Isolation of the middle- and long-wavelength-sensitive cones in normal trichromats

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Spectral sensitivity in the red–green spectral range typically reflects the joint influence of the middle-wavelength-sensitive cones (the M or green cones) and long-wavelength-sensitive cones (the L or red cones). The balance of M- and L-cone influence can be altered by presenting the test lights superimposed upon steady background fields of long or short wavelength. We find that presenting test stimuli just after an abrupt exchange between two colored backgrounds permits an easier and closer approach to cone isolation than presenting them either on a steady background or following an intense bleach. Background exchange drives the flicker detection or flicker photometric spectral sensitivities measured at 17 Hz to a limiting condition at lower intensities than do steady backgrounds. This condition is consistent with either M- or L-cone isolation. Steady backgrounds do not produce complete cone isolation: even on backgrounds that push spectral sensitivity closest to M or L, there are substantial phase differences between flickering lights of different color. In contrast, no phase differences remain following background exchange. The improvement in cone isolation produced by the exchange procedure is not confined to flicker measurements: the spectral range over which subjects are temporarily monochromatic is more extended following background exchange than on steady fields.

Key words: Color vision, M cones, L cones, red cones, green cones, spectral sensitivity, temporal sensitivity, phase differences, flicker photometry, luminance

1. INTRODUCTION

The spectral sensitivities of the three cone types are broad and overlap extensively, so that lights are seldom seen by one type alone. Because of this, the cone spectral sensitivities are most easily assessed in color-deficient individuals, in whom one of the cone types is assumed to be absent (see, for instance, Refs. 1–5). Such estimates, however, do not agree well with much of the available data from normal eyes (see, for instance, Refs. 6–9). In this paper we describe the development and validation of psychophysical procedures for isolation of the middle-wavelength-sensitive (M) and long-wavelength-sensitive (L) cone types in the normal observer. The resulting cone spectral-sensitivity estimates agree closely with the cone fundamentals of Vos and Walraven[10] and of Smith and Pokorny[5] at middle and long wavelengths. In our companion paper[9] we report the use of these procedures to measure spectral sensitivities in a group of normal and dichromatic observers and to derive new estimates of the cone fundamentals.

A. Two-Color Threshold Method of Stiles

Most cone-isolation techniques, including our own, owe much to the two-color threshold method of Stiles,[7,11] so called because the detection threshold for a target or test field of one color is measured on a larger adapting or background field, usually of a second color. Spectral sensitivity can be obtained either (1) by fixing the wavelength of the target and measuring the detection sensitivity as a function of changes in adapting field wavelength or, more directly, (2) by fixing the adapting-field wavelength and measuring the detection sensitivity as a function of changes in target wavelength. Stiles referred to such measurements made at a single threshold elevation as (1) field versus field wavelength or (2) threshold versus test wavelength measurements, whereas he referred to measurements made at a series of threshold elevations as (1) field sensitivity or (2) test sensitivity measurements. If cone isolation is achieved, the relative spectral sensitivities obtained by the short and the long methods should be the same, although the longer methods have the advantage of permitting a check that the spectral sensitivity remains invariant as the threshold level varies (see Subsection 1.E, below).

B. Field Sensitivities

In order for a field sensitivity to be a cone spectral sensitivity, the fixed-wavelength target must be detected by a single cone type, whatever the adapting field wavelength. Even if target isolation is achieved, however, it must also be true that each adapting field raises the target threshold solely by its effect on the single cone type that is mediating detection. This requirement of adaptive independence[12,13] must hold true even though changes in field wavelength cause large changes in the adaptive states of the two cone types that are not detecting the target (and thus in most postreceptoral pathways, since most receive inputs from more than one cone type).

For a few of the conditions used by Stiles to obtain his field sensitivity measurements, there is some evidence to suggest that adaptive independence is found, provided that the field intensities are kept below a certain level; but under many other conditions adaptive independence has been shown to fail (e.g., see Refs. 14–16). Yet even when adaptive independence does seem to hold, the field spectral sensitivities that are obtained are unlikely candidates for cone spectral sensitivities.[17]

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C. Test Sensitivities

Since the adapting-field wavelength is held constant in a test sensitivity determination, so too (for any particular adapting-field intensity) are any effects that the field might have through the fact that the two cone types do not mediate detection. Thus adaptive independence is not a requirement for a test spectral sensitivity to be a cone spectral sensitivity. All that is necessary is target isolation: a single cone type must mediate detection at all test wavelengths.

For target isolation to be achieved, the adapting-field wavelength (or combination of wavelengths) should be one to which the unwanted cone types are more sensitive than the cone type to be isolated, so that the former will be more desensitized by the field. Ideally, the color should be chosen to maximize the suppression of the two unwanted cone types. Yet, even if the optimal color is used, it is unlikely that a large steady field can desensitize the unwanted cone types enough to produce cone isolation at all test wavelengths. This argument is well illustrated by the "homochromatic" case, i.e., when the test field is of the same wavelength as the adapting field (as it must be in a complete test sensitivity determination). When the adapting-field wavelength, which differentially desensitizes the unwanted cone types, is used as a test field, it differentially favors detection by the same cone types that the adapting field is there to suppress. Indeed, if the sensitivities of the different cones are independently set in accordance with Weber's law, the selective effect of the test light will then merely cancel the sensitivity losses that are due to adaptation, resulting in completely unselective excitation rather than in the desired cone isolation (see Stiles's model of π_4 and π_5, his green- and red-sensitive π mechanisms: Sec. 7.4 of Ref. 18). For isolation under these worst-case homochromatic conditions, the sensitivity losses that are due to adaptation must exceed the selective effect of the test light.[17,19]

D. Background Exchange and Cone Suppression

In this paper we describe experiments designed to develop and validate a technique for measuring isolated M- and L-cone spectral sensitivities. In preliminary experiments we used steady chromatic adaptation and intense bleaching lights but found that both methods yield incomplete cone isolation (see Subsection 3.A). Subsequently we discovered that temporally modulating the adapting field in both color and intensity could improve cone isolation. We call this method, in which we measure spectral sensitivity immediately after the exchange of two background fields of different color, the exchange method [see Fig. 3(a) below]. Our results suggest that an abrupt change in background color can suppress the unwanted cone type(s) by a factor greater than that predicted by Weber's law, thus permitting the isolation of a single cone class throughout the visible spectrum.

Our method is much like one used by King-Smith and Webb[19] to isolate the L cones. To achieve isolation, these authors set the intensities of two colored backgrounds so that the background exchange was a silent substitution for the cone type to be isolated but caused an abrupt increase in the adaptation level of the unwanted cones. Given a cone-specific model of adaptation, these transient changes might be expected to reduce the sensitivity of the unwanted cone types relative to that of the type for which the exchange is invisible (see Refs. 20–22), thus improving isolation. Surprisingly, though, we found cone isolation for a range of background exchanges that included the exchange that was actually silent for the unwanted cone type. This unexpected result argues against isolation's being the result of a cone-specific transient sensitivity loss in the unwanted cones. Tentatively, we propose that the extra suppression of the unwanted cone signal depends on a chromatically opponent signal produced by the exchange in background color (see Fig. 11 below).

E. Evidence for Cone Isolation

We performed several standard tests for cone isolation. The first and simplest test was a comparison of our spectral sensitivities with previous estimates of the cone spectral sensitivities, such as those of Smith and Pokorny.[5] If any of our cone spectral-sensitivity estimates diverges from previous estimates by an amount that is too great to be explained by individual variability or error in the previous estimates, we can be fairly confident that cone isolation has failed. (Individual differences in cone spectral sensitivities are considered in more detail in the companion paper.[9])

The remaining checks for cone isolation rely on the assumption that the output of each cone (and thus of each cone type) is univariant, i.e., that it varies only according to the number of photons absorbed and is independent of their wavelength (see, e.g., Refs. 23 and 24).

The second check for cone isolation that we used was to measure spectral sensitivity over a range of background intensities (as in Stiles's test sensitivity method). On the assumption that cone spectral sensitivity is independent of background intensity (until photopigment bleaching becomes important), the measured spectral sensitivity should remain invariant whenever the experimental conditions successfully isolate the response of a single cone type. This check is known as a test of the displacement rules[14] or sometimes as a test of spectral or shape invariance. In general, we tested spectral invariance by measuring the sensitivity difference between 545- and 668-nm or 470- and 638-nm lights (see below). Since spectral invariance can also occur when more than one cone type mediates detection, this test is only suggestive of cone isolation.

The third check was to determine whether there were any phase differences between flickering targets of different wavelength. If both targets are detected exclusively by a single cone type, no phase differences should be found. This test proved to be particularly successful in demonstrating that steady chromatic backgrounds do not isolate single cones (see below). However, this test, like the previous one, does not conclusively demonstrate cone isolation. Phase differences would also not be found if cone isolation failed and the M- and L-cone signals were in phase.

The fourth check was to test whether two lights of different wavelength look identical. If the two lights are detected solely by one cone type, there should be no residual color differences when the two are matched in intensity. Like the previous tests, however, this test is also inconclusive. Color differences would also not be found if isolation failed, yet the lights were detected by a channel that signaled only intensity.

If any of the above tests fails, we can conclude that cone isolation has also failed. If all of them are passed, we can have some confidence that isolation has been achieved.

2. GENERAL METHODS

A. Apparatus

The optical apparatus was a conventional four-channel, Maxwellian-view system with a 2-mm entrance pupil. Test and field wavelengths were selected by use of interference filters (Ealing) that were placed in the first collimated part of each beam. Infrared radiation was minimized by heat-absorbing glass (Oriel) placed before the interference filters. Fixed neutral-density filters (Inconel) were added as required. Each channel contained a circular variable neutral-density wedge positioned almost conjugate with the pupil. The positions of the wedges, and therefore the beam intensities, could be controlled by the subject. Square-wave flicker was produced by interruption of the light beam close to an image of the lamp filament with mechanical shutters (Uniblitz). The shutters had rise and fall times of 0.6 and 0.9 ms, respectively. The observer's head was stabilized by a dental wax impression rigidly mounted on adjustable cross slides taken from a milling machine. Shutters were placed close to the first image of the arc.

B. Stimuli

The sizes of the test and field stimuli were defined by circular field stops. The observer foveally fixated the center of a 4°-diameter background field, on which one or two 2°-diameter test fields were superimposed. For the color-matching experiment (Subsection 3.E), two contiguous 2° half-fields formed a vertically bisected bipartite field.

C. Choice of Test Sensitivity Measure

In the majority of the experiments reported below, we used flickering test stimuli and required the subject either to set flicker threshold or to null one stimulus flicker photometrically with another flickering in opposite phase with it. Conventional wisdom holds that the M- and L-cone receptor signals can be transmitted either through chromatic pathways, which difference the signals from the various cone types, or through a luminance pathway, which adds them together. The two types of pathway can be distinguished psychophysically by their temporal resolution: when differently colored lights are alternated at low frequencies, the flicker can be perceived as a chromatic and luminance alternation, but at higher frequencies the flicker can be perceived only as a variation in luminance with no chromatic change (see, e.g., Refs. 25 and 26). This is taken as evidence that the chromatic pathway has a limited temporal resolution and is unable to follow rapid flicker. In the following experiments we used rapidly flickering test stimuli, so that our psychophysical tasks should depend on signals transmitted through the additive luminance pathway rather than on signals transmitted through slower chromatic pathways (see Refs. 27 and 28).

D. Choice of Adapting-Field Wavelength

For separation of the responses of the M cones from those of the L cones or vice versa, the adapting field should maximally suppress the unwanted cone types yet leave the cone type to be isolated relatively unadapted. Ignoring the short-wavelength-sensitive (S) cones for the moment, for L-cone isolation the wavelength of the adapting field ideally should be the one at which the sensitivity of the M cones relative to the L cones is greatest, and for M-cone isolation it should be the one at which the sensitivity of the L cones relative to the M cones is greatest.

In L-cone-isolation experiments, a number of workers (e.g., see Ref. 29) have used field wavelengths as long as 500 nm. Yet tritanopic color matches suggest that the greatest sensitivity difference between the M cones and the L cones is ~460 nm.[30] In our experiments we used a field wavelength of 485 nm. This choice of a slightly longer than optimal wavelength was guided by a concern that intense 460-nm bleaching backgrounds used in some experiments could produce unacceptably high levels of S-cone stimulation.[31] In a control experiment, flicker photometric spectral sensitivities measured on L-cone-equated 456- and 485-nm backgrounds were found to be identical.

For M-cone isolation we used a 678-nm field wavelength. At the red end of the visible spectrum, the sensitivity difference between the L and the M cones increases as the wavelength approaches 700 nm and thereafter slowly decreases.[32] Thus an adapting-field wavelength near 700 nm would be optimal for M-cone isolation. However, the sensitivity difference between M and L cones increases very little beyond ~670 nm, whereas the absolute sensitivities of both cones falls precipitously. To produce a long-wavelength adapting field of sufficient intensity, we used a deep-red Wratten #70 gelatin cutoff filter instead of an interference filter. In combination with the two HA3 heat-absorbing filters, the #70 filter produced a broadband field metameric with 678 nm. These two field wavelengths, 485 and 678 nm, became our standard isolating backgrounds.

E. Intrusion by Short-Wavelength-Sensitive Cones

Since we are comparatively insensitive to high-frequency S-cone-detected flicker, the use of high-frequency flickering stimuli has the added advantage of reducing S-cone contamination in our test sensitivity data. Nevertheless, we can detect moderately high-frequency S-cone flicker under some of the adaptation conditions used here. Furthermore, contrary to the conclusions of some workers,[33] the S cones can make a small contribution to flicker photometric sensitivity under some of the conditions that we used (see Refs. 34–36). It was therefore necessary to add an auxiliary 418-nm short-wavelength adapting field to desensitize the S-cones in some of our experiments (see Subsection 3.D).

F. General Procedures

Each subject light adapted to the background field(s) for at least 3 min before any data were collected. Sensitivity was measured mainly by 17-Hz flicker detection or by 17-Hz flicker photometry, but 10- or 200-ms flash detection and color matching were used; and, in a refinement of the flicker photometric procedure, we also determined the phase delay or phase advance needed to optimize the flicker photometric null.[28] These procedures are described in more detail below. The flicker was square wave. Since the measurements were generally made with

17-Hz flicker that was either at or near threshold, the weaker, higher harmonics of the square wave (at 51, 85, and 119 Hz, etc.) should be visually insignificant. The subject could control the intensities of the test fields by using the variable neutral-density wedges. In each experimental session, six settings were made at each test wavelength or adaptation level used. The data shown below are averaged from settings made during two, three, or four separate sessions (as noted). The subject was instructed to alternate the direction of the initial excursion of the wedge or phase control after each setting. In a spectral-sensitivity determination, test wavelengths were presented in ascending order of wavelength on the first run and in descending order on the second. If third and fourth runs were done, wavelengths were presented in descending and then in ascending order.

We used both steady and transient adaptation procedures. In the transient procedures we alternated two fields of different color or pulsed a single field on and off.

G. Calibration: General

The relative spectral radiant power distributions of all light source and spectral filter combinations were measured *in situ* with a calibrated EG&G spectroradiometer that had itself been calibrated against a reference mercury lamp and a reference light source. Daily measurements of the radiant fluxes of test and background fields were carried out with an EG&G radiometer/photometer that had been cross calibrated with a silicon photodiode (United Detector Technology) independently calibrated (by Optronics, Inc.) with a precision of 2% traceable to the U.S. National Institute of Standards and Technology. The test intensities are given below in $\log_{10}$ quanta $\sec^{-1}$ $\deg^{-2}$. The intensities of the backgrounds are given in $\log_{10}$ photopic trolands (abbreviated as Td throughout the paper). For the narrow-band 485-nm background (and all other backgrounds, except 678-nm), the photopic troland values were obtained by application of the appropriate formula to the quantal values. For the broadband 678-nm, deep-red background, the photopic troland values were obtained directly with the EG&G radiometer/photometer with its long-wavelength photometric filter (Model 550-4 LED photometric filter) attached. Neutral-density filters, fixed and variable, were calibrated *in situ* for all test and field wavelengths used.

H. Calibration: Test Wavelengths

The 10 test filters used in this study were spectrally calibrated at 2-nm steps *in situ* with the EG&G spectroradiometer. The bandwidths of the spectral test lights, defined as the width in nanometers between the two wavelengths at which the spectral output has fallen to one half of its maximum, varied from 10 to 13 nm. Typically, the wavelengths of such lights are described by the center wavelength of the transmitted band. This is generally an adequate description, except at the extremes of the visible spectrum where sensitivity is falling so rapidly that the physiologically equivalent monochromatic wavelength differs from the physical spectral centroid. To deal with this problem, we calculated, for each of our test lights, the wavelength of monochromatic light that would both have the same effect on the cone type of interest as our narrowband test light and be of the same total energy. We did this by finding the area under the spectral output curve for each test light (each spectral curve being a plot of wavelength against relative energy). Each spectral curve was cross multiplied with Smith–Pokorny M-cone or L-cone spectral-sensitivity functions [calculated from Ref. 5 with the Judd[37] and Vos[38] modified CIE color-matching functions (Table 1 of Ref. 38)], and the area under the resulting curve was then calculated. By dividing the area under this second curve by that under the first, and by looking again at the Smith–Pokorny cone sensitivities, we determined the wavelength of a monochromatic light that was equivalent to an equal energy of the test light in its effects on the cone type under consideration. The test wavelengths given below are these equivalent wavelengths. They differ from the physical spectral centroid in the direction of the spectral centroid of the pigment excitation distribution, differing from both centroids generally by less than 1 nm. Although it is small, this adjustment is important for ensuring that the differences between our measured sensitivities and the sensitivities expected on the basis of the Smith–Pokorny spectra are accurately represented.

We made self-screening corrections when necessary by assuming a peak optical photopigment density at 0.4 at λ_{max} and a half-bleach constant of 4.3 $\log_{10}$ Td for white light.[39] Negligible corrections were needed for the steady and exchange background M-cone isolation conditions; for the comparable L-cone conditions, the largest correction that was required was 0.04 $\log_{10}$ unit. Larger corrections of up to 0.15 $\log_{10}$ unit were necessary for the bleaching conditions shown in Fig. 2 below.

I. Subjects

Two of the authors (AS and JAV) served as the main observers in these experiments. Observers AS, JAV, and NEJ are emmetropic. NEJ is female; AS and JAV are male. Normal trichromacy was established for all three subjects by Rayleigh matches, by the Farnsworth–Munsell 100-hue test, and by Ishihara plates (and by the experiments themselves). Except where noted, AS and JAV carried out all the experiments reported below. NEJ carried out all the experiments except those described in Subsection 3.A and 3.B.2.

3. RESULTS AND DISCUSSION

A. Flicker Photometric Spectral Sensitivity on Backgrounds and after Intense Bleaches

1. *Introduction*

In this section we report conventional flicker photometric spectral-sensitivity measurements obtained with steady and bleaching backgrounds.

De Vries[40] demonstrated that steady chromatic adaptation can shift flicker photometric spectral sensitivity from V_λ toward an M-cone (protanopic) or an L-cone (deuteranopic) spectral sensitivity. Following up on this work, Eisner and MacLeod[41] measured 17-Hz flicker photometric spectral sensitivities on a variety of colored backgrounds and found that steady chromatic adaptation can depress the relative contribution of either the M or the L cones to flicker photometric sensitivity at least 10 times more than Weber's law predicts. A limitation of their study, however, was that the authors relied mainly on results obtained with test wavelengths away from the far-red and the blue regions of the visible spectrum, thus avoiding the regions where M- and L-cone test isolation is likely to be worst. One aim of this preliminary experiment was to extend the measurements made by Eisner and Macleod to include test wavelengths in the blue and the far-red parts of the spectrum. Moreover, by using 485- and 678-nm adapting fields of higher intensity, we also hoped to achieve better cone isolation than Eisner and MacLeod were able to obtain. For M-cone isolation we were disappointed. Small deviations still remained between our 17-Hz flicker photometric spectral sensitivities and the Smith–Pokorny M-cone spectral-sensitivity estimate even on the most intense deep-red field that we could produce.

When complete cone isolation is not achieved on steady adapting fields, an obvious recourse is to try more-intense adapting lights. Brindley[42] measured sensitivity following exposure to lights of bleaching intensity. He reported that combinations of bleaches can induce temporary or artificial monochromacy: i.e., over a limited spectral range, pairs of lights that match in intensity also match in color. Monochromacy is a condition that should ensue if vision is restricted to signals from only one type of photoreceptor (see above). Brindley found artificial monochromacy and an L-cone spectral sensitivity between 500 and 700 nm for 10–15 s following a 20-s, 4.39-$\log_{10}$-Td, 438-nm bleach and a 10-s, 4.90-$\log_{10}$-Td, 499-nm bleach; and he found artificial monochromacy and a plausible M-cone spectral sensitivity between 480 and 620 nm following a 20-s, 4.39-$\log_{10}$-Td, 438-nm bleach and a 10-s, 5.43-$\log_{10}$-Td 658-nm bleach (see also Ref. 43). However, the limited monochromacy found at long wavelengths following the red bleach (up to only 620 nm) suggests quite poor M-cone isolation.

In this section we also report measurements of 17-Hz flicker photometric spectral sensitivity following the offset of an intense deep-red, 678-nm or an intense blue, 485-nm bleaching light. We did not use the intense violet bleaches used by Brindley, who "even 8 months after the last experiment...[had] a faint after-image" (Ref. 42, p. 335). We find that M-cone isolation is worse following a deep-red bleach than it is on a much dimmer steady deep-red background.

2. Methods

Flicker photometry. In these experiments we used flicker photometry to measure the subject's spectral sensitivity (later we used flicker detection; see below). Two 2°-diameter test lights were alternated at a rate of 17 Hz. One light, the standard, was fixed in wavelength at 561 nm, while the other light, the test, was varied. For each background or bleach condition the intensity of the standard was set at four times the flicker threshold established in preliminary settings by the subject. Then at each test wavelength the subject adjusted the intensity of the test light to find the flicker photometric null, i.e., the intensity at which the flicker resulting from the alternation between the standard and the test light is minimized. Six settings were made for each condition. Flicker photometric spectral sensitivities were measured either with the two test fields superimposed upon a steady background or following a bleach.

Steady Background. The 678- and 485-nm steady backgrounds were provided by one of the optical channels of the main optical system. The flickering test lights were exposed continuously [see Fig. 1(a)]. There was no explicit time limit for subjects to make flicker photometric settings on the steady background fields.

Bleaches. The 678- and 485-nm bleaching lights originated from a separate optical channel with its own Maxwellian lens. The final filament image produced by this channel was focused on the subject's pupil when the subject looked 15° to the left of the axis of the main optical system. As above, the two flickering test fields were produced by the main Maxwellian-view optical system. Thus to see the bleaching lights the subject looked to the left, and to see the test lights the subject looked straight ahead. By using a bleaching channel entirely separate from the main optics of the Maxwellian view, we could produce a more-intense bleach.

The bleaching background was alternated with the two flicker photometric test fields: the bleaching background was exposed for 15 s, the two test lights for 5 s, and so on [see Fig. 1(b)]. The subject directed his or her gaze appropriately. Flicker photometric settings could be made only during the 5-s interval when the test lights were exposed. The subject adapted for at least 3 min before making any settings. As above, the standard test light was 561 nm. At the beginning of each new condition the standard was set to be four times flicker threshold near the end of the 5-s viewing interval.

The flicker photometric spectral sensitivities were averaged from six settings made on each of eight (AS) or four (JAV) runs. The 545–668-nm sensitivity differences measured as a function of either background or bleach luminance were averaged from two runs.

3. Results

Figure 2(a) shows 17-Hz flicker spectral sensitivities for subject JAV measured under various conditions: (1) following an intense blue, 485-nm bleach; (2) on a steady 485-nm background; (3) following an intense deep-red, 678-nm bleach; and (4) on a steady 678-nm background. Comparable results are shown for AS in Fig. 2(b).

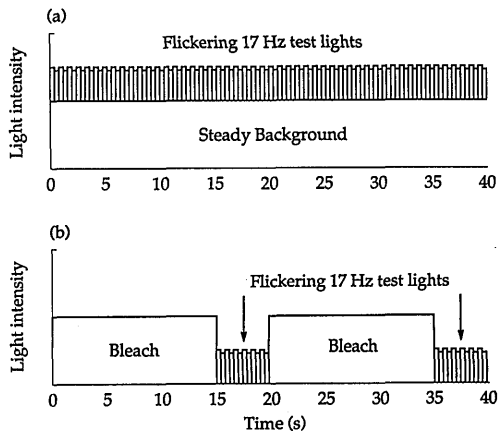

Fig. 1. Temporal sequence of stimuli. (a) Background condition: the two 17-Hz flicker photometric test lights and the steady background were exposed continuously. (b) Bleach condition: the bleaching background was alternated with the two flicker photometric test lights. The bleaching background was exposed for 15 s and the two test lights for 5 s. (Not to scale.)

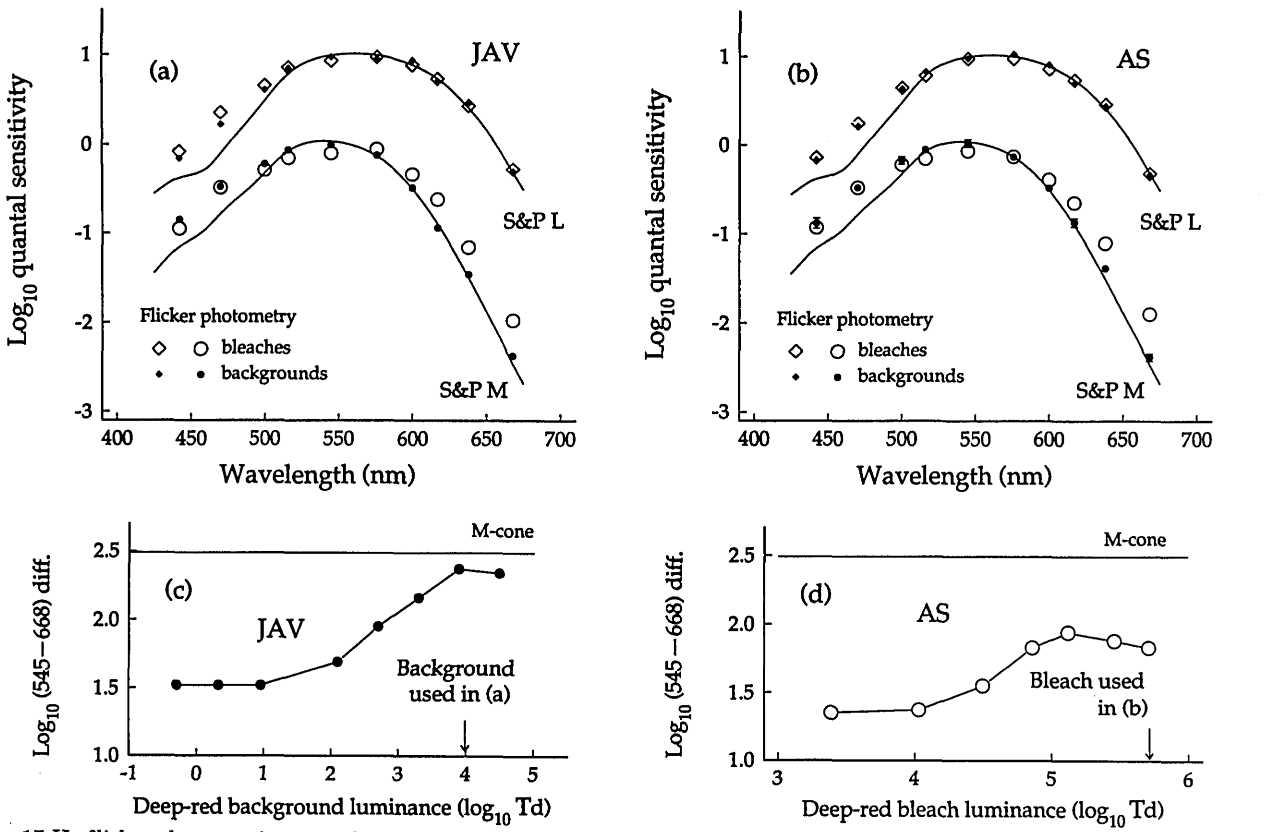

Fig. 2. 17-Hz flicker photometric spectral sensitivities for subjects (a) JAV and (b) AS measured following a 5.43-$\log_{10}$-Td, 485-nm bleach (open diamonds); on a steady 3.00-$\log_{10}$-Td, 485-nm background (filled diamonds); following a 5.75-$\log_{10}$-Td, 678-nm bleach (open circles); and on a steady 4.00-$\log_{10}$-Td, 678-nm background (filled circles). Standard stimulus: 561 nm at approximately 8 log quanta $\sec^{-1}$ $\deg^{-2}$. Curves are Smith–Pokorny L-cone (upper) and M-cone (lower) fundamentals. (c) Filled circles, 17-Hz flicker photometric sensitivity differences between 545- and 668-nm lights for JAV measured as function of the 678-nm background luminance. (d) Open circles, 545–668-nm sensitivity differences for AS as a function of the luminance of the 678-nm bleach. The horizontal lines in (c) and (d) represent the Smith–Pokorny M-cone-sensitivity difference. ±1 Standard deviation across sessions is shown when it is larger than the size of the plotted symbol.

To assess the degree of cone isolation implied by these spectral-sensitivity data, we fitted the measured sensitivities with a weighted linear sum of the cone sensitivities proposed by Smith and Pokorny.[5] We used a slightly different form of the equation for the fits to our M-cone data (S_M) and L-cone data (S_L):

$$\log S_M = \log\left(M_\lambda + \frac{w_L}{w_M} L_\lambda\right) + k_M,$$

$$\log S_L = \log\left(\frac{w_M}{w_L} M_\lambda + L_\lambda\right) + k_L. \quad (1)$$

M_λ and L_λ are the M- and L-cone sensitivities based on the work of Smith and Pokorny[5] and calculated by use of the CIE 2° color-matching functions modified by Judd[37] and by Vos[38] (see Table 1 of Ref. 38), and w_M and w_L are the relative M_λ and L_λ weights. The constants k_M and k_L are necessary only for expressing absolute sensitivity. A standard fitting program was used (Sigma Plot, Jandel Scientific). For simplicity, the results of the fits are given as percentage M_λ and L_λ weights. This is equivalent to rearranging the above equations into the following form:

$$\log S_\lambda = \log\left(\frac{100 w_M}{w_L + w_M} M_\lambda + \frac{100 w_L}{w_L + w_M} L_\lambda\right) + c, \quad (2)$$

where S_λ represents our cone-sensitivity estimates (S_M or S_L), $100w_M/(w_L + w_M)$ and $100w_L/(w_L + w_M)$ are the relative M_λ and L_λ weights, respectively, expressed as percentages, and c is a constant. The percentage weights are tabulated in Table 1. Implicit in the use of the above equations is the assumption that flicker photometric sensitivity depends on the linear combination of signals from the M and L cones. This assumption is apparently correct when the flicker photometric test lights are presented on intense backgrounds,[41] as is the case in these experiments. If isolation has been successful, and if the Smith–Pokorny cone sensitivities are applicable, the weighting factor for the suppressed cones in Eq. (2) should be zero.

We found the best-fitting forms of Eq. (1) for describing each of the eight (AS) or four (JAV) individual cone spectral-sensitivity estimates. We restricted the fits to test wavelengths between 516 and 668 nm to minimize the effect of individual differences in lens and macular pigmentation. Table 1 gives, as percentages, the mean, standard error, and 95% confidence interval of the best-fitting M- and L-cone weights.

For both subjects the flicker photometric spectral sensitivity measured on the 678-nm steady field is close to the Smith–Pokorny M-cone sensitivity; the relative M-cone influence is 98.76% and 98.97% for AS and JAV, respectively. Similarly, sensitivity measured on the steady 485-nm field is close to L; the relative L-cone influence is 93.46% and

99.63% for AS and JAV, respectively. The 95% confidence intervals (which we obtained conservatively by treating the fitting error as an estimate of random error) fix the relative M-cone contribution on the 678-nm field above 98.22% for AS and above 98.85% for JAV and fix the relative L-cone contribution on the 485-nm field above 85.68% for AS and above 87.08% for JAV. Going from steady adaptation to the blue field to steady adaptation to the deep-red field thus causes a change in the ratio of the M- to L-cone weights by at least a factor of 330 for AS and at least a factor of 580 for JAV. These factors are too large to be consistent with a simple reciprocal adjustment of sensitivity such as that implied by Weber's law ($\Delta I/I = k$), since the change in the relative M- and L-cone excitation caused by going from the 485-nm to the 678-nm field is by only a factor of ~27. If steady field adaptation for both cone types followed Weber's law, the change in w_L/w_M should also be by a factor of ~27. Clearly it is much larger, indicating a selective suppression well beyond that implied by Weber's law (see Section 4).

The M-cone spectral-sensitivity estimates after the 678-nm bleach clearly do not approach M-cone isolation (as defined by the Smith–Pokorny spectral sensitivity): the relative M-cone contributions are only 82.39% and 86.63% for AS and JAV, respectively. The L-cone spectral-sensitivity functions measured following the 485-nm bleach are closer to the Smith–Pokorny cone estimate: the relative L-cone contributions are 108.88% and 101.27% for AS and JAV. The suggested negative M-cone contributions (−8.88% and −1.27%, respectively) are not statistically significant (see Table 1).

It should be noted that a small-percentage L-cone contribution to an otherwise M-cone spectral sensitivity has a much larger effect on $\log_{10}$ sensitivity (between 516 and 668 nm) than does a similarly small percentage M-cone contribution to an L-cone spectral sensitivity. This is reflected in larger standard errors and confidence limits in Table 1 for the L-cone fits than for the M-cone ones. Thus seemingly large M-cone contributions to the L-cone spectral-sensitivity estimates may not be statistically significant.

Figures 2(c) and 2(d) show how the approach to M-cone isolation depends on the adapting luminance, in the cases of steady red adapting fields or of red bleaches, respectively. The $\log_{10}$ quantal flicker photometric sensitivity difference between 545- and 668-nm test lights is plotted in Fig. 2(c) (subject JAV) as a function of the luminance of the 678-nm background. It can be seen that the 545–668-nm difference asymptotes at a level just short of M and that the approach to M-cone isolation illustrated in Fig. 2(b) is not bettered at other adapting luminances. Similar results were obtained for subject AS (not shown). Measurements made with another system capable of producing more intense lights show that at still-higher background luminances, the curve in Fig. 2(c) declines further.[44,45] These results were disappointing; the results of Eisner and MacLeod[41] suggest a sensitivity ~0.1 $\log_{10}$ unit greater than the Smith–Pokorny M function at 668 nm on a red, 656-nm, 3.5-$\log_{10}$-Td field. We can do no better, despite using a longer-wavelength, more-intense field. It might seem tempting to ignore deviations as small as 0.1 $\log_{10}$ unit. However, in measurements described in our companion paper[9] we found a standard deviation of only 0.029 $\log_{10}$ unit in the 545–668-nm sensitivity differences of 13 subjects under M-cone-isolation conditions and a standard deviation of 0.076 $\log_{10}$ in the 545–668-nm sensitivity differences of 17 subjects under L-cone-isolation conditions.

Figure 2(d) shows how the 545–668-nm difference for AS varies as a function of the luminance of the deep-red bleach. The difference falls more than 0.5 $\log_{10}$ unit short of the assumed M-cone sensitivity difference at all bleach luminances. The bleaching results of Fig. 2 are in rough agreement with those of Brindley.[42] As he found, we find a close approach to L-cone isolation following a blue bleach but clearly incomplete M-cone isolation following a deep-red bleach. Surprisingly, bleaching is not more effective than steady adaptation in producing cone isolation: less-intense steady backgrounds can be more effective than bleaches.

In these early experiments the two targets were always flickered out of phase. For all the conditions described above, the subjects were easily able to set a flicker minimum by adjusting the intensity of the variable-wavelength test field to flicker photometrically match the standard field. Under most conditions, the flicker photometrically nulled target appeared quite steady. However, when the test field was deep red or violet, the subjects were sometimes aware of a small amount of residual flicker that could not be eliminated by intensity adjustments. The importance of this residual flicker became clear in the experiments described in Subsection 3.C, in which we found that it was caused, at least in part, by a phase difference between the signals generated by the two targets.

Table 1. Percentage L- and M-Cone Contributions That Best Describe the L- or M-Cone Spectral-Sensitivity Estimates for Subjects AS and JAV Obtained Either on Steady Backgrounds or Following Intense Bleaches

Subject	Estimate	%L Cone	%M Cone	Standard Error	95% Confidence
Steady Backgrounds					
AS	M cone	1.24	98.76	0.22	0.54
	L cone	93.46	6.54	3.29	7.78
JAV	M cone	1.03	98.97	0.04	0.12
	L cone	99.63	0.37	3.95	12.25
Bleaches					
AS	M cone	17.61	82.39	0.61	1.45
	L cone	108.88	−8.88	6.41	15.16
JAV	M cone	13.37	86.63	0.36	1.13
	L cone	101.27	−1.27	0.99	3.14

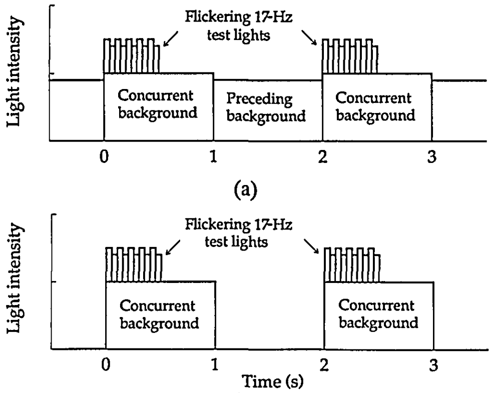

Fig. 3. Temporal sequence of stimuli. (a) Exchange condition: the two backgrounds, each on for 1 s, were exchanged once every 2 s. The two 17-Hz flicker photometric test lights were exposed only during the 500 ms immediately following the transition from the preceding background to the concurrent one. (b) Pulsed condition: like the exchange condition, except that the preceding background was absent. (Not to scale.)

B. Flicker Photometric and Flicker-Detection Measurements after Background Exchange

1. Introduction

The deviations of 0.1 $\log_{10}$ unit between our 17-Hz flicker photometric spectral sensitivities and the Smith–Pokorny M-cone fundamental are comparatively small, but they are too large to be attributable to experimental error. Since transient conditioning stimuli can produce greater modifications of sensitivity than is found under steady-state adaptation,[21,22,46] we next investigated the degree of M- or L-cone isolation under transient conditions of adaptation, in the hope that these would be more effective than steady-state adaptation. Our procedure was to alternate or exchange the two standard isolating backgrounds (678- and 485-nm) at a rate of 0.5 Hz [see Fig. 3(a)]. We call this the exchange method.

In the following experiments we varied the relative intensities of the exchanged backgrounds. This made it possible to adjust the size of the transients seen by the M- and L-cone types and to include background exchanges that were invisible to either the M- or the L-cones. A cone-specific model of adaptation predicts that isolation should be best when the exchange is invisible to the cone type to be isolated yet produces a large transient in the unwanted cone type,[19] but this need not be so if the signals attenuating one cone type's signals originate in part from other cones.

In some experiments we simply flashed or flickered a single adapting field at 0.5 Hz [see Fig. 3(b)]. We refer to this as the pulsed method.

The experiments described in this section were directed at M-cone isolation. In the first experiment we measured the 545–668-nm flicker photometric sensitivity difference as a function of the luminance of the concurrent 678-nm background and of the luminance of the preceding 485-nm background. In the second experiment we varied the wavelength of the preceding background. In the third experiment we determined the dependence of 17-Hz flicker threshold sensitivity on the luminance of the concurrent 678-nm background.

2. Methods

Exchange and pulsed procedures. In the exchange procedure the 678- and 485-nm backgrounds were alternated once every 2 s (i.e., they were flickered out of phase at 0.5 Hz). The test fields were presented during the 500 ms immediately following the transition from one field (which we refer to as the preceding field) to the other (which we refer to as the concurrent field). For M-cone isolation, the preceding field was 485 nm and the concurrent field 678 nm. For L-cone isolation (see Subsection 3.C), the reverse was the case. The exchange procedure is shown in Fig. 3(a). Figure 3(b) shows the pulsed procedure, in which the preceding field was absent. Sensitivity was probed either by a 17-Hz flicker photometric task (as illustrated in Fig. 3) or by a 17-Hz flicker-detection task.

In the second experiment in this section the wavelength of the preceding background was varied. Background wavelengths of 485, 530, 574, and 617 nm were selected by interference filters; the preceding deep-red field of 678-

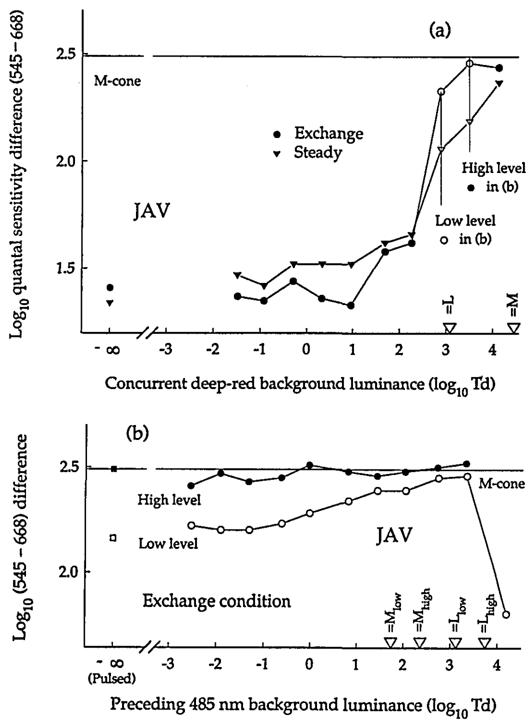

Fig. 4. Differences in flicker photometric sensitivity for 17-Hz, 545-nm, and 668-nm lights. (a) 545–668-nm sensitivity differences for JAV as a function of 678-nm background luminance, following an exchange of background from 485 to 678 nm (circles) or on a steady 678-nm field (triangles). The luminance of the preceding 485-nm background was 3.32 $\log_{10}$ Td. The horizontal line is the Smith–Pokorny M-cone sensitivity. The triangular symbols plotted along the abscissa denote the concurrent background luminances at which the exchange was invisible to the L cones (3.08 $\log_{10}$ Td) and to the M cones (4.46 $\log_{10}$ Td). (b) 545–668-nm sensitivity differences for JAV measured at two concurrent 678-nm luminances (open circles, 2.88 $\log_{10}$ Td; filled circles, 3.50 $\log_{10}$ Td) as a function of the preceding 485-nm background luminance. The squares denote the flashed condition, when the 485-nm background is extinguished. The triangular symbols on the abscissa denote the preceding background luminances at which the exchange was invisible to the M cones (1.74 and 2.36 $\log_{10}$ Td for the low and the high levels, respectively) and to the L cones (3.12 and 3.74 $\log_{10}$ Td for the low and the high levels, respectively).

nm, like the concurrent deep-red field, was broadband, produced by a Wratten #70 filter and heat-absorbing filters. The data points shown in Figs. 4–6 are averaged from six settings made on each of two separate experimental runs.

Flicker-detection thresholds. In the third experiment of this section (and in later experiments) we measured flicker threshold sensitivity rather than flicker photometric sensitivity. A single 2° test field was used. It flickered at 17 Hz and was presented in the center of the 4° adapting fields. The subject adjusted the intensity of the flickering light until he or she was satisfied that the flicker was just at threshold.

3. Results and Discussion

Varying the luminances of the concurrent and the preceding backgrounds. Figure 4(a) shows the $\log_{10}$ quantal flicker photometric sensitivity differences for 545-nm and 668-nm lights for JAV as a function of the luminance of the concurrent deep-red background. Measurements were made either following an exchange of background color or on steady fields. The triangular symbols on the abscissa denote the concurrent background luminances at which the exchange was invisible to the L cones and the M cones. Similar results (not shown) were obtained for AS and NEJ.

For both background exchange and steady adaptation, increasing the luminance of the deep-red background increases the 545–668-nm difference from a value roughly consistent with the standard luminosity curve, V_λ (1.52 $\log_{10}$ unit; see Table 1 3.3.1 of Ref. 18), toward an M-cone spectral sensitivity. Only following background exchange does the 545–668-nm difference reach the assumed M-cone spectral sensitivity, and it first does so at a background luminance at which the 545–668-nm sensitivity difference on the steady field is still shy of *M*.

Figure 4(b) shows the effect of varying the luminance of the preceding 485-nm background at the two concurrent deep-red luminances indicated by the line and the open symbols in Fig. 4(a). For the pulsed condition ($-\infty$ $\log_{10}$ Td), the preceding background is extinguished. In this panel the larger triangular symbols along the abscissa indicate the preceding background luminances at which the exchange was M- or L-cone equated for the high and low concurrent-background luminances.

At the higher concurrent-background luminance, increasing the luminance of the preceding background has little effect on the 545–668 sensitivity difference, which stays close to an M-cone spectral sensitivity. This suggests that if the deep-red field is intense enough, pulsing it is as effective in producing an M-cone spectral sensitivity as is exchanging it for a blue field. At the lower level, however, the presence of the preceding blue field clearly improves M-cone isolation, provided that the blue field is not too intense (the spectral sensitivity collapses back toward *L* if the preceding background luminance exceeds ~4 $\log_{10}$ Td).

If adaptation proceeds independently in the M- and L-cone pathways, then we should expect the closest approach to M-cone isolation when the transition from the 485- to the 678-nm fields produced a large transient in the L cones and little or no transient in the M cones. The results shown in Fig. 4(b) decisively refute this prediction. The approach to M-cone isolation (or to the complete suppression of input from L cones) is closer when the fields

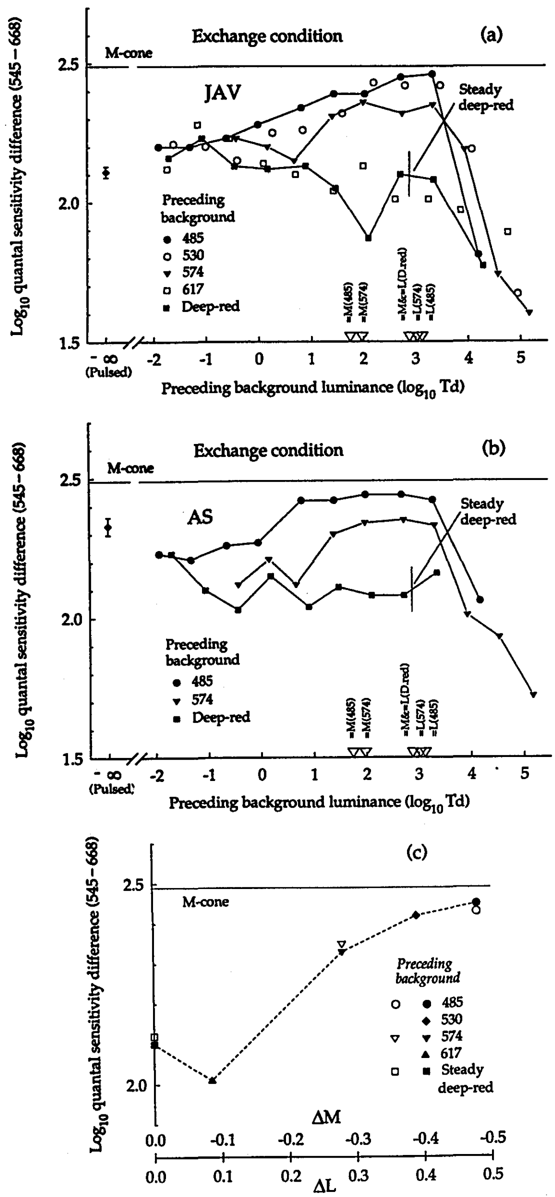

Fig. 5. 545–668-nm, 17-Hz flicker photometric sensitivity differences for (a) JAV and (b) AS measured with a concurrent 678-nm background of 2.88 $\log_{10}$ Td, as a function of the preceding background luminance for five preceding background wavelengths: 485 nm (filled circles), 530 nm (open circles), 574 nm (filled triangles), 617 nm (open squares) and a deep red, homochromatic with the concurrent field (filled squares). The vertical line corresponds to the luminance at which the deep-red concurrent and preceding backgrounds are equal in luminance. The horizontal line is the Smith–Pokorny M-cone sensitivity. The filled diamond is the average of the sensitivity differences obtained when the preceding backgrounds were absent. Error bars are ±1 standard deviation. The triangular symbols on the abscissa denote the preceding background luminances (485 nm, 574 nm, and deep red only) at which the exchange is M- or L-cone equated. (c) 545–668-nm, 17-Hz flicker photometric sensitivity differences for JAV (filled symbols) and AS (open symbols) for background exchanges of equal luminance (2.88 $\log_{10}$ Td) as a function of ΔL and ΔM, where ΔL and ΔM are the change in L- and M-cone excitations (expressed as a fraction of the total luminance) caused by the background exchange (see text for details). Preceding background wavelengths: 485 nm (circles), 530 nm (diamonds), 574 nm (inverted triangles), 617 nm (upright triangles), and deep red (squares).

are L-cone equated than when they are M-cone equated. If transience at the cone level *per se* were critical, these isolation conditions should have impaired M-cone isolation instead of enhancing it. Similarly, the results shown in Fig. 4(a) show that a background exchange that is L-cone equated pushes spectral sensitivity closer to M than does a steady field.

Varying the wavelength of the preceding background. Since the foregoing results suggest that transients produced by background exchange do not promote isolation by their action at the receptor level, it seemed useful to vary both the wavelength and the intensity of the preceding background in order to elucidate further the chromatic organization of the mechanisms responsible. We kept the luminance of the concurrent deep-red background at 2.88 $\log_{10}$ Td [the low level in Fig. 4(b)]. Figure 5(a) shows 545–668-nm, 17-Hz flicker photometric sensitivity differences for JAV for five different preceding field wavelengths: 485, 530, 574, and 617 nm and a deep red, homochromatic with the concurrent field. Figure 5(b) shows similar results for AS for preceding 485- and 574-nm and deep-red fields.

Use of the 485-, 530-, and 574-nm preceding backgrounds brings the 545–668-nm sensitivity difference closer to an M-cone spectral sensitivity than does pulsing the deep-red field (filled diamonds) or presenting it as a steady field. In fact, the 485- and 530-nm backgrounds push sensitivity very close to our assumed M-cone sensitivity, while the 574-nm background leaves sensitivity only ~0.1 $\log_{10}$ unit short. In contrast, introducing the 617- and 678-nm preceding backgrounds before the deep-red concurrent field makes M-cone isolation worse.

What is happening at the cone level during these background exchanges? L-cone equivalence occurs when the preceding field is 3.12 (485-nm), 3.13 (530-nm), 3.03 (574-nm), 2.92 (617-nm), or 2.88 (678-nm) $\log_{10}$ Td; and M-cone equivalence occurs when the preceding field is 1.74 (485-nm), 1.90 (530-nm), 1.97 (574-nm), 2.38 (617-nm), and 2.88 (678-nm) $\log_{10}$ Td. For the 485-nm, 574-nm, and deep-red fields, these intensities are indicated along the abscissas of Figs. 5(a) and 5(b) as inverted triangles. The generalization that previous exposure to light of 574-nm or shorter wavelength is helpful to M-cone isolation, whereas longer-wavelength exposure is not, holds across a range of preceding background luminances that spans equality with the concurrent background for both L- and M-cone types (as well as equality in luminance). These results can be understood if the change in background color acts at a chromatically opponent site that receives opposing inputs from the M and the L cones. At such a site the change in background color alters the direction of polarization from one extreme to the other and thus plausibly may transiently reduce sensitivity there. A loss in sensitivity might be incurred in this way for both the M- and the L-cone signals, but the improvement in M-cone isolation implies that the loss is greater for the L-cone signal.

Figure 5(c) shows the 545–668-nm sensitivity differences for background exchanges of equiluminant (2.88-$\log_{10}$-Td) fields plotted as a function of the change in L-cone excitation (ΔL) or in M-cone excitation (ΔM) when the deep-red background replaces the preceding one. The cone excitations here are expressed in units such that each represents the fraction of the total (constant) luminance derived from the cone type in question. For the deep-red background, $L = 0.961$ and $M = 0.039$. At isoluminance, ΔL and ΔM are equal and opposite, as shown by the dual abscissa, so a linear chromatically opponent channel would receive a change in excitation proportional to either ΔL or ΔM. The data for JAV and AS are interpolated from the data of Figs. 5(a) and 5(b). It can be seen that as ΔL increases (or ΔM decreases), so too does the degree of M-cone isolation implied by the 545–668-nm sensitivity difference.

Our proposal that there is chromatically opponent attenuation may seem to conflict with the finding that the most extreme adaptation drives the spectral sensitivity to an M- or an L-cone-dominated function rather than toward a spectrally opponent one. The resolution of this apparent contradiction is simple: signals derived independently from the M and the L cones may be attenuated to a degree that depends on the value of a chromatically opponent signal (see Fig. 11 below and, for instance, Ref. 41).

Flicker threshold versus intensity (f.t.v.i.) curves. We now have clear evidence that an exchange of background color from blue to deep red is more effective than a steady deep-red field in pushing flicker photometric spectral sensitivity toward M. In this experiment we looked at what is happening at the threshold level by comparing detection thresholds for 545- and 668-nm, 17-Hz flicker obtained

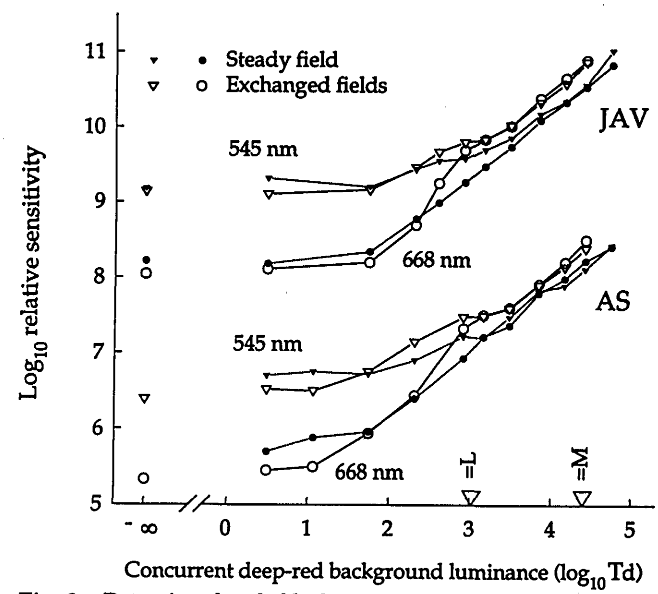

Fig. 6. Detection thresholds for 17-Hz, 545-nm (triangles) and 668-nm (circles) flicker measured as a function of background luminance on a steady 678-nm field (open symbols) or following an exchange of background from 485 to 678 nm (filled symbols). The luminance of the 485-nm preceding background was 3.26 $\log_{10}$ Td. The triangular symbols plotted along the abscissa denote the concurrent background luminances at which the exchange was invisible to the L cones (3.02 $\log_{10}$ Td) and to the M cones (4.40 $\log_{10}$ Td). For each subject, we shifted the 668-nm f.t.v.i. curve 2.46 $\log_{10}$ units downward relative to the 545-nm curve to equate the test lights for their effects on the M cones. The 545-nm f.t.v.i. curves for AS and the 668-nm f.t.v.i. curve for JAV are plotted correctly with respect to the scale of the ordinate. To obtain the correct threshold levels for the 668-nm f.t.v.i. curve for AS add 2.46 $\log_{10}$ units, and for the 545-nm f.t.v.i. curve for JAV subtract 2.46 $\log_{10}$ units.

after background exchange with thresholds obtained on steady fields.

Figure 6 shows $\log_{10}$ detection thresholds for 545-nm and 668-nm flicker on steady fields (filled symbols) and after background exchange (open symbols). The upper set of curves is for subject JAV and the lower for AS.

For each subject, the 668-nm f.t.v.i. curves have been shifted 2.46 $\log_{10}$ units downward relative to the 545-nm curves. This shift is our estimate of the M-cone sensitivity difference between 545- and 668-nm lights. Thus when the 545- and 668-nm flicker thresholds coincide in Fig. 6, the spectral sensitivity is an M-cone spectral sensitivity.

For both subjects the 17-Hz flicker exchange spectral sensitivity converges onto an M-cone spectral sensitivity as the 678-nm background luminance approaches 3.0 $\log_{10}$ Td (i.e., when the backgrounds are approximately equated for the L cones) and remains there as the background luminance is further increased. The approach to M-cone isolation is accompanied by a steep rise in the exchange f.t.v.i. curves. By 3.0 $\log_{10}$ Td, the exchange thresholds are $\sim$0.40 $\log_{10}$ unit above the steady-field thresholds at 668 nm and $\sim$0.25 $\log_{10}$ unit above them at 545 nm. The exchange f.t.v.i. slope in this region is much steeper than the Weber's law slope of 1. Between the background luminances of 2.31 and 2.91 $\log_{10}$ Td, the 668-nm threshold rises with a slope of 1.67 for JAV and 1.48 for AS. Since Weber's law is exceeded, the sensitivity losses resulting from adaptation can exceed the selective effect of the 668-nm test light in favoring detection by the unwanted L cones, thus making M-cone isolation possible (see Section 1).

What else can these results tell us? The background exchange is invisible to the L cones when the 678-nm field is 3.02 $\log_{10}$ Td (and to the M cones when it is 4.40 $\log_{10}$ Td). The largest elevation of the 668-nm exchange threshold above the steady-field threshold occurs, therefore, when the exchange is close to being invisible to the L cones. This implies a substantial elevation of L-cone threshold by transients seen only by the M cones. Other workers have reported similar findings. Sternheim *et al.*[47] and Reeves[48] found that exchanges that are silent for Stiles's π_5 (which has a roughly L-cone spectral sensitivity) still can raise π_5 threshold for flash detection; and Reeves[49] has reported similar findings for Stiles's π_4. Clearly, these results are inconsistent with a simple cone-specific model of adaptation.[47–49]

Again, our results can be explained if the L-cone flicker signal undergoes a chromatic attenuation caused by the change of background color. However, the fact that the background exchange elevates both the 545- and the 668-nm flicker thresholds above their steady-field levels (see Fig. 6) suggests that the chromatic attenuation is applied to both the M- and the L-cone flicker signals. Since spectral sensitivity changes in this region, the attenuation must be applied to some extent independently to the flicker signals from the two cone types.

For the exchange thresholds the attainment of M-cone isolation is accompanied by a reduction in the slopes of both the 545- and the 668-nm f.t.v.i. curves. This type of threshold transition is traditionally interpreted as a change in the mechanism determining threshold (see, for example, Ref. 7). No such transition can be identified in the f.t.v.i. curves measured on the steady 668-nm field.

The steady-field 17-Hz thresholds shown in Fig. 6 do not show the extended M-cone asymptote that the exchange thresholds do. Nevertheless, the data for AS in particular do reach (or even slightly exceed) the standard M-cone spectral sensitivity at high background luminances. Yet, as we shall see next, substantial phase differences can be demonstrated between the responses to 545- and 668-nm flicker under these conditions, indicating that isolation on steady backgrounds is less nearly complete than the spectral sensitivities suggest.

C. Flicker-Detection Thresholds and Phase Differences after Background Exchange and on Steady Fields

1. *Introduction*

In this experiment we considered both M- and L-cone isolation. To investigate L-cone isolation we measured the difference in sensitivity for the detection of 470- and 638-nm 17-Hz flicker (1) following an exchange of background color from deep red to blue and (2) on a steady blue field. To investigate M-cone isolation we measured the difference in sensitivity for detection of 545- and 668-nm 17-Hz flicker (1) following an exchange of background color from blue to deep red and (2) on the steady deep-red field (these M-cone measurements are also shown as f.t.v.i. curves in Fig. 6). As a further test of cone isolation, we determined the phase differences required for production of a flicker photometric null of the 17-Hz 545- and 668-nm lights (M-cone-isolation conditions) or the 470- and 638-nm lights (L-cone-isolation conditions). If cone isolation is achieved, there should be no phase difference between these lights.

Phase differences may be a particularly sensitive test of cone isolation, even when the spectral sensitivity is close to cone isolation. For example, on steady red adapting fields that push spectral sensitivity close to M, Swanson *et al.*[50] observed that substantial phase adjustments may be required for production of a flicker photometric null of alternating red and green test lights. Similarly, Stromeyer *et al.*[51] inferred large phase differences on red fields from the shapes of detection contours.

2. *Methods*

Sensitivity was measured with the 17-Hz flicker detection task. As above, test lights of 545 and 668 nm were used for the M-cone-isolation conditions. For L-cone-isolation conditions, 470- and 638-nm lights were used. We chose a light of 470 nm because it is close to the wavelength at which a failure of L-cone isolation should be most evident (see above).

Phase measurements. For the phase measurements, two 2° flickering test fields were presented in the center of the 4° adapting fields. In a refinement of the flicker photometric technique described above, the subject adjusted the relative phase difference between the two test fields as well as their relative intensity. To vary the relative phase of the two flickering test lights, we used two frequency generators. The first was set to the frequency of interest (usually 17 Hz), while the second, a phase-lockable generator with variable phase delay (Wavetek), was phase locked to the output signal of the first. The output of each generator drove the shutter in the one of the two test channels, so that, by adjusting the variable

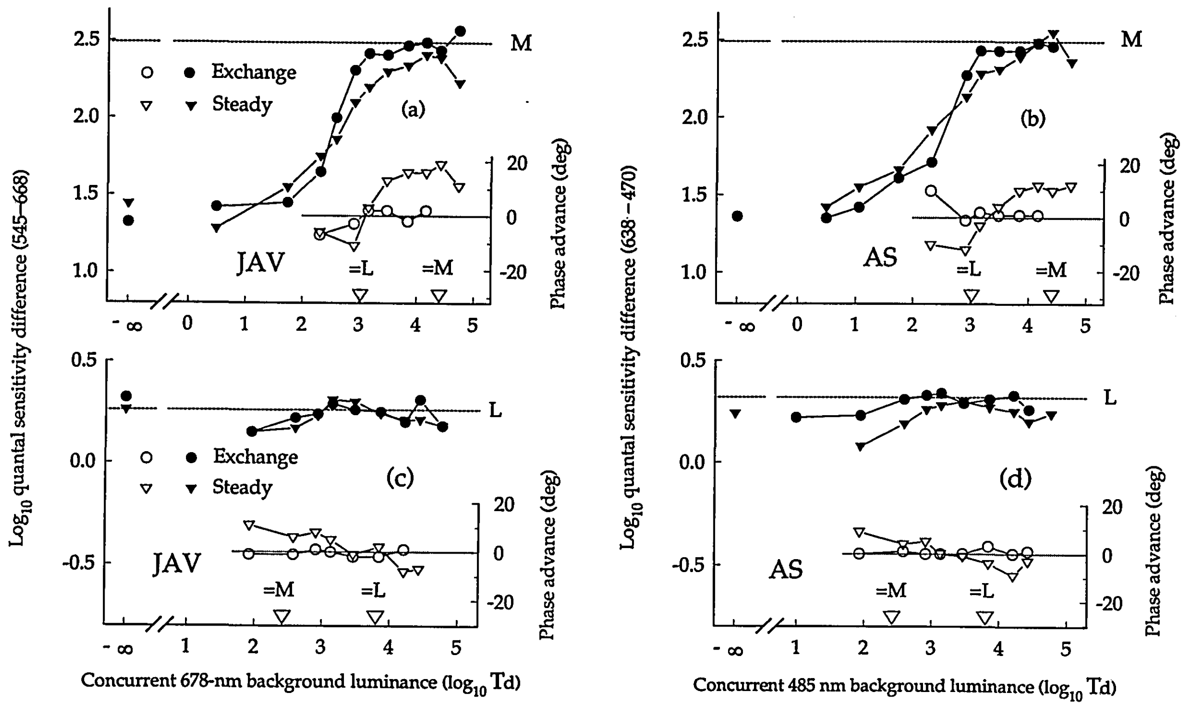

Fig. 7. (a) Upper curves are the difference in $\log_{10}$ sensitivity for detection of 545- and 668-nm, 17-Hz flicker for JAV either on a steady 678-nm background (filled triangles) or following an exchange of background from 485 to 678 nm (filled circles) plotted as a function of background luminance. The sensitivity differences are derived from the data of Fig. 6. The upper horizontal dashed line is the Smith–Pokorny M-cone sensitivity. The lower curves are the phase advances (from 180°) of the 545-nm flickering light required for a flicker photometric null of the 668-nm light on the steady 678-nm background (open triangles) or following the exchange of background from 485 to 678 nm (open circles), also plotted as a function of background luminance. The lower dashed line is the 0° phase advance that is expected if the two lights are detected by the same cone type. In the exchange procedure the preceding 485-nm background was 3.26 $\log_{10}$ Td. The triangular symbols plotted along the abscissa denote the concurrent background luminances at which the exchange was invisible to the L cones (3.02 $\log_{10}$ Td) and to the M cones (4.40 $\log_{10}$ Td). The flicker-detection sensitivity differences shown in (a) for JAV can be compared with his flicker photometric sensitivity differences shown in Fig. 4(a). (b) Like (a) but for subject AS. (c) L-cone isolation. The upper curves are the difference in $\log_{10}$ sensitivity for detection of 638- and 470-nm, 17-Hz flicker for JAV either on a steady 485-nm background (filled triangles) or following an exchange of background from 678 to 485 nm (filled circles) plotted as a function of background luminance. The upper horizontal dashed line is our estimate of the L-cone spectral sensitivity. The lower curves are the phase advances (from 180°) of the 638-nm flickering light required for flicker photometric null of the 470-nm light on the steady 485-nm background (open triangles) or following the exchange of background from 678 to 485 nm (open circles). The preceding 678-nm background was 3.56 $\log_{10}$ Td. The triangular symbols plotted along the abscissa denote the concurrent background luminances at which the exchange was invisible to the M cones (2.42 $\log_{10}$ Td) and to the L cones (3.80 $\log_{10}$ Td). (d) Like (c) but for subject AS. [See Figs. 1(a) and 1(b) of Ref. 9 for exchange sensitivity measurements in other subjects.]

phase delay of the phase-locked generator, the subject could continuously vary the relative phase of the two flickering test lights.

Before each phase measurement, a 561-nm standard field was set to flicker at approximately twice flicker threshold. The subject varied (1) the phase difference between the standard and test fields and (2) the intensity of the test field to produce the most compelling null. A switch on the phase-lockable generator flipped the relative phase of the two flickering stimuli by 180°. This allowed the subject to compare the phase at which the flicker appeared least with an opposite phase at which the flicker appeared maximal, thus ensuring that the null was not mistakenly set by a reduction of both of the flickering stimuli below threshold. Despite the apparent complexity of the task, experienced subjects could make settings easily and reliably after only a few practice trials. Four phase settings were made at each frequency and adaptation level. The data points are averaged from settings made during two separate sessions.

3. *Results*

M-cone spectral-sensitivity and phase differences. The filled symbols in Figs. 7(a) and 7(b) show the differences in $\log_{10}$ sensitivity for detecting 545- and 668-nm flicker; they are plotted relative to the left-hand ordinate. The phase adjustments that are required for nulling alternating 545- and 668-nm lights are shown as open symbols and are plotted against the right-hand ordinate. Measurements were made following background exchange (circles) and on steady backgrounds (triangles).

For both subjects the 545–668-nm sensitivity difference following background exchange reaches an M-cone spectral sensitivity by 3.0 $\log_{10}$ Td and remains fairly constant with further increases in luminance. On the steady field, however, the difference never reaches an M-cone spectral sensitivity for JAV and reaches it only above 4.0 $\log_{10}$ Td for AS.

Does a 4.0-$\log_{10}$-Td, steady 678-nm field produce M-cone isolation for AS? The phase differences shown at the bottom right of Fig. 7(b) suggest that it does not. The closest approach to M-cone isolation for AS is accompanied by a large phase difference of 12°. Similarly large phase differences are found for JAV. For phase differences of this magnitude to be present at all, more than one receptor type must be mediating the flicker detection of at least one of the test lights. In contrast, the phase differences are all close to 0° following background exchange.

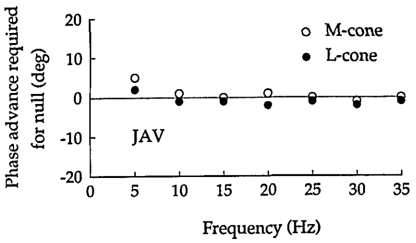

Fig. 8. Open circles are the phase advances (from 180°) of the 545-nm flickering light required for flicker photometric nulling of the 668-nm light following an exchange from a 3.26-$\log_{10}$-Td, 485-nm background to a 4.16-$\log_{10}$-Td, 678-nm background. Filled circles are the phase advances of the 638-nm flickering light required for nulling of the 470-nm light following an exchange from a 3.29-$\log_{10}$-Td, 678-nm background to a 3.91-$\log_{10}$-Td, 485-nm background. Subject: JAV.

L-cone spectral-sensitivity and phase differences. Figures 7(c) and 7(d) show the difference in $\log_{10}$ sensitivity for detecting 638- and 470-nm flicker following background exchange and on a steady field; the phase adjustments required for null alternating 638- and 470-nm lights under the exchange and steady adaptation conditions are shown plotted against the right ordinate.

Because of individual variability in macular and lens pigmentation at 470 nm, we cannot assume that the Smith–Pokorny L-cone estimate of the 638–470-nm sensitivity difference is valid for our subjects. The upper, horizontal dashed line in each panel is simply the 470–638-nm sensitivity difference for each subject obtained in the spectral-sensitivity determinations shown in Fig. 9 below. We believe that these represent the true L-cone spectral sensitivities for these subjects (see Ref. 9).

The 638–470-nm sensitivity differences shown in Figs. 7(c) and 7(d) change little with background luminance. This is because a change from the standard photopic luminosity curve to a pure L-cone sensitivity amounts to a shift of only 0.32 $\log_{10}$ unit for these test wavelengths. Since the changes in spectral sensitivity are relatively small, we do not show the separate f.t.v.i. curves for 470 and 638 nm as we did for M-cone isolation. However, consistent with the thresholds shown in Fig. 6, background exchange elevates flicker threshold by approximately 0.3 $\log_{10}$ unit above its steady-field level.

For the 678- to 485-nm background exchange that we used for L-cone isolation, the transition is invisible to the L cones when the 485-nm field is approximately 3.80 $\log_{10}$ Td and is invisible to the M cones when it is only 2.42 $\log_{10}$ Td. As for M-cone-isolation conditions, the additional elevation of threshold and the approach to L-cone isolation do not seem to depend critically on either L- or M-cone equivalence. Again, a chromatic attenuation is suggested.

Here, as with M cones, phase differences appear to be a more critical test for L-cone isolation. For both subjects the phase differences obtained on a steady 485-nm field vary continuously as a function of background luminance, changing from 10° to −9° as the luminance increases. These differences show that more than one receptor type is mediating flicker detection. Following background exchange, however, the phase differences are all close to 0°. By this criterion, background exchange gives L-cone isolation but steady adaptation does not.

For the exchange condition, the 17-Hz phase adjustments measured under both M- and L-cone isolation conditions all lie near 0°. If cone isolation is complete, a phase difference of 0° should be found at all frequencies, not just at 17 Hz. In a further experiment we varied the flicker frequency. The results for JAV are shown in Fig. 8. The measured phase differences following background exchange all stay close to 0° under both M-cone- and L-cone-isolation conditions. Comparable results were obtained for AS. In contrast, the phase adjustments on steady fields (not shown) vary by up to 50°. We note that even near threshold the higher harmonics of the square wave may be visually significant at square-wave frequencies as low as 5 Hz.

Pulsed backgrounds. All the experiments reported in this section were also carried out with a pulsed transient adaptational procedure, in which flicker thresholds and phase measurements were made during the 500 ms following background onset [see Fig. 3(b)]. Consistent with the results shown in Fig. 4 and with the results of King-Smith and Webb,[19] who showed that an M-cone spectral sensitivity can be produced by flashing a red field, we found that an intense pulsed deep-red, 678-nm field drives the 545–668-nm sensitivity difference close to M and requires minimal phase adjustments for completion of the 545–668-nm null. Pulsed 485-nm fields, however, are actually less effective in producing L-cone isolation than are steady fields of the same wavelength.

D. Flicker- and Flash-Detection Spectral Sensitivities Following Background Exchange

1. Introduction

Results presented in Subsection 3.C.3 indicate successful isolation at key wavelengths. In the experiment discussed below we extend the range of wavelengths by measuring 17-Hz flicker-detection spectral-sensitivity curves following the exchange of background color. We decided on 17-Hz flicker detection rather than flicker photometry as our primary sensitivity measure, because we found that naïve subjects had less difficulty in setting flicker thresholds than in setting flicker photometric nulls.[9]

We have seen that background exchange is effective in achieving M- and L-cone isolation for 17-Hz flicker detection. How effective is it if other tasks are used? In addition to flicker-detection spectral sensitivity, we also measured the M-cone spectral sensitivity for the detection of 200- and 10-ms-duration targets. While 17-Hz flicker detection is thought to depend mainly on the so-called luminance channel, the detection of 200-ms flashes is thought to depend also on chromatic pathways (see, for example, Ref. 52). (Comparable 10- and 200-ms L-cone spectral sensitivities were not measured, mainly because S-cone intrusion obscures the region where failures of L-cone isolation are most likely to occur.)

2. Methods

Thresholds were set by the method of adjustment. Each subject made six settings at each test wavelength. In the flicker-detection experiment there were four separate experimental runs, and in the target detection experiment there were two.

The choice of adapting-field luminances for each subject is based on the 545–668- and 638–470-nm sensitivity differences shown in Fig. 7. For each subject, we chose a

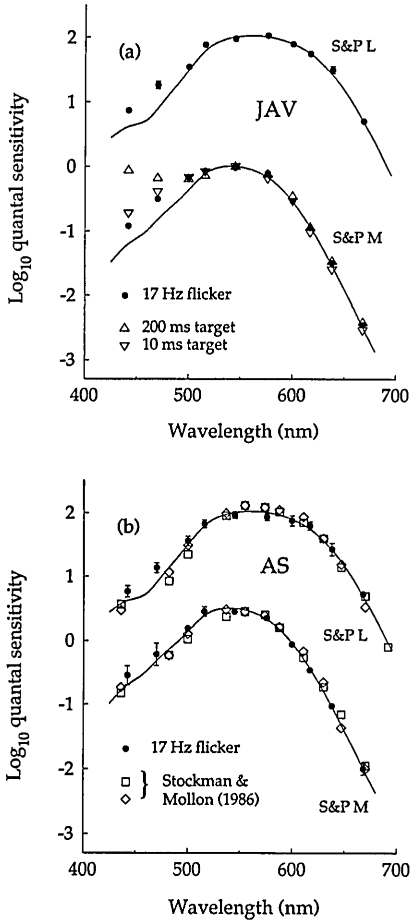

Fig. 9. Spectral sensitivities for 17-Hz flicker (circles) and flashes (triangles). (a) Subject JAV. M-cone flicker sensitivities (lower circles) measured following an exchange from a 3.26-$\log_{10}$-Td, 485-nm background to a 4.14-$\log_{10}$-Td, 678-nm background. L-cone flicker sensitivities (upper circles) measured following an exchange from a 3.56-$\log_{10}$-Td, 678-nm background to a 3.88-$\log_{10}$-Td, 485-nm background. Test sensitivities at 545 nm are -8.20 and -8.85 $\log_{10}$ quanta sec^{-1} deg^{-2} for the M- and the L-cone data, respectively. Flash sensitivities measured following an exchange from a 3.30-$\log_{10}$-Td, 485-nm background to a 3.79-$\log_{10}$-Td, 678-nm background. Test sensitivities at 545 nm are -7.52 and -8.07 $\log_{10}$ quanta sec^{-1} deg^{-2} for the 10- and the 200-ms functions, respectively. (b) Subject AS. M-cone flicker sensitivities measured following an exchange from a 2.94-$\log_{10}$-Td, 485-nm background to a 3.98-$\log_{10}$-Td, 678-nm background, and L-cone flicker sensitivities measured following an exchange from a 3.29-$\log_{10}$-Td, 678-nm background to a 3.91-$\log_{10}$-Td, 485-nm background. Test sensitivities at 545 nm are -7.96 and -8.69 $\log_{10}$ quanta sec^{-1} deg^{-2} for the M- and the L-cone estimates, respectively. The diamonds and squares are test sensitivity measurements for AS made in a different laboratory. They were obtained with a foveally fixated, 17-ms-duration, 3-min-diameter test flash presented in the center of a 7-min-diameter background (see text for details). Error bars in both panels are ± 1 standard deviation; curves are Smith–Pokorny M- and L-cone sensitivities.

concurrent background luminance that lies close to the middle of the range of the asymptotic sensitivity differences, i.e., in the middle of the range over which we assume cone isolation.

Target detection. In the target-detection experiments, the 200-ms flashes were presented 150 ms after the background exchange from the 678- to the 485-nm backgrounds, and the 10-ms flashes were presented 245 ms after the transition. Thus the 500-ms flicker presentation shown in Fig. 3(a) was replaced by a single 10- or 200-ms test flash centered in the middle of the 500-ms window during which the flicker was usually presented.

Auxiliary violet backgrounds. As we mentioned in Section 1, we found it necessary to add an auxiliary violet background to desensitize the S cones under M-cone-isolation conditions. The need for this was established during the course of these 17-Hz flicker spectral-sensitivity measurements. For each subject we remeasured the M-cone flicker-detection spectral sensitivities at 442, 470, and 545 nm in the usual way, except that we added either a 418- or a 436-nm steady violet adapting background. These backgrounds were 4° in diameter and were 9.68 or 10.11 $\log_{10}$ quanta sec^{-1} deg^{-2} (1.20 or 2.36 $\log_{10}$ Td), respectively. In general, we found that the auxiliary 418-nm background reduced flicker ssitivity at 442 nm by up to 0.25 $\log_{10}$ unit, at 470 nm by a lesser amount, and at 545 nm not at all. The 436-nm auxiliary field, which to the S cones is approximately 0.75 $\log_{10}$ more intense than the 418-nm field, caused comparatively little additional sensitivity loss at short wavelengths, suggesting that the 418-nm field was sufficient for suppression of the S cones. (No auxiliary background was used in the target-detection experiments.)

An auxiliary background was not needed for the L-cone-isolation conditions.

3. *Results*

In the red–green spectral range, the M- and L-cone 17-Hz flicker-detection spectral sensitivities shown in Fig. 9 agree well with the estimates of Smith and Pokorny. Only at short wavelengths, where there are substantial individual differences in macular and lens pigmentation, are the deviations large (see Ref. 9).

As in Subsection 3.A, we found the best-fitting forms of Eq. (1) to describe the four individual M- or L-cone spectral-sensitivity estimates for each subject. Again, the fit was restricted to test wavelengths between 516 and 668 nm and assumed the Smith–Pokorny M- and L-cone-sensitivity estimates. Table 2 gives, as percentages, the mean, the standard error, and the 95% confidence interval of the best-fitting M- and L-cone weights.

Under M-cone-isolation conditions, the relative M-cone influence is 100.05% for AS and 99.83% for JAV. Given the small confidence limits (0.70% for AS and 0.39% for JAV), these percentages imply excellent M-cone isolation. Under L-cone-isolation conditions, the relative L-cone influence is 112.42% for AS and 96.45% for JAV; however, these fits are associated with large confidence limits

Table 2. Percentage L- and M-Cone Contributions That Best Describe the L- or M-Cone Spectral-Sensitivity Estimates for Subjects AS and JAV Obtained Following an Exchange of Background Color and Intensity

Subject	Estimate	%L Cone	%M Cone	Standard Error	95% Confidence
AS	M cone	−0.05	100.05	0.22	0.70
	L cone	112.42	−12.42	2.65	11.38
JAV	M cone	0.17	99.83	0.12	0.39
	L cone	96.45	3.55	4.57	14.54

(11.38% for AS and 14.54% for JAV). The analysis for AS suggests a small negative M-cone contribution to his spectral sensitivity measured under L-cone-isolation conditions, but the comparatively minor deviation from the Smith–Pokorny fundamental [see Fig. 9(b)] could equally be caused by a variety of factors (including individual differences and experimental error).

Also shown in Fig. 9(a) for JAV are detection spectral sensitivities for targets of 10-ms and 200-ms duration. Similar functions were also obtained for AS (not shown). As in the case of the flicker-detection data, the agreement between the 10- and the 200-ms detection spectral sensitivities and Smith–Pokorny M is good at middle and long wavelengths. The larger deviations at shorter wavelengths are consistent with detection by the S cones. The similarities among these functions suggest that background exchange can produce M-cone isolation for a variety of tasks, even those that under normal conditions are assumed to depend on chromatic as well as on achromatic pathways.[52]

Figure 9(b) shows test sensitivity measurements for AS made in a different laboratory. By using very small test (3-min-diameter) and background (7-min) fields, Stockman and Mollon[17] were able to identify two branches in threshold-versus-intensity (t.v.i.) data that could be attributed to detection by either the M or the L cones. The open squares in Fig. 9(b) show how the sensitivities of the M- and the L-cone branches change with test wavelength. The open diamonds are test spectral sensitivities measured on a fixed-intensity background. As can be seen, the 17-Hz flicker spectral sensitivities and the 3-min-flash spectral sensitivities are very similar in shape. The small differences that are found are consistent with a higher density of macular pigment in the central 3 min of the fovea than over the central 2°.

E. Bipartite-Field Color Matching after Background Exchange

1. *Introduction*

Our results show that background exchange differentially suppresses either M- or L-cone flicker sensitivity to yield test spectral sensitivities that are close to those of single cones. Is the differential cone suppression caused by the background exchange specific to cone flicker signals, or is it more general, affecting also the cone inputs to the more-sluggish, chromatic channels? Our results for 200- and 10-ms detection suggest that the suppression may be general. To look specifically at chromatic signals, we used a color-matching paradigm.

In this experiment we determined the range of test wavelengths over which the subject can make two test fields match by adjusting their relative intensity. Such a match should be found over the spectral range over which cone isolation is complete, but it could also arise if vision were limited to signals from a single, color-blind postreceptoral channel that simply adds the cone inputs together. During the experiment we also recorded the spectral sensitivities for the matches. These should be consistent with cone spectral sensitivities if monochromacy results from cone isolation. Measurements were made following background exchange and on steady fields under M- and L-cone-isolation conditions.

We made no attempt to desensitize the S cones in these experiments. Thus the matches break down at short wavelengths because of S-cone intrusion. In the red–green range we found a more-extended range of artificial monochromacy following the exchange of backgrounds than on a steady background.

2. *Methods*

In the color-matching experiments the subject was presented with a vertically divided bipartite test field subtending 2° of visual angle. Each half-field was produced by a separate optical channel. The standard half-field was fixed in wavelength at 561 nm. At the beginning of each run, the subject set the intensity of the standard half-field to just above threshold. This intensity remained unchanged during a single pass through the spectrum. At each test wavelength the subject adjusted the intensity of the test half-field in an attempt to match the standard half-field. The subject was instructed to inform the experimenter if the color difference between the two half-fields could not be entirely eliminated by intensity adjustments. If a difference remained, the subject was asked to make a brightness match between the two half-fields. Matches were not made at short wavelengths, when the test half-field was too blue. As with the flickering test fields, the two half-fields were presented either for 500 ms following background exchange [i.e., they replaced the flickering test lights shown in Fig. 3(a)] or continuously on the steady backgrounds.

3. *Results*

Figure 10 shows the bipartite-field color-matching data. Matches made on a steady background are denoted by filled and open triangles, and those made following background exchange by filled and open circles. An open symbol denotes that at that test wavelength a perfect match could be made between the test and standard lights. A closed symbol denotes that even for the best match some residual color difference between the two fields remained.

The color-matching data show that the range of artificial monochromacy is greater following an exchange of backgrounds than it is on a steady background.

For M-cone isolation [Fig. 10(a)], the ranges over which monochromacy is found following background exchange are from 545 to 638, 516 to 668, and 516 to 617 nm for AS, JAV, and NEJ, respectively. At short wavelengths the matches fail because the test lights appear too blue or violet, presumably because of S-cone involvement. The color differences seen by AS and NEJ at long wavelengths were described as small or very slight, and they were accompanied by only minor deviations from the Smith–Pokorny M-cone spectral sensitivity. In contrast, the deviations on the steady 678-nm field are much larger, and the color differences were much more apparent. For AS, the range of monochromacy is smaller on the steady field than following background exchange.

For L-cone isolation [Fig. 10(b)], the ranges over which monochromacy is found for background exchange are 545 to 638, 516 to 668, and 500 to 668 nm for AS, JAV, and NEJ, respectively. Only AS sees any color differences at long wavelengths. On the steady 485-nm field the ranges collapse to 576–600 nm for AS and to 576–617 nm for NEJ. With the exception of the steady-field color matches

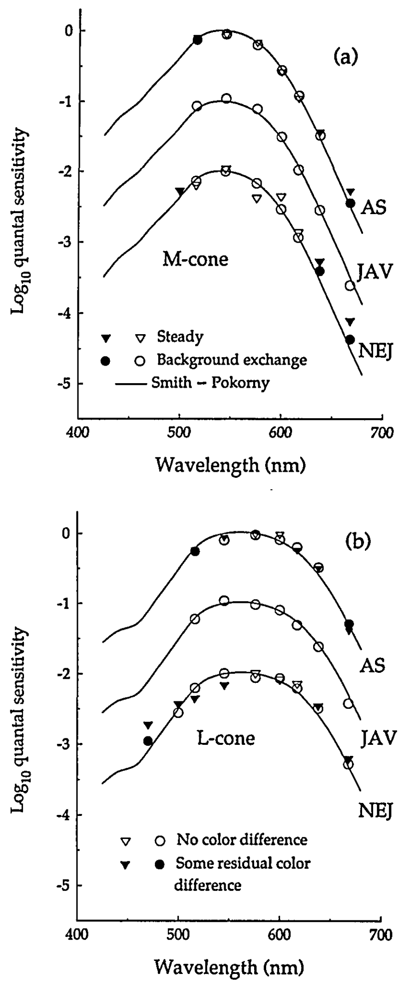

Fig. 10. (a) Bipartite field color-matching data for AS, JAV, and NEJ measured either following an exchange of background from 678 to 485 nm (circles) or on a steady 678-nm field (triangles), with Smith–Pokorny M-cone sensitivity (continuous curves). A standard of 561 nm was used. If there was a perfect match between the standard and the test light, an open symbol is plotted. If there was not, a filled symbol is plotted. The concurrent or steady 678-nm background luminances were 4.23, 4.16, and 4.16 $\log_{10}$ Td, and the preceding 485-nm background luminances were 2.94, 3.26, and 3.26 $\log_{10}$ Td for AS, JAV, and NEJ, respectively. The absolute sensitivities at 545 nm for the exchange condition are −8.36, −8.21, and −8.70 $\log_{10}$ quanta $\sec^{-1}$ $\deg^{-2}$ for AS, JAV, and NEJ, respectively, and for the steady condition are −8.06 and −8.42 $\log_{10}$ quanta $\sec^{-1}$ $\deg^{-2}$ for AS and NEJ, respectively. (b) Color-matching data for the three subjects measured either following an exchange of background from 485 to 678 nm (circles) or on a steady 485-nm field (triangles), with Smith–Pokorny L-cone sensitivity (continuous curves). The concurrent or steady 485-nm background luminances were 3.91, 3.47, and 4.21 $\log_{10}$ Td, and the preceding 678-nm background luminances were 3.29, 3.56, and 3.56 $\log_{10}$ Td for AS, JAV, and NEJ, respectively. The test sensitivities at 545 nm for the exchange condition are −9.52, −8.59, and −9.37 $\log_{10}$ quanta $\sec^{-1}$ $\deg^{-2}$ for AS, JAV, and NEJ, respectively, and for the steady condition are −9.34 and −9.17 $\log_{10}$ quanta $\sec^{-1}$ $\deg^{-2}$ for AS and NEJ, respectively. Other details as for (a). Subject JAV made matches only following background exchange.

for NEJ, the color matches all lie fairly close to the Smith–Pokorny L-cone estimate.

These color-matching experiments show that background exchange is more effective in producing artificial monochromacy than is steady chromatic adaptation. Complete cone isolation is found for only one of three subjects under M-cone isolation conditions and for two of three under L-cone isolation conditions. This is in contrast to 17-Hz flicker detection, for which our results suggest complete isolation.

4. DISCUSSION

A. Why Does the Exchange Procedure Improve Cone Isolation?

We have demonstrated that the exchange of two colored backgrounds can give better cone isolation than steady adaptation, intense bleaches, or flashing the field on and off. Background exchange seems to suppress the responses of the unwanted cone type to reveal the response of a single cone type. But why does this technique work?

Since we were concerned with achieving rather than explaining cone isolation, our experiments were not designed specifically to answer this question. Nevertheless, many of our results are suggestive. We believe that the M- and L-cone signals undergo, more or less independently, an attenuation by a color-opponent signal that depends on the change in background color. Large incremental transients at the cone level *per se* are not responsible for isolation. This is shown clearly by the fact that M-cone isolation is found when the background exchange is minimal or invisible to the L cones (Figs. 4 and 5) and is confirmed by f.t.v.i. curves that show the steepest loss of L-cone sensitivity when the background exchange is silent for the L cones (Fig. 6). Nor does isolation seem to depend on decrements at the cone level. Most of the preceding fields shown in Fig. 5 produce sizable M-cone decrements at some luminances, yet it is only the 485- and 530-nm fields that give M-cone isolation. The change in background color, as opposed to luminance, is what is critical for promoting isolation. This indicates, as we have argued, that color-opponent mechanisms are involved. It may be surprising, therefore, that the flicker spectral sensitivity does not itself become color opponent. This paradox can be resolved if pure M- and L-cone signals are independently scaled by other, color-opponent signals. One possible scheme of this sort would involve nonlinear compression of a signal formed by excitation from one cone type and inhibition from the other. If the inhibitory cone signal is a sluggish one that is unable to resolve rapidly modulated targets, the transmitted flicker signal will be traceable to the exciting cones alone, but its amplitude will depend on the color of the adapting field.[41] Such a model is illustrated in Fig. 11.

The additional loss in sensitivity that accompanies background exchange can be envisaged as being caused by a transient overload of the system that occurs because the sensitivity-regulating mechanisms are unable to adjust instantaneously to the change in adaptation level. This class of model is typically invoked to explain Crawford masking (see Ref. 21). To explain our data we would have to suppose that the transient overload occurs in a chromatically opponent mechanism. Equivalently, it could be argued that the system is slow in readjusting its operating range, so that the most sensitive part of the range is centered on the new adaptation level, as proposed by Craik[20] to explain the loss of differential sensitivity following abrupt increases or decreases in adaptation level.

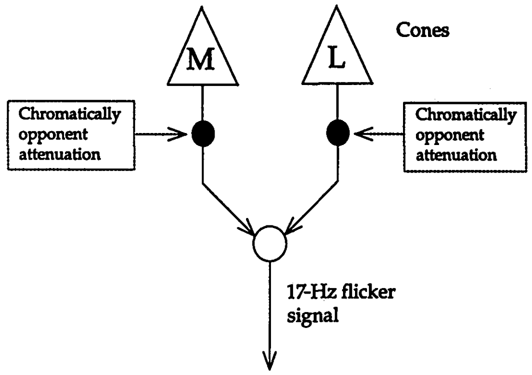

Fig. 11. How an opponent attenuation might independently suppress M- and L-cone 17-Hz flicker signals.

To explain our data, we would have to suppose that the slow readjustment is in a chromatic mechanism (see above).

Whatever its cause, the extra loss of sensitivity produced by background exchange must persist for at least 500 ms after the change of background. Our own control experiments indicate that this is indeed the case. Stronger evidence is provided by Reeves,[48,49] who showed that the sensitivity for large, long test flashes is elevated for up to 30 s following background exchange.

B. Approach to Isolation with Steady Adapting Fields

Although our experiments emphasize the improvement in isolation found with the background-exchange procedure, we also find a fairly close approach to isolation in the test spectral sensitivity under steady-state chromatic adaptation. There is ample precedent for this. Stiles, for instance, recognized in his analysis of his test sensitivities (Figs. 6–9 of Ref. 14) that the validity of Weber's law in the steady state makes cone isolation unlikely; yet his actual results for π_4' and π_5' show a closer approach to cone isolation than Weber's law would allow: π_4' is indeed quite similar to our estimate of the M-cone spectral sensitivity and to dichromat-based estimates. (Although π_4' and π_5' are referred to as field sensitivities, they were actually derived from test sensitivity measurements made on high-intensity fields.[7]) Wald[53] measured several test sensitivities on intense, steady chromatic backgrounds (though his stated background luminances may be incorrectly high; see Ref. 54, p. 552). He produced M-cone test spectral-sensitivity functions that, like π_4', are consistent with protanopic spectral sensitivities. His L-cone functions, however, are narrower than most deuteranopic spectral sensitivities.

The relationship of flash-detection spectral sensitivities to the underlying cone excitations is complex.[7,55] In contrast, flicker spectral sensitivities for test lights presented on a more-intense background can be described by a simple sum of M- and L-cone excitations.[41] This makes flicker experiments particularly useful in determining the extent of any selective suppression beyond that implied by Weber's law. Flicker sensitivity with steady colored backgrounds was investigated first by De Vries.[40] His results were consistent with cone isolation, though with some observer variation; but his theoretical framework, like that of Stiles, invokes only the suppression implied by Weber's law and consequently fails to describe his own data, a fact that his paper does not mention. Later Eisner and MacLeod[41] claimed, as did Wald,[53] an approach to isolated cone spectral sensitivities with the use of steady, chromatic adaptation. From the similarity between their flicker photometric test sensitivities and dichromatic data, Eisner and MacLeod argued that the suppression of cone signals by some fields must be considerably in excess of that predicted by Weber's law. Eisner and MacLeod reported that, on steady 3.5-$\log_{10}$-Td fields, flicker photometric spectral sensitivity on a 656-nm background can be described by $M_\lambda + 0.017L_\lambda$, and on a 500-nm field it can be described by $0.1\ M_\lambda + L_\lambda$ (see Table 1 of Ref. 41). This represents a change in relative cone weights of 588 times in going from the red to the green fields and compares with a change in the relative cone sensitivity to the two field wavelengths of only 19.6 times. As we noted above, if adaptation for both cone types follows Weber's law, the change in cone sensitivity to the two field wavelengths should be mirrored in the change in the relative contributions of the cones to flicker sensitivity. But, as the present results confirm, the cone type that is more sensitive to the field is suppressed considerably in excess of Weber's law. Comparable results have also been obtained by Ikeda and Urakubo.[56]

The issue of whether Weber's law is exceeded on steady fields has been reexamined in two other recent investigations. Stromeyer *et al.*[51] confirmed the "super-Weber" suppression of L cones by steady red fields, but they failed to find an equivalent suppression of the M cones by blue–green or green fields. This is surprising in view of the degree of L-cone isolation that we (and others) find on a steady 485-nm field (see Fig. 2). The degree of L-cone isolation may depend critically on the steady background intensity used, and observers differ in the intensity required (see Fig. 1 and Ref. 9). More recently, Yeh *et al.*[57] measured flicker thresholds against broadband colored backgrounds. Although they conclude that their "analysis does not indicate any sign of the 'super-Weber' behavior postulated by Eisner and MacLeod for a similar paradigm" (p. 2084), their data actually give clear support for super-Weber behavior under both M- and L-cone-isolation conditions. They used three observers, one male and two females. The male observer (and the female observer, who was a known protan carrier) yielded spectral sensitivities in which the relative M-cone contribution to spectral sensitivity changed by a factor of 1,000 or more between the best M- and L-cone-isolation conditions (a 1.6° test field on a 3.4-$\log_{10}$-Td background). Yeh *et al.*[57] gave no information about the cone excitations produced by their chosen backgrounds, but even if we make the unlikely assumption that each background was actually optimal for selective adaptation of the unwanted cone type, Weber adaptation would allow the M-cone weight to change by only a factor of 34. Thus, while it is true that the dependence of sensitivity on background luminance is roughly consistent with Weber's law, the dependence of relative M- and L-conesensitivity on background color is quite inconsistent with Weber's law, in the same way that is implied by the results of De Vries,[40] Eisner and MacLeod,[41] and the present study. It is clear, however, that observer variation may be substantial; we consider this further in the following paper.[9]

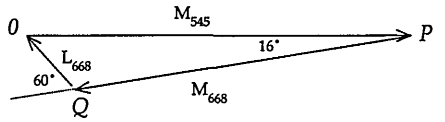

Fig. 12. Vector diagram illustrating how a 16° phase difference between 545- and 668-nm flickering lights and a near-M-cone spectral sensitivity implies a much larger phase difference between the underlying M- and L-cone signals. Each cone's response to a stimulus component is represented by a vector, the length of which represents its amplitude and the direction its phase. *OP*, pure M-cone response to 545-nm stimulus; *PQ*, M-cone response to 668-nm stimulus (retarded from opposite phase by 16°), *QO*, L-cone response to 668-nm stimulus (advanced by 60° relative to the M-cone response); *PO*, resultant vector for 668 nm stimulus exactly cancels M-cone response to 545-nm stimulus. We assume that under near-M-cone isolation the M-cone response to the 668 nm light (*QP*) is 2.5 times that of the L-cone response (*QO*).

C. Role of Phase Differences between M- and L-Cone Signals

Like Swanson *et al.*,[58] we required substantial phase adjustments between red and green flickering test lights to optimize flicker photometric nulls made on steady colored backgrounds. Given that the associated spectral sensitivities suggest that the red and the green test lights were acting mainly through the same cone type (M cones on red backgrounds, L cones on blue backgrounds), the actual phase differences between the cone signals themselves may be much larger. For example, suppose that on the deep-red field the 545-nm flicker produces only an M-cone signal and that the 668-nm flicker produces a signal in the M cones that is 2.5 times greater in amplitude than that in the L cones. Suppose also that the signal that is nulled in our flicker photometric settings is the vector sum of the M- and L-cone contributions. It can be calculated that a nulling phase difference of, say, 16° between the 545- and the 668-nm lights then implies a phase difference of ~60° between the M- and the L-cone signals evoked by the 668-nm stimulus. This effect is illustrated in Fig. 12.

In the presence of such large phase differences, the smaller of the two cone signals has less influence on the magnitude of the resultant signal. Thus the flicker sensitivity at 668 nm is less, and the flicker-detection spectral sensitivity will be as close to M as we observed it to be, despite the relatively moderate two-and-a-half-fold suppression of the L cones above Weber's law. Perhaps here we have one reason, though not the only one, that flicker measurements give rise to such good isolation on steady fields.

Our findings on the red field are consistent with phase differences indirectly inferred (without experimental phase adjustments) from the shapes of threshold-detection contours in cone-contrast space by Stromeyer *et al.*[51] At 22.4 Hz on a 4-$\log_{10}$-Td, 640-nm field, they calculate a phase difference of 75° or 85° between the M- and the L-cone signals and a relative suppression of the L-cone signal three or four times above that expected from Weber's law. We can use these values to predict the flicker nulling phase corrections that we should expect for our conditions. If we assume that on our intense deep-red field the 17-Hz, 668-nm test light produces M-cone and L-cone signals in the ratio 3:1 (and that the 545-nm light produces a signal only in the M cones), then a phase difference of 80° between the cone signals would give rise to a phase difference of 17° between 545- and 668-nm flicker. This is similar to what we find.

D. Other Techniques for Improving Isolation

A shortcoming of studies such as those of Wald[53] and of Eisner and MacLeod[41] is that they present no independent evidence that the unwanted cones have been suppressed, i.e., that Weber's law is exceeded under their experimental conditions. They assume that it is, simply because the spectral sensitivities that they obtain agree with some preconception of what the cone spectral sensitivities ought to be. Yet the variation of threshold with the intensity of large steady adapting fields does not generally reveal sensitivity losses in excess of Weber's law, since the logarithmic slopes of t.v.i. curves seldom exceed one. For example, the 17-Hz, 668-nm f.t.v.i. curves shown in Fig. 6 reach a slope of only 0.85, even though the 545–668-nm sensitivity difference in the same range implies a more-than-Weber's-law suppression of the L cones.

The case for cone isolation can be made more persuasively if the conditions are such that adaptation exceeds Weber's law independently for each cone type. Two studies fulfill this requirement. Stockman and Mollon[17] obtained threshold changes that exceed Weber's law by using very small test (3-min-diameter) and background (7-min) fields. In addition to measuring test spectral sensitivities, these authors also varied the intensity of the background at each test wavelength to produce a set of t.v.i. functions. Consistent with an independent attenuation of the M- and L-cone signals, Stockman and Mollon found that some t.v.i. curves had distinct M- and L-cone branches. From the changes in the sensitivity of the M- and L-cone branches as test wavelength was varied, they derived the M- and L-cone test sensitivity functions shown in Fig. 9(b), which agree well with dichromatic spectral sensitivities and the present results.

In an earlier study more closely related to the present one, King-Smith and Webb[19] measured the threshold for a 20-ms target, 250 ms after the onset of a 500-ms-duration, pulsed background. They found that threshold rose more steeply than predicted by Weber's law, and they too found a double-branched M- and L-cone t.v.i. function on a red background. Measuring test spectral sensitivities, King-Smith and Webb claimed M-cone isolation following the onset of a purple background, but they were unable to isolate the L cones after the onset of a blue background. Our results are consistent with theirs. We also found good M-cone isolation on a flashed deep-red field but poor L-cone isolation on a flashed blue field (see Subsections 3.B and 3.C.3). To achieve L-cone isolation King-Smith and Webb[19] used a method similar to our exchange procedure. They presented a red background for 1 s followed by a green background for 500 ms. The 50-ms-duration target was presented 50 ms after the replacement of the red field by the green.

E. Cone Spectral Sensitivities

To the extent that our experiments were successful in achieving the isolation of the M and L cones, the results support the proposition that the normal cone sensitivities are close to estimates made with use of data from dichromatic observers, such as the dichromat data of Smith and

Pokorny.[5] The results shown in Figs. 4–7 suggest that those sensitivities represent opposing asymptotes for the flicker sensitivity of normal observers under transient chromatic adaptation.

For the companion paper[9] we used the exchange technique to estimate the M- and L-cone spectral sensitivities, using the exchange technique in a group of normal and dichromatic observers; and, from the mean spectral-sensitivity data, we derived new cone fundamentals based on either the CIE or the Stiles–Burch 2° color-matching functions. The new Stiles–Burch-based cone fundamentals agree well with protanopic and deuteranopic spectral sensitivities and tritanopic color matches as well as with the two subjects' spectral sensitivities shown in this paper.

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