Analysis of visual modulation sensitivity. V. Faster visual response for G- than for R-cone pathway?

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To determine the linear, unadapted responses of the cone pathways, we have measured the critical fusion frequency (CFF) for green (555-nm) and red (642-nm) flicker as a function of retinal illuminance. Both functions obeyed the Ferry–Porter law (CFF proportional to log illuminance) to high accuracy over a ≥5-log-unit range. In both foveola and periphery the CFF/illuminance functions were significantly steeper for green light than for red light. The peripheral 555-nm function had an average slope 1.26 times the average slope of the 642-nm function. An additive model of flicker detection could not account for the observed differences in slope. A threshold independence model, in which detection is based on the most sensitive mechanism, accurately fits the data. Whichever model is assumed, the presence of different slopes for the two wavelength flicker conditions strongly implies that the R- and G-cone pathways have different temporal properties. The occurrence of steeper CFF/illuminance slopes in response to green light implies that the linear (near-CFF) response of the G-cone pathways is inherently faster than that of the R-cone pathways at both retinal loci. These differences in R- and G-cone-mediated temporal properties complicate the fundamental concept of luminance and invalidate it for precise application over the full illuminance range.

1. INTRODUCTION

Temporal resolution is not the same for all classes of photoreceptors. The rod system is much more sluggish than the cone system, with most reports giving a maximum critical fusion frequency (CFF) value of approximately 20 Hz,[1–3] in comparison with cone-mediated CFF's, which can exceed 100 Hz in the periphery.[4,5] Even reports of a higher-frequency component in the rod response do not cite values beyond 30 Hz.[6] In addition, some psychophysical measurements of the short-wavelength-sensitive (B) cone system indicate that it has a slower temporal response and a lower contrast sensitivity than either of the other two cone systems,[7–12] although direct physiological recordings from blue cones[13] suggest that the temporal limitations in the B-cone system may be postreceptoral. However, the literature does not provide a clear answer regarding the question of any differences that may exist between the temporal properties of the long-wavelength-sensitive (R) and midwavelength-sensitive (G) cone pathways. A significant group of studies[2,8,14–23] indicates that the temporal properties of the visual system depend on wavelength for wavelengths beyond 540 nm; these findings are consistent with the existence of differences between R- and G-cone-mediated temporal responses. Another group finds no such wavelength dependence.[3,10,11,24–28] We address this question in more detail by examining the unadapted (linear) temporal responses of the R- and G-cone pathways in patches of retina that are homogeneous with respect to cell density and morphology[29,30] and temporal properties.[4,31]

A. Temporal Response near CFF Remains Unadapted by Background Luminance

In 1961 Kelly[32] and Levinson and Harmon[33] established that at high temporal frequencies the visual system behaves linearly. Both their models and their psychophysical data showed that in the high-frequency region of the temporal-modulation threshold function (TMTF), detection of temporal modulation depends solely on the absolute amplitude of the fundamental Fourier frequency of the modulation and is independent of both the mean illuminance level and the higher harmonic content of the waveform.

This linear behavior is depicted schematically in Fig. 1, showing a linear function that relates stimulus to internal response. Two sinusoidal flicker stimuli are shown, one at 20 Td (100% contrast) and one at 100 Td (20% contrast). In both cases an equal, just-detectable internal response ΔR is generated. Thus 20% modulation at a mean illuminance of 100 Td yields the same CFF as 100% modulation at a mean illuminance of 20 Td, since the modulated component has an amplitude of 20 Td in each case. Another way of thinking about this is that the CFF is unaffected by adaptation: If 100%-modulated flicker of a 20-Td light is at psychophysical threshold, it will remain detectable even when a steady adapting light up to four times brighter (80 Td) is added to it. The visual system is thus operating in a completely linear fashion in detecting the modulated signal for temporal frequencies near CFF (although it would exhibit strong adaptation for lower frequencies).

Previously we provided an empirical demonstration of such linear behavior.[5] Four CFF/illuminance functions were obtained by using three contrasts of sinusoidal modulation (20%, 50%, and 100%) plus one 100%-contrast temporal square wave with a fundamental amplitude of 127% contrast. Long-wavelength stimuli were presented at 35° eccentricity, 5.7° in diameter. When the data were plotted in terms of the absolute amplitude of the Fourier fundamental, they collapsed onto a single linear function (CFF proportional to log amplitude, i.e., the Ferry–Porter law) with the same slope, in keeping with the linear pre-

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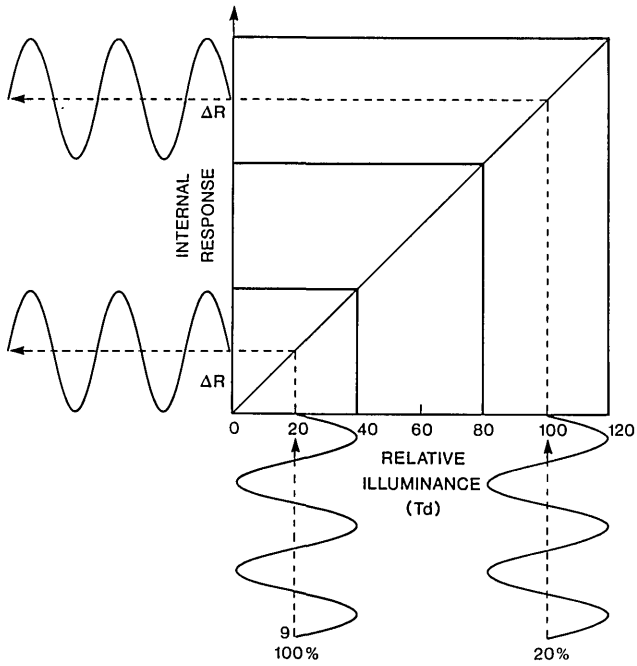

Fig. 1. Schematic representation of linear, unadapted behavior of the visual system. Two sinusoidal inputs are depicted, one at a mean luminance of 20 Td and 100% modulation and the other at a mean luminance of 100 Td and 20% modulation. In both cases the absolute amplitude of modulation is the same. Near CFF, when the visual system is responding linearly,[5,32,33] the fivefold increase in mean luminance will not decrease the detectability of the modulation, i.e., the two inputs will result in the same internal response (ΔR).

diction of independence from the adapting level. We discuss these data in more detail in Subsections 4.B.1 and 4.C.1.

We have pointed out[5,23] that, because of the linear nature of the visual response near CFF, measurement of CFF as a function of illuminance allows one to characterize the linear temporal response over a large dynamic range (>5 log units in the peripheral retina). When stimulus conditions were chosen so as to stimulate a retinal region that was homogeneous with respect to cone morphology, receptor density,[29,30] and temporal properties,[4,31] we found that the CFF/illuminance data were fitted extremely well by a straight line corresponding to the Ferry–Porter law.[5,23] Even those who dispute the generality of the Ferry–Porter law[34] confirm its applicability under the conditions that we define. The slope of the Ferry–Porter line provides a reliable estimate of the inherent response speed of the underlying receptor mechanism(s): in general, a steeper slope implies a faster underlying temporal response.

B. Chromatic Backgrounds Are Not Appropriate to Isolate the Unadapted Temporal Response of a Cone Mechanism

An important and somewhat surprising implication of the linear behavior near CFF is that chromatic adaptation[35–37] is not an appropriate technique to isolate the linear temporal response of individual cone mechanisms. If a given cone mechanism is contributing to the detection of flicker, addition of a background that does not push the mechanism out of its linear range will not adapt it. Thus moderate backgrounds will not eliminate that cone mechanism's contribution to the detection of flicker in the region near CFF. Conversely, once a background is sufficient to adapt the high-frequency temporal response of the particular cone class, the response has been driven out of its linear range and is therefore no longer an unadapted response.

The consequence of this is that the applicability of chromatic adaptation techniques in flicker studies is restricted to a much narrower range of adapting retinal illuminances than in studies that measure increment thresholds, as in the classic work of Stiles[35,36] and Wald.[37] In such studies the cone mechanism being studied may be adapted, as long as the remaining cone classes are kept less sensitive at the test wavelength. When the linear responses of a cone mechanism throughout the luminance range are studied, however, the chromatic adaptation technique is not appropriate to isolate the linear response of the cone mechanism if the cone class being tested is the most sensitive at the test wavelength. If, on the other hand, the cone class is not the most sensitive class at the test wavelength, chromatic adaptation can, in principle, help to isolate its linear response as long as the adapting light does not also adapt the cone class under investigation. However, as is illustrated by the final experiment presented in this paper, CFF's may be so resistant to adaptation that chromatic isolation of a cone mechanism is difficult to achieve in practice.

C. Goals of the Present Study

In the present study we reexamine the question of possible temporal differences between the R- and G-cone pathways. By choosing stimulus conditions carefully (see Section 2) and emphasizing CFF measurements, we measure the linear temporal responses dominated by each of the two cone types. This approach specifically minimizes the contribution from chromatic (color-opponent) pathways. Our general findings are as follows:

1. We reconfirm[5,23,31,38] that the peripheral retina is inherently faster than the central retina.
2. The CFF/illuminance data for red- and green-light flicker imply that the R- and G-cone pathways indeed appear to have significantly different temporal properties, with the G-cone pathway being the faster of the two.
3. Several alternative interpretations of our data, including an additive model of flicker detection, as well as a model assuming suppressive interactions between R and G cones, are evaluated. Finding 2 survives such an evaluation.
4. We discuss the implications that differing R- and G-cone pathways' temporal properties have for the procedure of flicker photometry and for the definition of luminance.

2. METHODS

A. Stimulus Conditions

The experiments were conducted under conditions that ensured that the eye was in a constant adaptation state for all stimuli. The stimulus was an array of 25 LED's with a dominant wavelength of either 642 or 555 nm viewed through a diffuser so as to form a uniform stimulus. It

was set in a hemispheric white surround of equal photopic illuminance, so that the achromatic pathway of the visual system would remain at a constant level of light adaptation even if fixation moved in relation to the stimulus. In addition, the white surround, which was approximately 3 log units brighter than the red stimulus in scotopic units, made it unlikely that thresholds were determined either by rods or by cones detecting stray light in regions of retina outside the test locus.[5,23,39]

The sinusoidal flicker modulation was presented with a gradual onset and offset in the form of a raised cosine envelope, so that flicker could not be detected by transients at the beginning or end of the presentation.[40] The stimulus duration was brief enough (1 s) to avoid adaptation to flicker during the CFF determination.[41]

The observers' pupils were dilated with 1% tropicamide (Mydriacil) to hold them constant at all illuminance levels, which were set by means of calibrated Wratten 96 neutral-density filters mounted in a light-tight mask worn over the eyes. One eye viewed the stimulus through the appropriate filter density, while the other was occluded and in darkness.

The test stimuli were presented so as to stimulate retinal regions that were uniform in structure. The foveolar region at the center of the foveal pit has constant receptor size, outer segment length, and axon length.[30] The stimulus for central viewing was therefore chosen to be 0.5° in diameter to stimulate the homogeneous central foveola. The peripheral stimulus was placed on the horizontal temporal meridian at 35° in the temporal visual field (tvf), since this had been determined to be a retinal region of high flicker sensitivity in prior experiments.[4,5,23,31] In peripheral experiments an auxiliary steady LED was used to provide a fixation point. Fading of the peripheral stimulus was avoided by instructing the observers to shift fixation between trials within a range of approximately 2° from the fixation point.

The peripheral stimulus size (5.7° diameter) was set so as to equate the number of ganglion cells stimulated in relation to the foveolar stimulus (42, 43). This also stimulated similar numbers of cones in the foveola and periphery (3000 in the foveola versus 6000 at 35°; see Ref. 29). Thus absolute threshold should be approximately the same for both stimuli on the grounds of summation over both photoreceptor and ganglion cell populations. Remaining differences should therefore reflect differences in either the absolute sensitivity or the temporal response properties of the cells in these retinal regions.

B. Procedure

The experiments consisted of measurement of CFF as a function of illuminance of the entire display over a ~5-log-unit range for 642- and 555-nm light. CFF thresholds were determined by using a yes/no forced-choice staircase method, with stimulus or no-stimulus trials having equal probability on each trial.[5] Three threshold estimates were obtained at each luminance for each of the two wavelength conditions. CFF's were always measured in an increasing luminance series. Full TMTF's were also measured for each of these two wavelengths throughout the temporal frequency range, with intensities adjusted to equate the sensitivities for the two wavelength conditions relative to their respective absolute thresholds.

3. RESULTS

A. CFF/Illuminance Functions Obey the Ferry–Porter Law: The Slope Depends on Wavelength

The CFF/illuminance functions for 642-nm (open circles) and 555-nm light (filled circles) are shown in Figs. 2 and

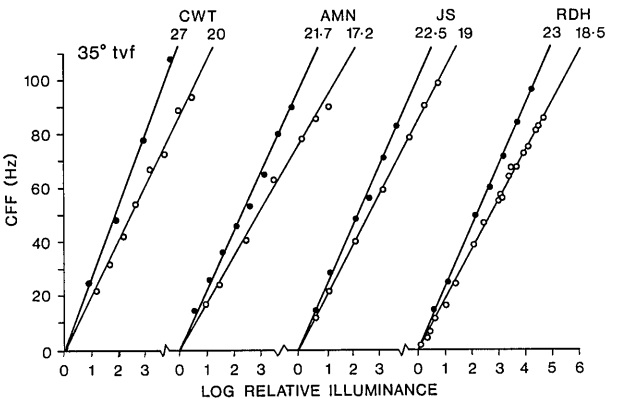

Fig. 2. CFF/illuminance functions for four subjects tested at 35° in the temporal visual field (5.7°-diameter test field). Data obtained by using green (555-nm) and red (642-nm) lights are indicated by filled and open circles, respectively. The slopes of the individual function, in hertz/decade, are denoted by the numbers above each best-fitting Ferry–Porter line. To illustrate the slope differences, we have plotted all the data on a relative illuminance abscissa. Note that no simple shift on the illuminance axis can equate the 642- and 555-nm data.

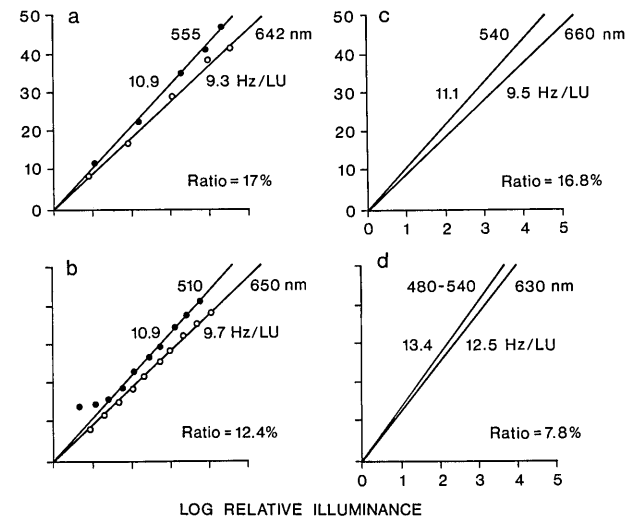

Fig. 3. (a) CFF/illuminance functions for one subject (RDH) tested in the foveola (0.5°-diameter test field) for red (642-nm, open circles) and green (555-nm, filled circles) flicker. The green-light function is steeper by 17%. (b) CFF data from Ives.[44] Green- (510-nm) and red-light (650-nm) flicker stimuli, which were presented in a 5.2° × 8.6° rectangular field, were produced by a spectroscope and were viewed centrally through a 1 mm × 1 mm artificial pupil. The green-light function is steeper by 12.4%. (c) CFF/illuminance functions for narrow-band green (540-nm) and red (660-nm) light for a normal observer (RS) tested by Pokorny and Smith.[15] The stimulus was a 1° field, viewed foveally through a 3-mm-diameter artificial pupil. Only the slopes of this observer's functions were reported. The green-light function is steeper by 16.8%. (d) CFF/illuminance functions for green-light (mean of narrow-band 480- and 540-nm data) flicker and red-light (630-nm) flicker obtained by Giorgi.[14] The average slopes for three observers are shown for each of the wavelength conditions. Stimuli were presented as 1° 40′ foveal fields viewed through an artificial pupil. The average green-light function is steeper than the average red-light function by 7.8%.

3. The data in all cases are fitted extremely well by the Ferry–Porter lines, as we have shown.[5,23] For all the functions except one (Observer JS, 555 nm, Fig. 2, r = 0.996), the correlation coefficient was 0.999 or greater.

At 35° in the temporal visual field, the average 555-nm slope for four subjects (23.6 Hz/decade) was 26% steeper than the average 642-nm slope (18.7 Hz/decade). On the basis of the t test for differences between the regression coefficients, the slope of the 555-nm function was significantly steeper than the slope of the corresponding 642-nm function for each of the four subjects. The highest p value (for subject JS) was less than 0.005 after adjusting to protect for multiple t tests.

One of the four subjects (RDH) was also tested in the foveola [Fig. 3(a)]. Here the 555-nm slope (10.9 Hz/decade) was 17% steeper than the 642-nm slope (9.3 Hz/decade). A t test of the regression coefficients for these two data sets also showed these slopes to be significantly different ($p < 0.025$ after adjustment for multiple t tests).

Also shown in Fig. 3 are data from three prior studies in which slope differences as a function of wavelength were observed for centrally viewed targets.[14,15,44] Figure 3(b) shows CFF data taken from the pioneering study of Ives.[44] The CFF/illuminance for green light (510 nm) was 12.4% steeper than the red-light (650-nm) function. A similar relationship between green-light and red-light CFF/illuminance functions was found also by Pokorny and Smith [Ref. 15, Fig. 3(c)] and by Giorgi [Ref. 14, Fig. 3(d)]. The data for the latter two studies are represented in Fig. 3 by the average slopes reported in each case. Thus our foveolar CFF data are consistent with those from at least three prior classical studies in which green-light CFF/illuminance functions were found to be steeper than red-light functions.

In summary, because slopes of the CFF/illuminance functions are different for red and green light, the two functions cannot be equated by a shift along the retinal illuminance axis. As we argue below, these data therefore imply that the cone pathways underlying the flicker responses in both the foveola and the periphery cannot have the same temporal properties.

B. Temporal Properties with Sensitivities Equated for Red and Green Light

Another approach to demonstrating that the underlying cone mechanisms have different temporal properties is to measure 555- and 642-nm TMTF's that have been equated at low frequencies, i.e., in their nonlinear range, where absolute modulation thresholds vary with adaptation level according to Weber's law.[32] If the underlying cone systems have identical temporal properties, than the 555- and 642-nm TMTF's should be congruent at all temporal frequencies. Once the two functions have been equated along the sensitivity axis, if the 642- and 555-nm TMTF's differ as a function of temporal frequency, the implication is that separate mechanisms with different temporal properties are being tapped.

The adaptation levels may be equated for the two wavelength conditions by setting their intensities an equal factor above their respective absolute thresholds. The absolute thresholds were estimated for these wavelengths by extrapolating the CFF/illuminance functions down to the abscissa (i.e., to 0 Hz; see Refs. 5 and 45), on the assumption that only one cone mechanism was determining CFF along the entire illuminance range.

The data from one observer (RDH) who was tested at 35° eccentricity and in the foveola are shown in Fig. 4. The 642-nm (open circles) and 555-nm (filled circles) intensities were set 4 log units above the respective absolute thresholds as established by the CFF estrapolation. It is apparent that, although the 642- and 555-nm TMTF's have equal peak modulation sensitivities, they are not identical; the 555-nm function has a higher inherent temporal cutoff frequency.

C. Relationship between the Ferry–Porter Function and the TMTF

Also shown in Fig. 4 are CFF/illuminance data (measured in the same session as the TMTF measurements) for the two wavelengths, along with their corresponding best-fitting Ferry–Porter lines. So that the CFF data could be plotted as frequency responses,[5,23,38] each value on the illuminance axis of the CFF/illuminance plots was converted to its equivalent value of absolute modulation sensitivity (1/absolute modulation amplitude) on the basis of the illuminance and percent modulation (100%) for the value. The data thus appear on these axes as straight lines with negative slopes. The validity and implications of this procedure are discussed in more detail in Subsection 4.C.

The 642-nm data were set in each case so that the best-fitting Ferry–Porter lines for the two wavelengths were equated at zero frequency. When we compared the CFF data with the corresponding TMTF's, it was evident that the substantial difference in sensitivity at high temporal frequencies between the 555- and 642-nm TMTF's was predicted by the corresponding unadapted linear CFF responses when these were equated for low-frequency sensitivity.

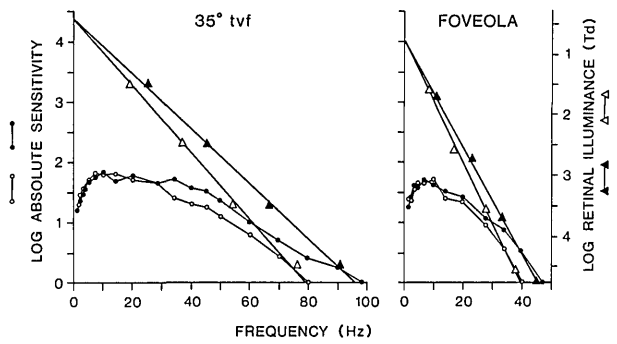

Fig. 4. 642-nm (open circles) and 555-nm (filled circles) TMTF's obtained at 35° (left) and in the foveola (right) for one observer (RDH). Also shown are the corresponding CFF/illuminance data obtained in the same session (open and filled triangles represent the 642- and 555-nm data, respectively) along with their best-fitting Ferry–Porter lines, all transformed appropriately for a frequency-response plot. The TMTF's were obtained in each case by setting the stimulus illuminance 4 log units above the respective 642- and 555-nm absolute thresholds, as determined by extrapolation of the corresponding Ferry–Porter lines to zero frequency.[45] This procedure resulted in the 642- and 555-nm TMTF's having equal sensitivities at low temporal frequencies. At frequencies beyond the peak sensitivity (around 10–15 Hz in the periphery and around 7 Hz in the foveola), the 642- and 555-nm TMTF's are increasingly divergent. This indicates that systems with different temporal properties underlie the responses to the 555- and 642-nm stimuli. The response to 555-nm light clearly has the higher temporal cutoff at both locations.

4. DISCUSSION

We have measured CFF/illuminance functions at two wavelengths, 555 and 642 nm, under conditions that sample loci that are homogeneous with respect to cone morphology and cone density.[29,30] For each wavelength condition, the data conform closely to the Ferry–Porter law over a 4-log-unit dynamic range in the foveola and over more than 5 log units in the periphery. The slopes of these functions are invariant with moderate changes in adaptation level (see Fig. 1 in the present paper, and Ref. 5). Previously we showed[5,23] that the slopes are also invariant when the stimulus area is varied by a factor of 10,000:1, a manipulation that involves the corresponding variation of the neural, spatial integration of the physical energy that is incident upon the receptor array. Invariance of the slope of the CFF/illuminance with changes in stimulus area has also been shown in x-linked dichromats.[46] However, simply changing the wavelength from 642 to 555 nm causes as much as a 26% increase in the slope of the CFF/illuminance function over the entire five-decade range. It is clear that this change in slope does not represent a change in adaptation level or effective illuminance, since illuminance is the abscissa of the function. Only a rescaling of the frequency axis, corresponding to adjustment of the time constants, would equate the 642- and 555-nm data. Thus the present results provide strong evidence that at least two cone mechanisms with different temporal properties underlie the responses for the two wavelength conditions. We argue in Subsection 4.B that a parsimonious interpretation of our CFF data is that the two wavelength conditions reveal the unadapted responses of the R- and G-cone pathways and that the G-cone pathway is inherently faster than the R-cone pathway.[47]

A. Relation to Previous Research

Our data are in agreement with several prior studies (already cited) that demonstrate the dependence of the slope of the CFF/illuminance function on wavelength.[14,15,44] More recently Stromeyer *et al.*[21] found that CFF increased more rapidly with increases in illuminance for middle wavelengths than for long-wavelength flicker presented to the fovea. Two observers showed 6.5% and 19% steeper slopes, respectively, for green (555-nm) flicker than for red (658-nm) flicker (both at 60% modulation) for retinal illuminances up to ~3 log Td. Their results are comparable to the 17% steeper G slope found in the foveolar data in the present study (see Fig. 3).

At retinal illuminances above ~3 log Td, Stromeyer *et al.* found saturations of CFF that our data do not replicate. It is possible that such saturation is related to their use of a constant number of cycles, which resulted in a decreasing stimulus duration as temporal frequency was increased. We discussed this issue in more detail in an earlier paper (see Appendix C in Ref. 5).

The classic study of Hecht and Schlaer[3] claimed that photopic CFF/illuminance functions were invariant with wavelength. However, Landis[48] reanalyzed Hecht and Schlaer's data and concluded that they contained evidence for systematic wavelength dependence.

Pokorny and Smith[15] measured CFF/illuminance in both dichromats and normals. Their data from normal subjects are in agreement with ours, with long-wavelength stimuli yielding 16% shallower slopes than midwavelength stimuli. However, the protanopes' CFF/illuminance functions (presumably based on G-cone responses) were shallower than the deuteranopes' functions (presumably based on R-cone responses), implying that the deuteranope R-cone pathway has a faster response than the protonope G-cone pathway. This picture for dichromats, which is the opposite of what could be predicted from the normal data, was recently reconfirmed by Lutze *et al.*[46] The switch between the dichromats' data and the data from normal trichromats suggests the possibility that dichromats' residual cone mechanisms may have temporal properties that are different from those of their counterparts in the normal eye. This calls into question the validity of assuming that dichromats' cones and associated neurons are functionally identical to those of the normal trichromat. Resolution of this issue will require testing a sizable population of both normals and dichromats under more controlled stimulus conditions such as those of the present study.

A powerful implication of the linear visual response at CFF[32] is that traditional chromatic adaptation techniques are not appropriate to study these responses. Previous studies of R- and G-cone-mediated temporal responses that used chromatic adaptation[8,10,21,25–28,49] therefore may not have been measuring linear, unadapted responses of the cone mechanisms. To the extent that previous studies were measuring these responses in the operating range controlled by an adaptive gain control, such studies have no bearing on the present conclusions. Furthermore, proper comparison of R- and G-cone-mediated temporal responses over their full frequency range requires that they be tested with their sensitivities equated, i.e., at equivalent states of light adaptation (as shown in Fig. 4). This condition was clearly not met in some of the earlier studies that used chromatic adaptation (e.g., Refs. 8 and 10).

If CFF is determined principally at the most peripheral level of the visual system, i.e., in the photoreceptors (as has been suggested by us and others[5,9–11,23,31,49] and implied by physiological data[50,51]), then one would expect some physiological measurements to reflect significant temporal differences between R- and G-cone-mediated responses. Two recent physiological studies support the notion of distal locus for such temporal differences (see Subsection 4.D below for further discussion of this issue).

First, Schnapf *et al.*[52] measured membrane-current impulse responses from individual human R and G cones. We analyzed the time to first zero crossing in the published records (see Fig. 1 of Ref. 52). Owing to the steepness of the membrane-current response at that point, the first zero crossing is the most robust temporal landmark to use. Estimates of the time to peak are more subject to the variability in photocurrent amplitude that tends to distort the waveform. For all the G-cone responses, the first zero crossing occurred at 109 ms after the stimulus. For all but one of the R-cone responses (i.e., the topmost response, which is saturated, thus delaying the zero crossing), the time to the first zero crossing occurred 36% later, i.e., at 148 ms. Moreover, all the temporal features of the G-cone responses could be made to be congruent with those of the R-cone responses simply by scaling the time axis by a factor of 1.36. Although the timing of R- and

G-cone responses in macaques does not appear to be different,[13] our analysis of the human cone flash responses published to date[52] are consistent with G-cone responses' being inherently faster than R-cone responses.

Second, Gouras *et al.*[53,54] have found recently that both focal (3°) and full-field electroretinograms are faster in response to midwavelength (544-nm) than to long-wavelength (633-nm) flickering (5-Hz square wave) helium–neon laser light. This result is also consistent with our psychophysical data and with the hypothesis that the G-cone pathway has an inherently faster response.

B. Identification of Cone Mechanisms Mediating Flicker Responses

If the pathways underlying the present CFF data had identical temporal properties, then the slopes of the two CFF/illuminance functions would be the same for any two wavelengths. However, as is evident in Figs. 2 and 3, no simple shift on the illuminance axis can make the 555- and 642-nm functions congruent. This implies that at least two receptor mechanisms with different (linear) temporal properties are responsible for the difference in slopes observed for the 642- and 555-nm conditions. We can rule out the role of B cones in flicker detection at these long wavelengths, since B-cone sensitivity is 3.9 log units less than G-cone sensitivity at 555 nm.[55] In addition, it is highly unlikely that these flicker thresholds are rod mediated. Rod-mediated CFF/illuminance functions characteristically have a much shallower slope[56] corresponding to their slower temporal properties. Furthermore, the present CFF data adhere tightly to characteristically different slopes at temporal frequencies (>30–100 Hz) to which rods are incapable of following.[1–3,6] Thus we conclude that the flicker responses measured in the present experiment were mediated by R- and G-cone mechanisms and that these must have different temporal properties.

We seek to identify which of these two mechanisms is faster. Clearly the faster of the two mechanisms dominates the 555-nm CFF data, since these have the higher CFF/illuminance slope (higher temporal cutoffs in the TMTF's as shown in Fig. 4). In the following four subsections we consider four models of how R- and G-cone responses may contribute to the flicker thresholds shown in Figs. 2 and 3: in Subsection 4.B.1, a nonlinear (inhibitory) interaction model, in which it is hypothesized that the difference in CFF/illuminance slopes is due to some form of suppressive interaction between the R- and G-cones; in Subsection 4.B.2, a supra-Weberian adaptation model, which predicts either paradoxical isolation of G-cone responses by the mean luminance of the red LED's (and isolation of the R-cone responses by the green LED's) or a strong adaptation of the red-light CFFs; in Subsection 4.B.3, an additive model, in which flicker detection is based on a linear summation of R- and G-cone signals; and in Subsection 4.B.4, an independence model, in which flicker detection is based on the most sensitive of the two cone types.

1. Nonlinear (Inhibitory) Interaction Model of Flicker Detection

It is possible that the different CFF/illuminance slopes result from some form of inhibitory interaction between R- and G-cone pathways (see, e.g., Ref. 57). For example, under such a model, shallower CFF/illuminance slopes in the 642-nm condition could result from interactions between R- and G-cone mechanisms that increase with frequency and/or illuminance. These mechanisms could be either the result of direct neural inhibitory interactions or due to a phase cancellation at high temporal frequencies, as has been proposed by Drum.[58]

We address this class of model by considering the effect of both homochromatic and heterochromatic backgrounds on CFF's. The homochromatic data (660-nm modulation on 660-nm backgrounds) are shown in Fig. 5. CFF's as a function of retinal illuminance were measured for four modulation depths (20%, 50%, 100%, and square-wave with 127% modulation of the Fourier fundamental). These data come from one of our previous studies (Fig. 9 of Ref. 5), replotted on more familiar ΔI versus-I-axes, i.e., flicker-threshold-versus-illuminance (tvi) functions. The absolute amplitude of each of the four modulations is plotted as a function of the amplitude of the red background for five temporal frequencies. The frequency range (5.5–65.4 Hz) spans the majority of the 5-log-unit dynamic range for flicker detection in the periphery. Because the response to 660-nm light is dominated by the R-cone contribution, these functions can also be considered to be Δ(R-cone excitation) versus (R-cone excitation) functions.

The data in Fig. 5 demonstrate that, over the full range of homochromatic backgrounds tested (i.e., up to five times the amplitude of the modulating component at each tem-

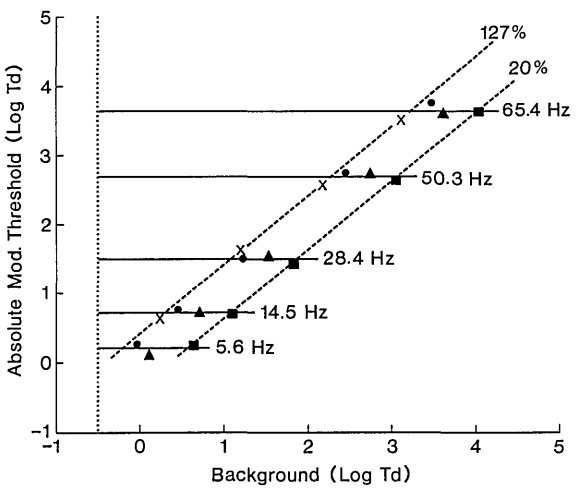

Fig. 5. Demonstration of linearity of CFF responses in the presence of homochromatic (660-nm) backgrounds. Here we have plotted the amplitude of the modulating component as a function of the base (background) upon which these were measured. This plot was derived from data presented in a previous paper (Ref. 5, Fig. 9) in which CFF/illuminance functions were measured at four modulation depths: 20%, 50%, 100%, and 127% (square-wave modulation). Data shown here were derived from horizontal cuts through the CFF/illuminance functions at five temporal frequencies: 5, 14.5, 28.4, 50.3, and 65.4 Hz. When there was no actual data point at that frequency, a value was determined by interpolation between the two nearest neighboring points. Within experimental error, the modulation sensitivities are independent of background level. The horizontal lines placed at the mean modulation threshold for each frequency have been extrapolated leftward to the approximate absolute, dark-adapted threshold for these conditions (~ −0.5 log Td, vertical dashed line). The oblique dashed lines through the 20%- and 127%-modulation data represent the slope of the Ferry–Porter function for these data sets.

poral frequency), the absolute sensitivity for modulation is unaffected by the background. In other words, there is no evidence for any adaptation of modulation sensitivity. This is simply another way of depicting the linearity of the visual response for detection of modulation near the CFF (see Fig. 1). It will be important for Subsection 4.B.2 to note that the total lack of adaptation of CFF's in the presence of homochromatic backgrounds eliminates the possibility of supra-Weberian adaptation within the R-cone pathway under our testing conditions.

For comparison with the homochromatic case, we have also measured red-light CFF's in the presence of heterochromatic backgrounds. We compared the red-light CFF/illuminance functions both in the absence of and in the presence of a steady green background light. For two observers (RDH and CWT), we measured flicker thresholds for red light (642-nm LED's, 356 cd/m^2 before attenuation) at 35° tvf, using a 5° field. Thresholds were measured over a ~4.5-log-unit range of retinal illuminances with and without a steady green background light (Kodak Carousel ELH projector lamp filtered by a Wratten 58 filter, dominant wavelength 538 nm, at ~2000 cd/m^2 before attenuation, $x = 0.368, y = 0.606$). The green background was rearprojected onto the same screen that diffused the red LED light. The stimulus (red light alone or red light plus the green background) was presented in a white surround that was equiluminant with the red light. Illuminance variations were obtained by means of calibrated neutral-density filters that attenuated the surround together with the modulating (642-nm) and steady (green) stimuli; this attenuation kept the surround and the stimuli in the same ratio.

The background conditions were designed to reduce the R- and G-cone modulations from full to ~20% (R cones) and <3% (G cones) modulation. On the basis of the near-CFF linearity in the presence of homochromatic backgrounds (see Fig. 5), we would predict that the green background would have no effect on CFF's if R-cone responses were dominating the detectability of the red-light flicker, since the R-cone modulation would still be within the CFFs' linear range (≥20%). However, since the background reduces the G-cone modulation to <3%, which is well into the G-cone Weberian adaptation range,[32] any G-cone contribution to red-light CFF's should be significantly reduced.

The results of this experiment are shown in Fig. 6. Here we have plotted the difference between CFF's without and CFF's with the heterochromatic background for the two observers (RDH and CWT). The abscissa is the mean retinal illuminance of the red LED's. The horizontal dashed lines indicate the 99% confidence limits for a difference between two CFF measures.

It is evident that, for both observers, the green background light had virtually no effect on the red-light CFF's until the overall mean retinal illuminance (red plus green light) approached cone half-bleaching levels, which were assumed to be 4.3 log Td for each cone type (vertical arrows on the abscissa). This experiment demonstrates that a steady, heterochromatic (green) background light that reduces the modulation of the R cones to ~20% has no effect on the detection of red flicker over their entire (subbleaching) dynamic range. Thus, whether caused by homochromatic (Fig. 5) or heterochromatic (Fig. 6) backgrounds, reduction of R-cone modulation to as little as 20% causes no adaptation of absolute modulation sensitivity: in either case, near-CFF linear visual responses are maintained. Moreover, since the green background was strongly stimulating to the G cones, reducing their modulation to <3%, the resistance of red-light CFF to the green background implies that it was not contaminated by the influence of interactions with G cones. If some form of suppressive interaction between the R- and G-cone pathways were influencing the red-light CFF's, the intense green background light should have revealed this in the form of a significant change in CFF's.

It is worth noting that this experiment provides a vivid illustration of why chromatic adaptation is ineffectual in isolating the linear (near-CFF) temporal responses of a cone class (see Section 1).

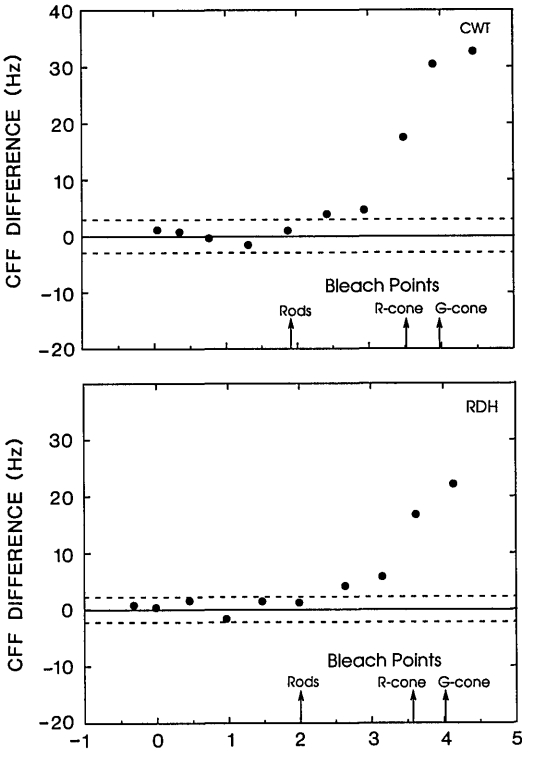

Fig. 6. Detection of red-light flicker in the presence of a green background light for two observers (RDH and CWT). The ordinate is the difference between CFF's obtained without and with the background light. (See text for details regarding the stimuli.) The abscissa is the mean retinal illuminance from the red LED's for each observer. Pupil sizes for RDH and CWT were 7 and 10 mm, respectively. The horizontal dashed lines indicate the 99% confidence limits for the difference between two CFF measures. The vertical arrows mark the illuminance of the red LED's at which the overall (red light plus green background) mean retinal illuminance caused significant bleaching of rods and each of the two cone types. (Half-bleaching levels were assumed to be 4.3 log Td for each cone type.) Rod responses are severely saturated at 3 log scotopic Td (i.e., ~2 log photopic Td for 540-nm light,[55] well below levels at which the green background begins to affect red-light CFF's. For both observers a steady green background light that reduced the modulation of the R cones to ~20% and the modulation of the G cones to <3% did not affect the detection of red flicker until overall mean retinal illuminance approached R-cone bleaching levels.

2. Paradoxical Cone Isolation by Means of Supra-Weberian Adaptation

It has been suggested that the combination of flicker photometry and the use of chromatic backgrounds can result in apparent suppression of the more sensitive mechanism beyond that expected from Weber's law.[18,59] Thus, for example, Eisner and MacLeod[18] found, using heterochromatic flicker photometry (HFP) and a moderate long-wavelength adaptation field, that the photopic spectral sensitivity function matched Vos and Walraven's[60] green fundamental from 500 to 620 nm, implying a supra-Weberian adaptation of the R-cone mechanism and consequent isolation of the G-cone mechanism.

Under a threshold-independence model, if the R and G cones have the same Weber fraction, and if the adapting and test lights are the same wavelength (642 nm, in this example), then it is not possible to use a chromatic background to shift detection exclusively to the less-sensitive mechanism (G cones, in this example). Under these conditions, chromatic adaptation at the test wavelength can, at most, equate the two sensitivities.[61] However, if supra-Weberian adaptation (inhibition) were operating, it theoretically would be possible for increments (or flicker) of a deep red light to be detected by the G cones, even though G cones are ~1.2 log units less sensitive at this wavelength than are R cones.[52]

Such paradoxical cone isolation is unlikely to occur under the conditions used in the present experiments. First, we are working at 100%-modulation CFF throughout the luminance range tested. As illustrated vividly by the results of the experiments of Figs. 5 and 6, the visual response near CFF is linear; this means that near CFF, modulation sensitivity does not adapt to either homochromatic or heterochromatic backgrounds but depends solely on the absolute amplitude of the Fourier fundamental.[5,32,33] This effectively eliminates the supra-Weberian adaptation hypothesis because it shows that no adaptation occurs and thus argues strongly against paradoxical cone isolation's occurring under our testing conditions. The heterochromatic condition (Fig. 6) strengthens the case against red-light CFF's being dominated by G-cone responses, since the green background reduced the modulation of the G cones to <3% over the entire illuminance range. If G-cone responses were underlying the red-light CFF's, adding the green background should have significantly altered the CFF's. However, this did not occur.

We thus conclude that the 642-nm CFF/illuminance functions shown in Figs. 2 and 3 are dominated by R-cone pathway responses and that therefore the 555-nm functions predominantly reflect the responses of the faster G-cone pathway.

3. Additive Model of Flicker Detection

It is commonly assumed that midwavelength and long-wavelength photopic flicker thresholds are determined by the so-called luminance (or achromatic) channel.[55,62] The output of the luminance channel is assumed to be proportional to a linear sum of R- and G-cone input signals. Evaluation of an additive model must be considered not only on psychophysical and theoretical grounds but also in light of physiological data.[63-73] For example, several studies have shown that both the center and the surround of receptive fields of magnocellular-pathway cells in macaque retinal ganglion cells[63-70] and in lateral geniculate nucleus cells[71-73] receive summed input from R- and G-cone signals. Thus we evaluate an additive model in which flicker detection is based on a linear summation of R- and G-cone outputs[74-77] forming an (R + G) luminance signal.

The additive model is depicted schematically in the top panels of Fig. 7. To relate the additive model to our CFF/illuminance data, we must assume some quantitative relationship between stimulus illuminance and the cone output modulation. We assume that the output of each cone type before summation obeys the Ferry–Porter law. In addition, the relative sensitivities of the R and G cones to the 642- and 555-nm stimuli must be set. It is well known that the R- and G-cone sensitivities for static targets are similar at midwavelengths.[55,62] Although the exact relationship between the R- and G-cone sensitivities

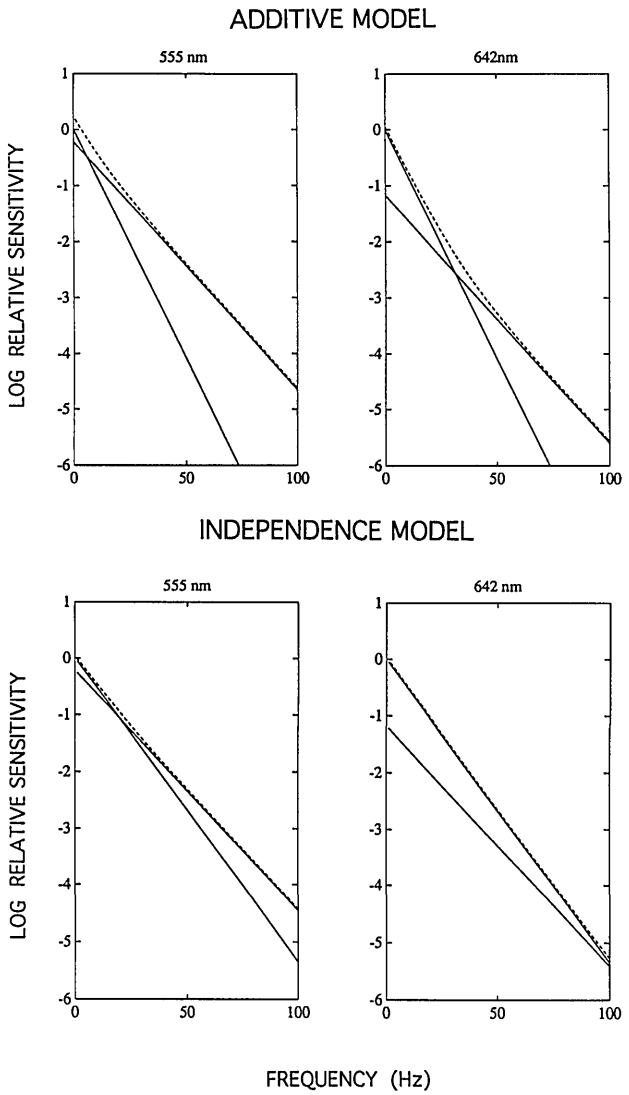

Fig. 7. Schematic depiction of the additive (top panels) and independence (bottom panels) models of flicker detection for 555- and 642-nm light. The solid curves represent underlying R- and G-cone-mediated Ferry–Porter lines shown here as frequency responses. In each panel the steeper curve is for R cones with a slope $-1/m_r$ and the shallower curve is for G cones with a slope $-1/m_g$ (corresponding to a faster G-cone response). The dashed curves indicate the outcome of the model predictions for the two wavelength conditions. The relative sensitivities of the R and G cones at 0 Hz were set according to the Smith–Pokorny[76] cone-sensitivity functions.

is not known for peripheral retina, we used the Smith–Pokorny[76] ratios, according to which the R cones are more sensitive than the G cones by 0.22 log unit at 555 nm and by 1.17 log units at 642 nm. We assumed maximal summation between the cone types.

Using these assumptions, we then attempted to fit the output of an (R + G) mechanism to the empirical sensitivities to 555- and 642-nm light by allowing the assumed underlying R- and G-cone Ferry–Porter slopes m_r and m_g to vary freely.

First we considered the case where $m_g = m_r$. We found that no linear sum of the cone signals of the same slope could predict CFF/illuminance functions with different slopes for the two wavelengths. Therefore, to interpret our CFF data using this additive model, we must assume that the underlying slopes of the R- and G-cone CFF/illuminance responses are different.

We next sought solutions for the case $m_g \neq m_r$. Two pairs of simultaneous linear equations defined the additive model for the two wavelength conditions. To solve for m_g and m_r we attempted to evaluate the equations at two temporal frequencies spanning the empirical range of the data (0 and 80 Hz). The Smith–Pokorny cone sensitivity values[76] were used to fix the predicted levels for the underlying temporal responses at 0 Hz. The empirical values were obtained by extrapolation for 0 Hz and by interpolation for 80 Hz from linear regressions fitted to the high- and low-frequency portions of the CFF data, respectively, for each observer. We then averaged these values to obtain a mean estimate for each frequency at each of the two wavelength conditions. From these values the reduction in sensitivity at 80 Hz relative to 0 Hz can be derived and used in an attempt to find solutions for the two simultaneous equations.

We found that over the full range of possible ratios of m_g to m_r, from equality to $m_g \gg m_r$, no solution existed; that is, no real values of m_g and m_r satisfied all the conditions of these experiments.

Real solutions for m_g and m_r could be found, however, if we allowed the relative R- and G-cone sensitivities to vary. For example, if the G cones were assumed to be more sensitive than the R cones at 555 nm (contrary to the Smith–Pokorny cone sensitivities[76]), then real-valued solutions for m_r and m_g could be found. However, the difference between these slopes was always greater than the difference between the empirical Ferry–Porter slopes. Under these conditions, then, an additive model forces an interpretation of the empirical slope difference as an underestimate of the true difference between the underlying mechanism temporal properties.

We also considered the possibility that the input to the additive stage does not follow the Ferry–Porter law but instead follows a square-root law such as that proposed by Kelly.[78] This modification of the additive model also failed to provide real-valued solutions for m_g and m_r. Moreover, it predicted significantly more curvature than was observed in the CFF data.

Thus we find that an additive model of high-frequency flicker detection cannot account for the difference in CFF slopes that we observe for the 555- and 642-nm conditions without a difference in the underlying mechanism response speeds. If anything, such a model predicts that the temporal properties of the underlying R- and G-cone pathways differ by more than the ratio of empirical CFF/illuminance slopes, and this only if the relative R- and G-cone (0-Hz) sensitivities are allowed to deviate from the Smith–Pokorny[76] sensitivities for the dominant wavelengths of our LED's. A more plausible explanation, in which the most sensitive mechanism determines flicker threshold, is considered next.

4. *Independence Model of Flicker Detection*

A threshold-independence model is depicted in the bottom panels of Fig. 7. This model assumes that, for any given set of wavelength, illuminance, and temporal-frequency conditions, detection of flicker will be determined by the receptor mechanism that is most sensitive to this stimulus. The only other refinement of an independence model is to include an evaluation of the effect of probability summation on the flicker thresholds.[79,80] Given the slopes of our psychometric functions (typically $\beta = \sim 4$), this effect would be small.[80]

According to an independence model, the CFF/illuminance function may take on one of two forms: (1) an unbroken line on CFF-versus-log I axes, implying adherence to the Ferry–Porter law by a unitary cone mechanism or by more than one mechanism with identical sensitivities and temporal properties or (2) a line with a distinct transition to another line of unequal slope, implying transition from detection by one mechanism to detection by another with different temporal properties. It may be emphasized that such a transition from flicker detection by one mechanism to detection by another would occur only by virtue of the faster response properties of one of the mechanisms and not because of adaptation.[61] Thus the slope of the CFF/illuminance function at intensities above the break can only be steeper than the slope below the break.

The CFF/illuminance data shown in Figs. 2 and 3 do not show any distinct breaks. Instead, the two wavelength conditions yield CFF data conforming to two distinct Ferry–Porter functions, implying dominance by one cone pathway in each case. According to the independence model, the empirical slopes for the two wavelength conditions correspond directly to the underlying cone-mechanism slopes.

5. *Summary of Additive and Independence Models*

Interpretation of our CFF data according to either an additive model or an independence model leads to the conclusions that (1) two cone mechanisms having inherently different temporal properties underlie flicker detection for the two wavelength conditions and (2) the G-cone mechanism has an inherently faster response than the R-cone mechanism. However, if an additive model is proposed, the difference between the underlying R- and G-cone-pathway temporal properties must be greater than is implied by the ratio of empirical CFF/illuminance slopes.

C. Determination of the Linear Time Constants of R- and G-Cone Pathways

1. *CFF/Illuminance Function As an Estimate of the Dark-Adapted (Linear) Frequency Response*

In this section we derive an estimate of the overall time constant of the linear (unadapted) visual response for the two wavelength conditions by converting the CFF/

illuminance functions (Figs. 2 and 3) into equivalent frequency responses (see Fig. 4 and Refs. 5 and 38). This procedure is illustrated in Fig. 8.

At the left in Fig. 8 is shown the best-fitting Ferry–Porter function (solid curve) to one of the data sets from Fig. 2 (RDH, 35°, 642 nm), plotted as a frequency response function on the more familiar log–log coordinates. Since the data are fitted so well by the Ferry–Porter line, we use this function to represent the data in order to estimate the linear frequency response. From the 3-dB point on the transformed Ferry–Porter line we fixed the time-constant parameter of a nine-pole linear filter model for the data. In lieu of an explicit phase function for these frequency responses, we have adopted this classical procedure,[81] allowing us to describe the data to within experimental error by a physically realizable model whose response characteristics are known in both the time and the frequency domains.[5,38] The dashed curve in the left-hand part of Fig. 8 is the corresponding best-fitting filter function for nine poles with equal time constants.

A classical frequency response is not usually defined or measured by using different mean levels for different frequency ranges. The transformed Ferry–Porter function, however, is an equal-response measure obtained at a different mean retinal illuminance for each temporal frequency measured. Nevertheless, because of near-CFF linearity this function may be considered equivalent to a frequency response obtained under fully dark-adapted conditions. To help in understanding this, we refer back to the homochromatic flicker data of Fig. 5. A dark-adapted frequency response could be derived algebraically by a vertical cut through the family of flicker tvi functions at the absolute photopic threshold (vertical dotted line, Fig. 5). Experimentally, data are unattainable here by means of modulation thresholds, since illuminance modulation cannot exceed 200%. However, the dark-adapted function may be estimated by extrapolation of the horizontal trend of the data at each frequency to the required illuminance level (horizontal solid lines, Fig. 5). These extrapolations correspond to the horizontal portion of Stiles's tvi curves,[35,36] so there is every reason to expect them to remain constant as retinal illuminance is reduced to absolute threshold.

Since the CFF's are independent of the background illuminance, the modulation thresholds derived from a vertical cut would be identical to those derived from any oblique cut through the data. In particular, oblique cuts corresponding to the slope of the Ferry–Porter line (oblique dashed lines, Fig. 5) will yield the same frequency response as a vertical cut through the data. Therefore an important consequence of near-CFF linearity is that, in their linear range, modulation thresholds not only represent unadapted responses; they are estimates of responses at absolute (dark-adapted) photopic threshold. It is entirely because of the linear visual response near CFF that a dark-adapted frequency response can be estimated from the CFF/illuminance measurements.

2. *Linear Impulse Responses for the R- and G-Cone Pathways*

According to the above interpretation of the CFF/illuminance function, and our arguments regarding the cone mechanisms underlying each wavelength condition (see Subsection 4.B, above), we regard the filter curve in Fig. 8 (dashed curve, left-hand side of Fig. 8) as an analytic estimate of the fully dark-adapted frequency response of a mechanism dominated by the R-cone pathway operating in its linear range. An inverse transform[81] of this filter characteristic yields the corresponding linear, dark-adapted impulse response.[5] This process was repeated for all four subjects for both wavelength conditions. The means of the derived linear impulse responses are shown at the right in Fig. 8. The striking feature of these linear impulse responses is the distinct separation of the impulse responses for the two wavelength conditions: the 555-nm response reaches its peak significantly earlier than the 642-nm response. In the foveola (dotted curves), the mean time to peak is 93 ms for the 555-nm data and 109 ms for the 642-nm data. At 35° eccentricity (solid curves), the average times to peak are 43 and 54 ms for the 555- and 642-nm data, respectively. These times to peak are comparable with the times to peak measured electrophysiologically from single human cones.[52]

Furthermore, for the 35° data, the distribution of the individual observers' times to peak (not shown in Fig. 8) for the 642-nm condition did not overlap at all with their

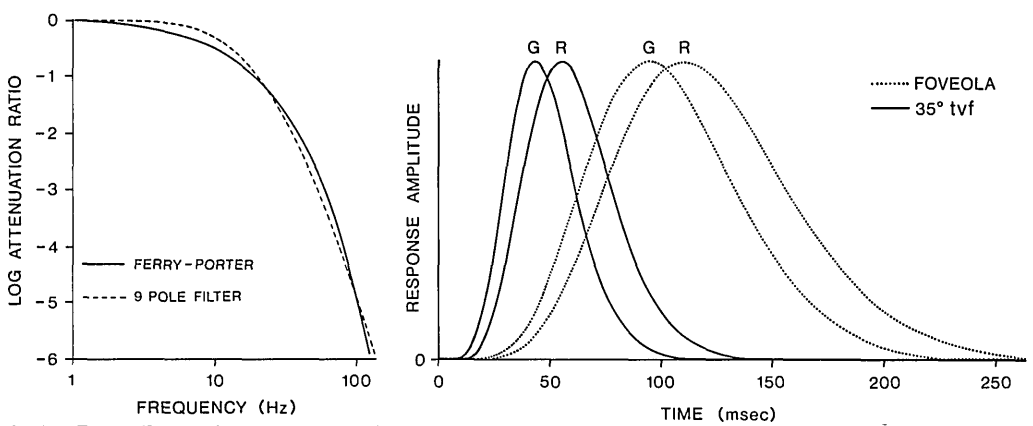

Fig. 8. (a) Best-fitting Ferry–Porter function to RDH's 642-nm, 35° data replotted as a frequency response (as in Fig. 4), with a logarithmic frequency axis (solid curve). The dashed curve depicts the frequency response of the corresponding nine-pole filter.[81] (b) This procedure was applied to the data in Figs. 2 and 3, with the time constants of the resulting nine-pole fits determined in each case by the average Ferry–Porter slope.[81] Inverse Laplace transform of these frequency responses yielded the four linear, dark-adapted impulse responses shown here. Solid curves, 35°; dotted curves, foveola. The 555-nm data and the 642-nm data are labeled G and R, respectively.

555-nm times to peak. These impulse responses thus depict in the time domain that the linear visual responses underlying the two wavelength conditions have different temporal properties. The 642- and 555-nm TMTF's confirmed this picture in the frequency domain, since the 555-nm TMTF had a higher temporal cutoff even though the red and green stimuli had been adjusted so as to equate the two sensitivity functions at low frequencies (see Fig. 4).

D. Receptoral Locus of Temporal Differences between R- and G-Cone Pathways: A Working Hypothesis

The linear visual response, as assessed by the CFF/illuminance measurements,[5,23,32,33] may be viewed as a psychophysical probe of early stages of photoreception, because it is only at these early stages that the photochemical response remains linear, without distortion by nonlinear adaptation processes.[10] We hypothesize that the differences in R- and G-cone-mediated linear responses derive from functional differences between the R- and G-cone photoreceptors, assuming that no differential filtering occurs subsequent to the early linear processing stages. We, and others, have proposed this notion previously.[5,9–11,23,31,49] Moreover, as we have noted above in the present paper, there are some electrophysiological data[52–54] that are consistent with a distal retinal locus for CFF responses and thus for the temporal differences as a function of wavelength that we have observed.

In summary, although R- and G-cones are currently ultrastructurally indistinguishable, they may be functionally different in ways other than their spectral sensitivity. A more comprehensive identification of the mechanisms underlying the differences in temporal properties between the R- and G-cone pathways awaits future research in both physiology and psychophysics.

E. Implications for Photometry

1. *HFP and the Current Concept of Luminance*

The fundamental operation in photometry is to match the internal responses to two lights of different wavelength composition by varying them along the intensive continuum. We may call that which is matched "luminous sensation."[55] In practice it is difficult to abstract the luminous sensation from an internal response that also has dimensions of hue and saturation. In direct[83] heterochromatic brightness matching, the two stimuli may differ greatly along the chromatic and the saturation continua, leading to an unacceptable variability in the ratio of radiances accepted as equiluminant.

HFP is designed to minimize the variability of matching radiance ratios by collapsing the perceived internal response space to a single dimension. HFP is at the core of traditional psychophysical photometry, which has generated the numerical standards for all practical (applied) photometry. A significant portion (490–540 nm, and all wavelengths of >650 nm) of V_λ, the CIE photopic spectral luminosity function, were determined by HFP.[55]

2. *Linearity Requirement in Flicker Photometry*

In studies using HFP it is traditionally explained that the use of high temporal frequencies (10–40 Hz) is necessary to exceed the temporal cutoff of the chromatic opponent channels to minimize perceived color variations. This is valid. However, this literature has apparently not recognized that there is a nonadaptive requirement for determination of photopic luminosity by HFP. In fact, some studies (e.g., Ref. 18) specify that Weber's-law adaptation must be operating in HFP.

It is well established that temporal modulation sensitivity obeys Weber's law at low temporal frequencies as long as the light level is sufficient to bring the cone mechanism out of the linear portion of its tvi curve. However, the flicker methods of determining equiluminance implicitly require that the R- and G-cone mechanisms are behaving, at least to some extent, nonadaptively (i.e., $\Delta I \propto I + k$, where k is a substantial proportion of the background, I). In HFP the subject adjusts the mean light level of one of the alternating wavelength components until a flicker null or minimum is achieved. In this adjustment both the dc and the ac components of the stimulus are affected. However, the meaning of Kelly's[32] result is that whenever the temporal frequency is near CFF for the light level being tested, adjustments in the dc component have no effect on flicker detectability. Only the change in the modulating component produced by the adjustment of the overall light level actually affects the flicker sensitivity and hence the ability to achieve a null. The greater the ratio of $k:I$, the more effective should be the nulling procedure.

Conversely, if the mechanism were operating entirely according to Weber's law, adjustment of the mean light level of the test (or of the standard) would fail to cause any change in the ac response of the mechanism: this is the meaning of $\Delta I/I$ = constant. Thus adjustment of the test radiance would fail to affect the flicker percept. The flicker-minimum technique thus requires an unadapted component in the response of the R and G mechanisms at the input to the site of their (suprathreshold) summation (i.e., the achromatic channel), which is precisely what Weber's-law adaptation eliminates. The focus of the present study was on the linear temporal responses (CFF) of the cone mechanisms, and the results imply that these are different for R- and G-cone mechanisms. This directs our findings at the heart of both the method and the theory of flicker photometry.

3. *Dependence of the Current Definition of Luminance on Temporal Frequency and Mean Radiance*

It is implicitly assumed in the traditional conceptualization of photometry that the luminance of a light will not change if the temporal frequency of the light is altered. This invariance is a sensible property for any metric of light to have: a light with a mean luminance of 100 cd/m^2 ought to remain at 100 cd/m^2, whether it is modulating at 30, 100, or 0 Hz. This property, of course, would apply if the outputs of the cone pathways contributing to achromatic flicker perception changed in exactly the same way as temporal frequency was changed. However, the data shown in Figs. 2–4 imply that the visual sensitivities of the R- and G-cone pathways change very differently when either temporal frequency or mean radiance is changed.

Another way of viewing this is to note that the different slopes for the 642- and 555-nm stimuli shown in Fig. 2 imply that the threshold illuminance for the detection of 100% flicker at a given frequency can differ by as much as a factor of 10 depending on the wavelength used (e.g., note

the horizontal separation of the CFF/illuminance functions at the 100-Hz level in Fig. 2). The consequence of this is to restrict the traditional luminance metric to one temporal frequency.

We are not the first to note a relationship between spectral luminous efficiency and the temporal frequency or mean radiance at which it is measured. Bornstein and Marks[20] found that photopic luminous efficiency measured by using CFF depends on the temporal frequency used to measure it. From the results of Giorgi,[14] who found that the slopes of CFF/illuminance functions varied with wavelength, these authors drew the conclusion that "luminosity determined by critical frequency varies with frequency of intermittence." They then directly investigated this dependence of luminous efficiency on temporal frequency. Foveal luminous-efficiency functions measured at high temporal frequencies (40–45 Hz) were found to be narrower than those measured at low frequencies (20–25 Hz). For example, at 620 nm the high-frequency function was lower than the low-frequency function by ~0.3 log unit.

Bornstein and Marks did not relate this narrowing in the luminous-efficiency function to differences in the time constants of the underlying cone mechanisms. However, our results imply that R-cone sensitivity decreases more rapidly with temporal frequency than does G-cone sensitivity (see Fig. 4). The luminous efficiency determined by HFP with a high-frequency minimum-flicker criterion therefore should fall more sharply at long wavelengths than with a lower-CFF criterion. The slope difference that we have measured between the 555- and 642-nm CFF/illuminance functions predicts the degree of spectral-sensitivity narrowing that Bornstein and Marks observed.

Ingling *et al.*[22] found that flicker matches used in HFP were substantially nonadditive when investigated over a 3-log-unit range of illuminance. Specifically, HFP displayed additivity only at ~20 Td. At 10 Td, subadditivity was found. Above 50 Td, achieving a flicker null required progressively more red light, corresponding to a progressive increase in superadditivity with increasing illuminance. Ingling *et al.*[22] proposed that the additivity failures of HFP resulted from a static, compressive nonlinearity in the visual pathway before the site of summation of cone signals to form an achromatic (luminance) signal. However, since the visual response is linear and unadapted near CFF,[5,32,33,38] one need not posit nonlinear mechanisms to explain HFP nonadditivity: the CFF/illuminance data in the present study predict such nonadditivity of HFP.

4. *Dependence of the Current Definition of Luminance on Retinal Locus*

Further complicating the picture is the fact that the retina is not spatially homogeneous in either structure or function. Of particular relevance in the context of an HFP definition of luminance is the substantial increase in temporal response speed of the retina with eccentricity.[5,23,38] Moreover, the present results indicate that the difference between the response speeds of the R- and G-cone pathways is more pronounced in the periphery than in the fovea. Thus, in the periphery, the shape of any photopic spectral-sensitivity function defined by HFP will depend more strongly on the temporal frequency of measurement than will the current definition, which has been developed essentially for the fovea. Any complete definition of luminance must take these locus specificities into account.

F. Toward a Redefinition of Luminance

Clearly the present results introduce further complexity to the conceptual framework of photometry and to the very definition of luminance. If the present definition of luminance were to be expanded to accommodate fully the results of the present study, the definition would have to be specific to both temporal frequency and retinal locus. A more serious matter is that the current definition is functionally dependent on the mean radiance of the light at which the spectral luminosity is measured. This amounts to a frank violation of Abney's laws of additivity. Thus the present results force us to seek a more general definition of luminance.

1. *Threshold-Based Definition*

To accommodate these complexities, we propose consideration of a new definition in which equality between two lights always refers to a unique ratio of their radiances, regardless of their mean radiance or temporal frequency (or retinal locus, to good approximation). Two monochromatic (primary) lights would be defined as equal when both were at absolute threshold, and they would remain equal at any suprathreshold level as long as they were set an equal factor in radiance above their respective thresholds.

The differences in sensitivity between wavelength conditions at high frequencies (Figs. 2–4), which are a manifestation of the different temporal properties of the R- and G-cone systems, are thus not confounded for a new definition in threshold-based units. Thus lights of an equal number of units above threshold will not, in general, have equal flicker sensitivities at nonzero frequencies. Our approach requires the measurement of absolute threshold for primary lights spanning the color space. The threshold-based flux,[84] $^*L$, of each primary light with radiant flux R_λ is given by

$$^*L = {}^*\kappa_m \int_\lambda R_\lambda T_\lambda d\lambda , \tag{1}$$

where R_λ is the radiant flux (watts), $^*\kappa_m$ is the maximum spectral efficiency, T_λ is the threshold spectral efficiency, λ is the wavelength (nm), and * indicates a threshold-based measure in each case.

The above integral is virtually identical to the CIE definition for photopic luminous flux; the only difference is that instead of V_λ it contains T_λ, a relative spectral efficiency based on absolute thresholds. Since T_λ is slightly broader than V_λ, the value of spectral efficiency $^*\kappa_m$ will be slightly less than the traditional value of κ_m (i.e., 683 lm/W). This definition may be incorporated, as is the current standard, into the design of any photometric light-measurement device. Rather than introduce a new term for the units of threshold-based flux at this time, we will simply refer to "threshold units," keeping in mind that such units must be expressed in terms of the external stimulus; they may be expressed in radiometric quantities or in appropriately adjusted photometric quantities, but they must always be referenced to T_λ. The concept of threshold units is not a new one; its counterpart in psychoacoustics, sensation level (the sound-pressure level in

decibels relative to the level at psychophysical threshold), has been in use for nearly a century.[86]

2. Threshold-Based Fluxes Obey Additivity

It is important to distinguish between additivity in two general domains: the theoretical (algebraic) and the empirical. Additivity of threshold-based fluxes in the first domain is strictly implied by the above integral [Eq. (1)]. This equation implies that lights specified in terms of threshold units obey the principle of superposition; that is, the total threshold-based flux (in threshold units) of a sum of lights equals the sum of the threshold-based fluxes of the component lights. The conventional definition of luminance is implicitly nonadditive, because the luminosity function defined by HFP depends on the light level at which it is measured.[22]

The question of empirical additivity may be expressed by two complementary questions: (1) Is there any psychophysical (perceptual) procedure in which algebraic additivity is preserved, i.e., in which two lights of differing wavelength composition that are algebraically equal also appear equal along some perceptual dimension? and (2) What perceptual dimensions of light will not obey the algebraic additivity of threshold-based fluxes? i.e., how may two lights that are equal in threshold-based flux differ in appearance?

The first question really leads one to consider the practical (psychophysical) determination of the equality of two lights specified in terms of their respective threshold-based fluxes. An elegant procedure to determine the threshold-based flux of any arbitrary test light at a given suprathreshold light level is by metameric matching to a mixture of three primaries, which can be performed with extreme precision by trichromats. First the absolute thresholds for the three primaries are established. These define the threshold-based scale for each primary. The threshold-based flux of any test light will then be equal to the sum of the three primary threshold-based fluxes that are required for achieving a metameric match with the test light. If the test light falls outside the space defined by the three primaries, the standard procedure of adding blue light to the test will be required for achieving a perfect match.

Suppose, for example, that test light A requires 100 $\mu W/cm^2$ of an r primary plus 50 $\mu W/cm^2$ of a g primary plus 0 $\mu W/cm^2$ of a b primary and that test light B requires, respectively, 0, 50, and 100 $\mu W/cm^2$ of the r, g, and b primaries to achieve metameric matches in each case. For the purposes of this example, suppose that the threshold for each primary were determined to be 1 $\mu W/cm^2$. The numbers above would then be in threshold units and proportional to threshold in any units desired. The total threshold-based flux of A and B is thus 150 threshold units each. If we now combine A and B, the principle of univariance for cone quantal absorptions ensures that the sum of the original primaries (100 $\mu W/cm^2$ of r, 100 $\mu W/cm^2$ of g, and 100 $\mu W/cm^2$ of b) will remain a metameric match to the sum of the test lights.

The advantage of a metameric (as opposed to a brightness) matching procedure is that, because of the principle of univariance, metamers result in equal quantal absorption across all receptor types. Thus this procedure constitutes a precise psychophysical way of measuring what a good (additive) photometer would measure if it were equipped with the exact T_λ filter for the particular observer being tested.

We point out that both the definition of threshold-based flux and the metameric procedure are conceptually equivalent to the traditional definition as expressed by Boynton: "...[T]wo lights may be said to be of equal luminance when each causes the same rate of photon capture in the combined population of R and G cones, without regard to their relative distribution." (Ref. 62, p. 308). Clearly the generality of the latter formulation is sacrificed if the radiances leading to equivalent photon capture at the psychophysical (flicker) null must vary with temporal frequency (and/or retinal locus).

The second question, regarding empirical additivity, has long been an issue in color science; that is, algebraic additivity does not imply perceptual (empirical) additivity along any or all dimensions. The most infamous example of this in the field of photometry is that, in general, the brightness (and/or saturation) of test lights will not be additive by any empirical procedure because of neural interactions subsequent to quantal absorption. Our threshold-based definition of luminance does not eliminate this complication from color science: two lights, each of which is set to be an equal number of units above threshold, may have very different brightnesses and/or saturations. However, our approach, like the traditional HFP-based approach, is not intended to equate brightnesses. Nonetheless, it is an empirical fact that even static, suprathreshold lights that are equal in threshold-based flux will be approximately equal in perceived brightness, since the shape of the absolute threshold spectral-sensitivity function more nearly approximates the brightness-matching spectral luminosity than HFP-spectral luminosity.[87,88]

One might question how chromatic interactions (e.g., color opponency leading to nonadditive color appearance) might influence the psychophysical procedure for measuring threshold-based flux. However, the elegance of the metameric matching procedure is that all interactions occurring subsequent to quantal absorption will be identical for both the test and the standard lights and therefore have no influence on the inherent additivity of the procedure. Thus additivity is built into both the analytic definition and the psychophysical procedure for measurement of threshold-based flux.

3. Other Advantages of Threshold-Based Flux

There are other factors that could, in principle, affect the measurement (and definition) of flux, such as the size of the stimuli, their retinal location, and their duration. However, with proper choice of stimulus conditions, a threshold-based definition may be immune to variations in these factors.[89]

Stimulus Duration: If, indeed, the response speed of R- and G-cone pathways differs, traditionally defined equiluminance between two lights that differentially stimulate R- and G-cone pathways must, in principle, vary with stimulus duration[90] for durations of the order of the peak of the impulse response (see Fig. 8). In this case a given change in the duration of the stimulus will represent a different proportion of the R- and G-cone pathway impulse response and thus will be subject to different

amounts of temporal integration. Threshold-based flux will not depend on stimulus duration.

Stimulus Size and Location: Traditional equiluminance also depends on the size and locus of the stimuli. This is because, among other possible factors, the time constant of cone pathways is as much as a factor of 2 less in the peripheral retina than in the foveola (see Figs. 2–4 in the present study and Refs. 5, 23, and 38). Thus to the extent that spatial parameters of the stimulus interact with this spatial gradient in cone-pathway response speed, flicker-defined equiluminance must depend on stimulus size and locus. Stimuli that are equal in threshold-based flux should be immune to retinal locus parameters if the ratio of absolute R-cone/G-cone-mediated thresholds does not vary significantly with retinal locus.

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$$F(s) = A(n - 1)!/(T + s)^n,$$

where s is complex frequency, n is the number of poles, and A and T are constants. The time constant T is inversely proportional to the Ferry–Porter slope. This filter equation was fitted to the 555- and 642-nm data of Figs. 2 and 3, with $n = 9$ and with T values derived from the average Ferry–Porter slopes in each case. Taking the inverse Laplace transform of the resulting frequency responses yields the nine-pole linear impulse responses shown in the left-hand portion of Fig. 8.
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Flicker photometry is termed an indirect method because the fields being equated are spatially contiguous but alternate in time. This distinction seems artificial. It is traditional to think of stimuli unchanging in time as probes of a single point on a temporal continuum. Wyszecki and Stiles[55] suggest the use of the term "flicker brightness" to refer to that which is matched in indirect (flicker) methods of photometry. We might propose that stimuli matched by this method be called "equimodulant." The concept of equimodulance explicitly includes a dependence on the temporal parameters of the stimuli but may be extended to zero frequency (i.e., the temporal domain of so-called direct measures).

84. Kaiser[85] has recently proposed the term "sensation luminance" or "s luminance" when an individual subject's spectral sensitivity (as determined by HFP, for example) is the basis of a light measurement. The term "luminance" would be reserved strictly for the photometric units based on the CIE photopic luminous efficiency function. A well-calibrated photometer can measure luminance; however, s luminance, which is inherently subject dependent, must be measured by a suitable (i.e., one in which additivity holds) psychophysical technique. Thus, for example, a 570-nm reference stimulus at 10 cd/m^2 can be matched by HFP (or minimum distinct border) to a series of test spectral stimuli. These will then all be at the same s luminance for that subject, in this case 10 Ives/m^2 (the unit Kaiser proposed for s luminances).

Although the concept of s luminance is a sensible one, it does not solve the problem that we are addressing here, namely, that for an individual subject the shape of the spectral-sensitivity curve itself varies with the temporal frequency (and the mean retinal illuminance) used to measure it, because of the underlying differences between R- and G-cone temporal properties. Thus two stimuli that have been matched at 10 Ives/m^2 at a low temporal frequency will not match at a high frequency.

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