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Paradoxical shifts in human color sensitivity caused by constructive and destructive interference between signals from the same cone class

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Abstract

Paradoxical shifts in human color (spectral) sensitivity occur on deep-red (658 nm) background fields. As the radiance of the deep-red background is increased from low to moderate levels, the spectral sensitivity for detecting 15-Hz flicker shifts toward shorter wavelengths, although by more than is predicted by selective chromatic adaptation (e.g., Eisner & MacLeod, 1981; Stromeyer et al., 1987; Stockman et al., 1993). Remarkably, though, at higher background radiances, the spectral sensitivity then shifts precipitously back towards longer wavelengths. Here, we show that both effects are due in large part to destructive *and* constructive interference between signals generated by the same cone type. Contrary to the conventional model of the human visual system, the M- and L-cone types contribute not just the customary fast signals to the achromatic or luminance pathway, but also slower signals of the same or opposite sign. The predominant signs of the *slow* M- and L-cone signals change with background radiance, but always remain spectrally opposed (M-L or L-M). Consequently, when the slow and fast signals from one cone type destructively interfere, as they do near 15 Hz, those from the other cone type constructively interfere, causing the paradoxical shifts in spectral sensitivity. The shift in spectral sensitivity towards longer wavelengths is accentuated at higher temporal frequencies by a suppression of fast M-cone signals by deep-red fields.

Keywords: Color vision, Spectral sensitivity, Postreceptoral channels, Flicker sensitivity, Phase differences, Luminance, Chromatic

Introduction

Human daytime vision depends on three types of light-sensitive photoreceptors with different spectral sensitivities called long-, middle-, and short-wavelength-sensitive (L-, M-, and S-) cones. According to the conventional model of the first stages of the human visual system, signals from the M- and L-cones feed into the fast, luminance pathway (L+M), while signals from all three cones feed into the more sluggish, spectrally opponent chromatic channels (L−M) and (S−[L+M]) (e.g., Schrödinger, 1925; Luther, 1927; Walls, 1955; De Lange, 1958; Guth et al., 1968; Smith & Pokorny, 1975; Boynton, 1979; Eisner & MacLeod, 1980).

The detection of flicker of moderate to high temporal frequencies is traditionally assumed to be mediated by the fast, additive luminance pathway. Thus, the spectral sensitivity for flicker detection should be a simple weighted sum of the M- and L-cone spectral sensitivities. Since long-wavelength lights adapt the L-cones more than the M-cones, the long-wavelength backgrounds used here should shift the flicker detection spectral sensitivity of the human observer towards shorter wavelengths (i.e.,away from a $V(\lambda)$ spectral sensitivity towards an M-cone one). Paradoxically, however, on very intense red fields, the flicker detection spectral-sensitivity shifts back the *wrong* way towards an L-cone spectral sensitivity—as we first reported several years ago in abstract form (MacLeod et al., 1985; Stockman et al., 1991*b*).

As we shall demonstrate, this paradox is caused by a substantive failure of the conventional model of the visual system. It results from destructive *and* constructive interference between fast and slow L- and M-cone signals, all of which contribute to achromatic or luminance flicker detection. The existence of these slow signals is evident not only in spectral-sensitivity data, but also in the sometimes sizeable phase adjustments that are required to flicker-photometrically-null luminance-equated alternating lights (see Stockman & Plummer, 2005*a*; Stockman et al., 2005). Such exceptions are important because they provide vital clues about the

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[4]Deceased. Dedicated by his coauthors in his memory (1966–2006).

signals underlying achromatic flicker perception, and can be used to build up a more realistic "standard" psychophysical model of the early human visual system.

To interpret our data, we adopt an operational model of the channel (or channels) that subserves the perception of achromatic flicker. We assume that the channel generates a color-blind or univariant flicker percept such that two flickering lights of any wavelength composition can be flicker-photometrically cancelled by adjusting their relative amplitude *and phase*. Applying this model, we have identified seven inputs to this channel: +fM, +fL, −sM, +sM, −sL, +sL, and −sS (Stockman et al., 1991*a*, 1991*b*; Stockman & Plummer, 1994; Stockman, 2001; Stockman & Plummer, 2005*a*, 2005*b*; Stockman et al., 2005). The nomenclature "S," "M," or "L" identifies the signals according to the cone type from which they originate, prefixed by either "f" or "s" for fast or slow, and by either "+" or "−" for their sign with respect to the fast signals. We identify signals by cone type, because we monitor them separately using cone-isolating stimuli. However, given that the slow M- and L-cone signals invariably occur as opponent pairs, we further identify them as being spectrally opponent: +sM−sL and +sL−sM. When restricted to the achromatic channel, these spectrally opponent signals generate an *achromatic* percept, and so can be flicker-photometrically nulled. The fast +fM and +fL signals are always of the same sign, as expected of the conventional fast inputs to luminance: +fM+fL. Slow and fast are used as descriptive terms to distinguish between the two categories of inferred cone signals, one of which is substantially phase delayed with respect to the other, without necessarily implying any underlying mechanism. In the model, we account for the differences between the slow and fast signals by a simply time delay (with, therefore, no difference in temporal frequency response). This simplification does a remarkably good job of accounting for the data (see Stockman & Plummer, 2005*a*, 2005*b*; see Stockman et al., 2005). An additional stage of low-pass filtering applied to the slow signal does improve the fits, but not substantially so.

Materials and methods

Subjects

The two primary observers in this work were both male (the authors, AS and DP). Both had normal color vision and were emmetropic. Informed consent was obtained in writing. These studies conform to the standards set by the Declaration of Helsinki, and the procedures have been approved by local ethics committees both in the UK and in the USA.

Apparatus

The optical apparatus was a conventional Maxwellian-view optical system with a 2-mm entrance pupil illuminated by a 900-W Xenon arc. Target and background fields were defined by circular field stops, and their wavelengths were selected by interference filters with full-width at half-maximum bandwidths of between 7 and 11 nm. Infrared and ultraviolet radiation were removed by glass absorbing filters. The radiance of each beam could be varied by the insertion of fixed or variable neutral density filters. Sinusoidal modulation (flicker) was produced by the pulse-width modulation of fast, liquid crystal light shutters (Displaytech, Longmont, CO) at a carrier frequency of 400 Hz. The position of the observer's head was maintained by a dental wax impression. The apparatus is described in more detail elsewhere (Stockman et al., 2005).

Stimuli

In all experiments, target stimuli of 4 deg of visual angle in diameter were presented superimposed in the center of a steady background field or fields of 9 deg in diameter. The observer was instructed to fixate the center of the field. All stimulus radiances given here are time-averaged. The targets were flickered at frequencies of between 2.5 and 25 Hz.

Monochromatic targets (Fig. 1)

Two monochromatic targets were used. The first was a 520-nm target, which favored detection by the M-cones. The second target was a single 650-nm light. On an intense 658-nm background, this target is detected by both M- and L-cones (see below). The 650-nm target was used as the reference flicker against which we measured phase delays. Given that it is roughly "equichromatic" with the background, it is unlikely to generate a substantial spectrally opponent or chromatic flicker signal. We assume, therefore, that it generates predominantly fast, +fM and +fL, signals. In the experiments, the results of which are shown in Fig. 1, the 658-nm background was varied in radiance from 10.39 $\log_{10}$ quanta s^{-1} deg^{-2} to 12.38 $\log_{10}$ quanta s^{-1} deg^{-2} (3.07 to 5.06 $\log_{10}$ phot. tds). Given the relative insensitivity of rods and S-cones to the long-wavelength background, it was important to ensure that the rods and S-cones did not detect the 520-nm target. To desensitize the rods and S-cones, an auxiliary 410-nm background of 10.30 $\log_{10}$ quanta s^{-1} deg^{-2} (1.43 $\log_{10}$ phot. tds) was superimposed on the 658-nm background. This background ensured that any modulation of the S-cones by the 520-nm target was well below S-cone modulation threshold. As expected, therefore, no evidence could be found for an S-cone response under these conditions.

Cone-isolating targets (Fig. 2)

The cone-isolating targets were paired sinusoidally alternating targets (a 650- and 550-nm pair equated for the M-cones to give L-cone isolation, and a 540- and 650-nm pair equated for the L-cones to give M-cone isolation) chosen so that the alternation was invisible either to the M-cones or to the L-cones. The chosen radiances were based on the Stockman and Sharpe (2000) M- and L-cone fundamentals. The equichromatic flicker against which M- or L-cone phase delays was measured was produced by a 656-nm monochromatic target. Two adapting background levels were used: 11.18 (Lower Level) and 12.50 (Higher Level) $\log_{10}$ quanta s^{-1} deg^{-2} (3.86 and 5.18 $\log_{10}$ phot. tds, respectively). To suppress the S-cones and rods at the Lower Level, an auxiliary 410-nm field of 10.30 $\log_{10}$ quanta s^{-1} deg^{-2} (1.43 $\log_{10}$ phot. tds) was superimposed on the 658-nm field. To suppress the S-cones at the Higher Level, an auxiliary 410-nm field of 10.80 $\log_{10}$ quanta s^{-1} deg^{-2} (1.93 $\log_{10}$ phot. tds) was superimposed on the 658-nm field.

Calibrations were carried out with the use of a radiometer (UDT Instruments, Orlando, FL) and a spectroradiometer (Gamma Scientific, San Diego, CA).

Procedures

Subjects light adapted to the target and background fields for at least 3 min prior to data collection. During the experiment, subjects interacted with the computer by means of eight buttons on a keypad. The computer provided instructions and gave verbal and other auditory feedback by way of a voice synthesizer and tones.

Flicker thresholds

Flicker thresholds were obtained by the method of adjustment. Each subject adjusted the stimulus radiance (at the maximum possible stimulus modulation of 0.92) until they were satisfied that the flicker was just at threshold.

Phase measurements

Phase differences were measured between two flickering stimuli (either between two monochromatic lights for the results shown in Fig. 1C or between a cone-isolating pair of lights and a monochromatic light for those shown in Fig. 2) using a flicker-cancellation technique. First, each subject adjusted the modulation of each of the two flickering stimuli separately (with the other stimulus set at zero modulation) until its flicker modulation was just above threshold (typically *ca.* 0.2 $\log_{10}$ above threshold). Then the subject adjusted the phase difference between the two stimuli as well as their relative modulation to find the best flicker null. Subjects could also reverse the relative phase of the two stimuli by 180 deg to help them find the correct nulling phase.

Except where noted, all data points are averaged from three or four settings made on at least four separate runs. Further details of the methods can be found elsewhere (Stockman & Plummer, 2005*a*; Stockman et al., 2005).

Results

Fig. 1A shows the effect of long-wavelength adaptation on the sensitivity ratio for detecting 15-Hz green (520 nm) and red (650 nm) flicker for subjects AS (dotted circles) and DP (dotted squares). Four horizontal lines are also shown. The lower grey line, labelled L-cone, is the expected ratio if detection is mediated solely by L-cones, while the upper black line, labelled M-cone, is the expected ratio if it is mediated by M-cones (Stockman & Sharpe, 2000). Fig. 1B illustrates how the 520/650 ratios are related to the underlying spectral-sensitivity functions, which for ease of illustration have been vertically aligned at 650 nm. Two vertical dashed lines are shown at 520 and 650 nm. The horizontal dashed lines have been aligned with the intersections of the 520- and 650-nm lines and the four spectral-sensitivity functions. The 520/650 nm differences for each spectral-sensitivity function are indicated by the arrows and numbers to the right.

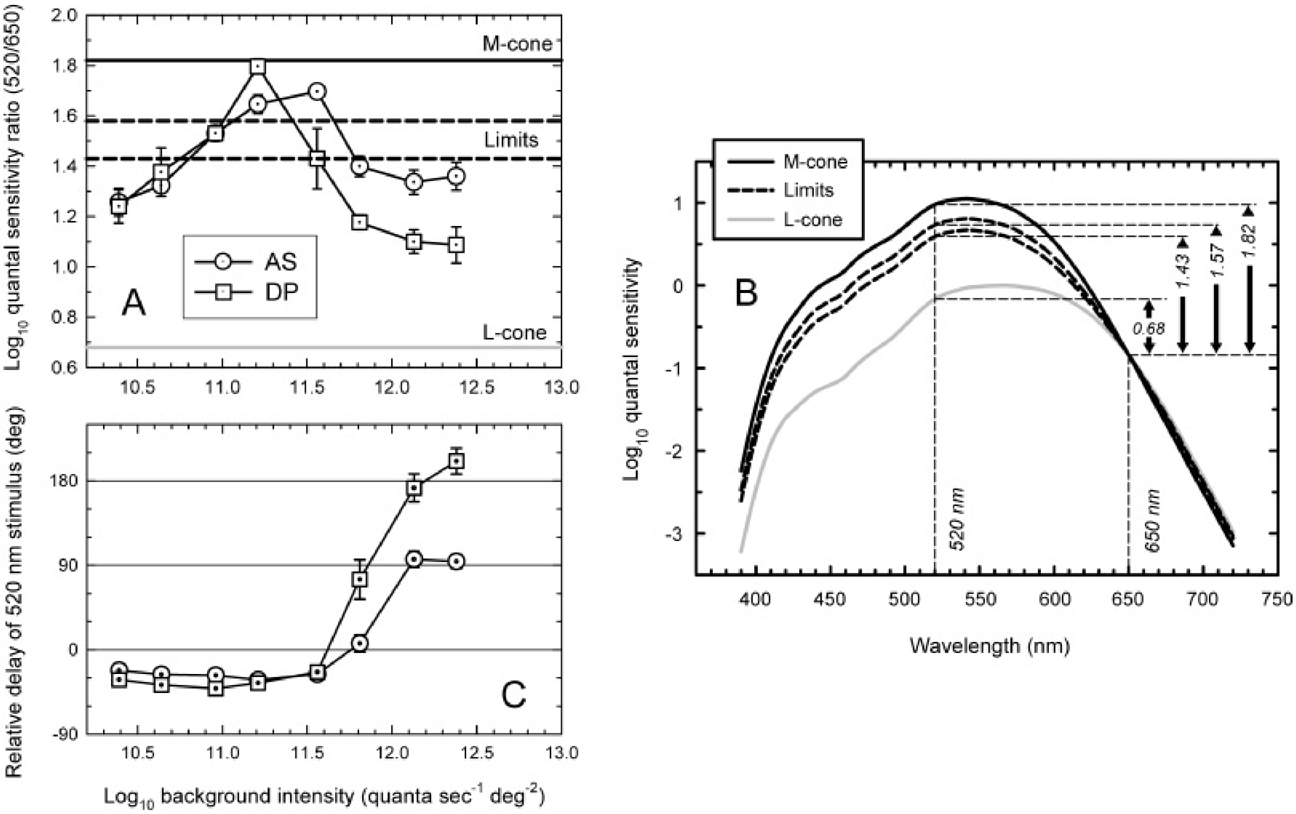

Fig. 1. A: Logarithmic quantal sensitivity ratios for detecting 520 and 650 nm, 15-Hz flicker measured as a function of the 658-nm background radiance. Subjects: AS (dotted circles); DP (dotted squares). The horizontal lines are the predicted 520/650-nm sensitivity ratios for detecting 15-Hz flicker based on the M-cone (black line), L-cone (grey line), and the Weber limiting (dashed lines) spectral sensitivities. B: The predicted ratios in A are the differences between logarithmic spectral sensitivities at 520 and 650 nm (labelled arrows and dashed lines) shown here. Four spectral sensitivities are shown: M-cone (black line), L-cone (grey line), and the Weber limiting functions (dashed lines). The Weber limiting spectral sensitivities are calculated by scaling the linear M- and L-cone spectral sensitivities to be equal at the adapting wavelength of 658 nm, and then adding them together in the L:M ratios of 1:1 (upper dashed line) or 2:1 (lower dashed line). All spectral sensitivities are based on the Stockman and Sharpe (2000) cone fundamentals. C: Phase advances at 15 Hz away from opposite phase required to null the 520-nm and 650-nm targets measured as a function of the radiance of the 658-nm background. Subjects: AS (dotted circles); DP (dotted squares).

The two spectral-sensitivity functions shown by the black dashed lines are the predicted *asymptotic* spectral sensitivities that should be reached on the 658-nm field by an additive (L+M) "luminance" mechanism with L:M cone input weights of either 1:1 (upper dashed line) or 2:1 (lower dashed line) when the M- and the L-cone sensitivities are both independently controlled according to Weber's Law. When Weber's Law holds, the sensitivity losses for each cone mechanism increase in proportion to the adaptation level. Consequently, if the L-cones are 12.9 times more sensitive to the 658-nm field than the M-cones, the 658-nm field will *reduce* the sensitivity of the L-cones by 12.9 times more than the sensitivity of the M-cones. As a result, the M- and L-cones become equally sensitive to the background wavelength (before any luminance input weights are applied). The Weber spectral-sensitivity limits shown in the figure were calculated by normalizing the L- and M-cone spectral sensitivities at 658 nm and then linearly combining them with L:M cone weights of 1:1 or 2:1. Those weights were chosen to illustrate the variation in luminance input weights found in the population, which on average favor L, but exhibit substantial individual differences (e.g., De Vries, 1948; Vos & Walraven, 1971; Walraven, 1974; Stromeyer et al., 1987; Cicerone & Nerger, 1989; Sharpe et al., 2005). Subject AS is known to have a weight of about 1.7 L:M on a white daylight background (Sharpe et al., 2005). The limiting Weber spectral-sensitivity differences between 520 and 650 nm have been transferred to Fig. 1A, where they are shown as the horizontal dashed lines. If adaptation is limited by Weber's Law, the 520/650 nm spectral-sensitivity difference should not exceed the appropriate Weber limit for a given subject.

As the 658-nm background radiance first increases, the selective attenuation of the L-cones by the deep-red field also increases, causing the spectral-sensitivity ratios shown in Fig. 1A to move away from L toward the Weber limits. Two unexpected things then happen. First, at about 11.0 $\log_{10}$ quanta s^{-1} deg^{-2} the ratio crosses the Weber limits (instead of asymptoting there), and approaches M (Eisner & MacLeod, 1981; Stromeyer et al., 1987; Stockman et al., 1993). Second, at still higher radiances above 11.3 log quanta s^{-1} deg^{-2}, the ratio falls precipitously, crosses the Weber limits again, and approaches L. Both effects are the result, at least in part, of destructive and constructive interference between slow and fast cone signals.

The existence of slow cone signals mediating sensitivity is evident in unexpectedly large phase delays between monochromatic flickering lights. Fig. 1C shows the phase adjustments of 520-nm flicker away from opposite phase (180 deg) required to perceptually null 650-nm flicker as a function of the radiance of the deep-red background for AS (dotted circles) and DP (dotted squares). A phase adjustment of 0 deg, for example, represents physically counterphase flicker. We assume that the two lights generate flicker signals in the L- and M-cones, which are subsequently combined within a common postreceptoral pathway that mediates flicker detection. Consequently, the phase adjustments of the two flickering lights required for the perceptual null reveal the relative *internal* delays that occur between the flickering lights at the input to the visual system and the postreceptoral stage at which their corresponding neural signals cancel. The phase adjustments required for a null at low to moderate adaptation levels are *ca.* −30 deg, but then change abruptly by about 120 deg for AS and by about 210 deg for DP at high levels. Significantly, these abrupt changes correspond to the precipitous changes in spectral sensitivity seen in Fig. 1A. Abrupt phase changes coupled with large changes in sensitivity often indicate underlying signals that are in opposite phase and destructively interfere. We can reveal more about the origin of these abrupt changes by measuring the phase delays of L- and M-cone-isolating lights. Isolation was achieved by alternating pairs of lights, the alternation of which was invisible (silent) to either the L- or the M-cone type, but visible to the other (Rushton et al., 1973; Estévez & Spekreijse, 1974).

Fig. 2 (A, B for AS; C, D for DP) shows the phase delays for the M- and L-cone isolating stimuli measured as a function of temporal frequency at two deep-red background radiances. They are the adjustments away from 180 deg required to null the M- or L-cone flicker with 656-nm flicker. Some of the phase adjustments are substantial, particularly for the M-cone lights. Moreover, the *direction* of the phase adjustments change abruptly between the lower and higher levels (11.18 and 12.50 $\log_{10}$ quanta s^{-1} deg^{-2}, respectively). These abrupt changes correspond to the abrupt change in the phase delay seen in Fig. 1C. The 15-Hz M-cone data obtained at these two levels agree well with the 520/650 nm phase data. Again, since the 656-nm flicker is "equichromatic" with the 658-nm background, it is unlikely to generate slow spectrally opponent flicker signals. Given that it generates predominantly fast cone signals, we can use it as a reference against which we can separately model the M- and L-cone phase data.

We generated simple models of signal combination to account for the M- and L-cone data and thus identify the types of underlying signals that might produce them. In the simplest version of our model, we assume that each isolated cone signal is a linear combination of a slow and a fast cone signal with some ratio of slow/fast signal amplitude (m) and with some delay (Δt) between them. Implicit in this "time-delay" model, is the assumption that Δt and m are not frequency dependent; that is, that the shapes of the logarithmic temporal modulation sensitivities of the slow and fast signals are identical. These values were fixed at any one adaptation level but were allowed to vary between adaptation levels. Model predictions for various values of m are shown in Fig. 3. (For further details, see Stockman & Plummer, 2005*a*; Stockman et al., 2005). Crucially, the sign of the slow signal can be the same as (Panel A) or opposite to (Panel C) that of the fast signal. The horizontal and diagonal lines, respectively, represent the phase delays of the fast signal alone ($m = 0$) and the slow signal alone ($m = \infty$) signals. The relative delay of the slow signal in this example is 33.3 ms, so that slow and fast 15-Hz signals of the *same* sign are in *opposite* phase, whereas slow and fast 15-Hz signals of the *opposite* sign are in the *same* phase. Predictions are shown in Fig. 3 for several values of m. The upper panels (A & C) show the predicted phase delay of the combination (resultant) of the slow and fast signals, and the lower panels (B & D) their amplitudes. The phase delays are related to the phase adjustments required to null flickering lights (Figs. 1C & 2), while the amplitudes are related to the flicker detection sensitivities (Fig. 1A). The amplitude predictions illustrate the effects of destructive and constructive interference and its dependence on flicker frequency (see below).

The phase predictions are characteristic "signatures" that should be found in experimental data that reflect the simple combination of slow and fast signals. A comparison between the phase signatures and the phase data shows that the two are indeed similar, which shows that the phase data are broadly consistent with the model. The continuous lines in Figs. 2A–2D are the best-fitting versions of the model, the parameters of which (Δt and m) are given in the figure legend. In general, for these and other background radiances (not shown) m is smaller for L-cones than for

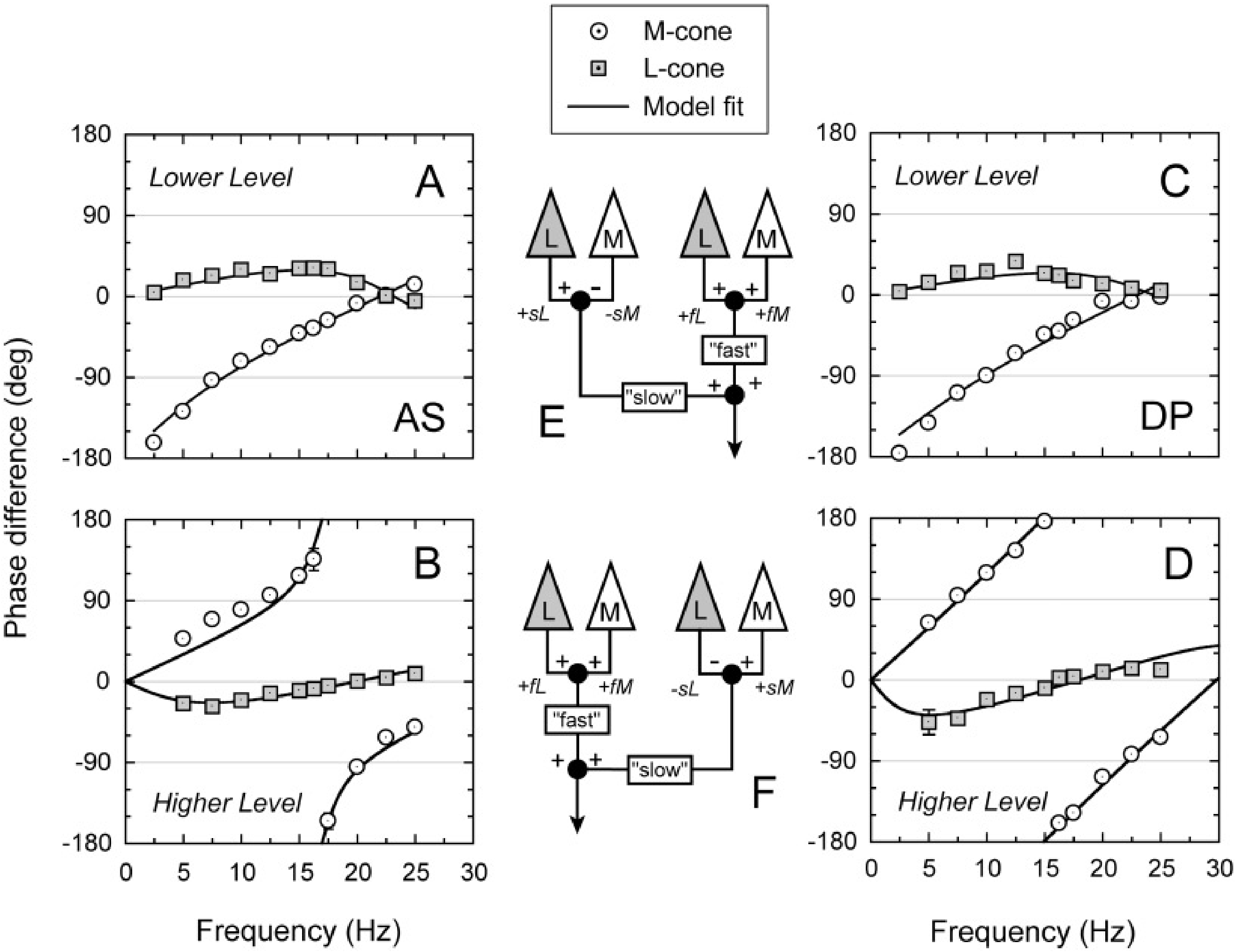

Fig. 2. Phase advances of M-cone (dotted white circles) or L-cone (dotted grey squares) stimuli required to null a 656-nm target measured on 658-nm backgrounds of 11.18 (Lower Level, A, C) or 12.50 (Higher Level, B, D) $\log_{10}$ quanta s^{-1} deg^{-2}. The M-cone stimuli were alternating pairs of L-cone-equated 540- and 650-nm targets; and the L-cone stimuli were pairs of M-cone-equated 650- and 550-nm targets (see Methods). The continuous lines are best fits of a model in which the cone signals are assumed to be the resultant of a fast signal and a delayed slow signal of the same or opposite sign. Best-fitting model parameters [M-cone: m, Δt (ms), minus/plus; L-cone: m, Δt (ms), minus/plus]: (A) M: 2.87, 22.72, minus; L: 0.49, 21.60, plus; (B) M: 1.31, 29.50, plus; L: 0.40, 25.08, minus; (C) M: 4.51, 21.71, minus; L: 0.41, 20.57, plus; (D) M: 27.96, 33.56, plus; L: 0.63, 27.79, minus. Subjects: AS (A, B), DP (C, D). E: Predominant cone signals at Lower Level. F: Predominant cone signals at Higher Level.

M-cones, while Δt varies between 20 and 35 ms. The crucial change that occurs between the two intensity levels shown here is that the sign of the slow M- and L-cone signals both *reverse*. The slow signals that predominate at the lower level are $-$sM and $+$sL (where "s" means "slow"), whereas at the higher level they are $+$sM and $-$sL.

Thus, in addition to the expected fast signals, $+$fM$+$fL (where "f" means "fast"), achromatic flicker perception depends on slow, *spectrally opponent* signals, which change abruptly from $+$sL$-$sM (Fig. 2E) to $-$sL$+$sM (Fig. 2F) as the long-wavelength adaptation level increases. The paradoxical frequency-dependent shifts in the observer's spectral sensitivity can now be easily explained: they are caused by destructive interference between signals from one cone type *combined with* constructive interference between signals from the other cone type (the slow M- and L-cone signals at any level are always 180 deg apart in phase, so the effects are opposite). We can use the 15-Hz results in Fig. 1A as an illustration. The 15-Hz spectral sensitivity first approaches M because at lower adaptation levels the predominant signals are $+$sL$-$sM and $+$fL$+$fM. Thanks to the delay of the slow signals, which adds an extra phase delay of *ca.* 180 deg at 15 Hz, the $+$sL and $+$fL signals *destructively* interfere, whereas $-$sM and $+$fM *constructively* interfere. Consequently, the spectral sensitivity becomes more M-like, as we find. At high adaptation levels, the 15-Hz spectral sensitivity falls back toward L because the predominant signals are $-$sL$+$sM and $+$fL$+$fM. Again the time delay adds an extra phase delay of *ca.* 180 deg to the slow signals at 15 Hz, so that now $-$sL and $+$fL *constructively* interfere, whereas $+$sM and $+$fM *destructively* interfere. Consequently, the spectral sensitivity is now more L-like, as we find.

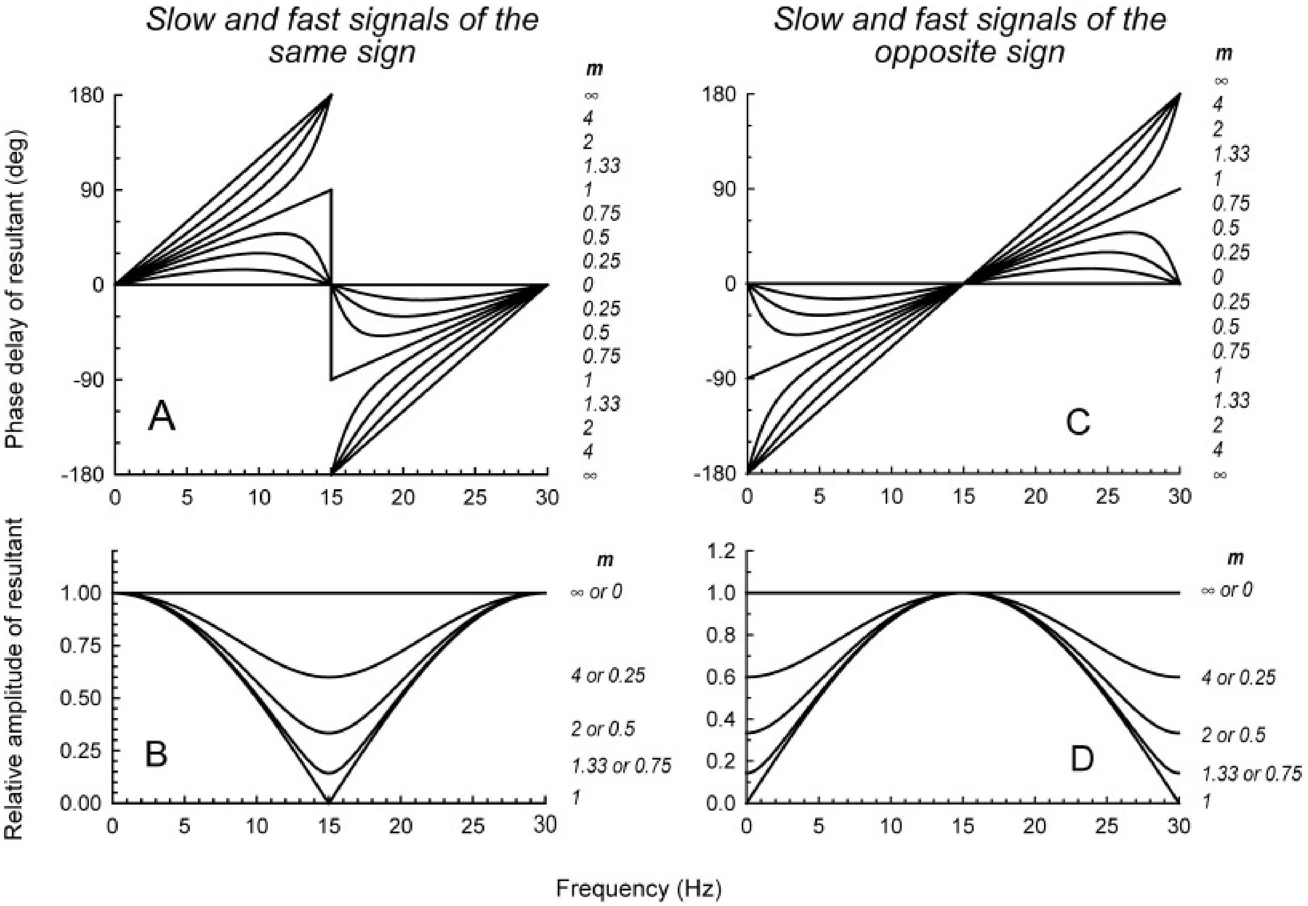

Fig. 3. Model predictions of the phase delay (A, C) and relative amplitude (B, D) of the combination (resultant) of slow and fast signals of the same sign (A, B) and of opposite sign (C, D). Predictions are shown for several slow to fast signal ratios, m, and for a time delay, Δt, between the slow and fast signals of 33.33 ms. 180 and -180 deg are equivalent in panels A and C, so that the phase delays for $m > 1$ are continuous.

Discussion

In addition to the expected effects of selective chromatic adaptation, flicker spectral sensitivity on long-wavelength backgrounds depends on constructive and destructive interference between fast and slow M- and L-cone signals. The fast signals are the conventional, additive cone inputs to luminance (+fM+fL), whereas the slow signals are spectrally opponent inputs, which change from being predominantly +sL−sM on low to moderate intensity red fields to being −sL+sM on high intensity ones. The presence of these signals gives rise to destructive or constructive interference that depends upon adaptation level and temporal frequency. The changes in spectral sensitivity associated with this interference can be substantial, because the effects on the signals from the two cone types are opposite. When the fast and slow M-cone signals constructively interfere, the fast and slow L-cone signals destructively interfere, and *vice versa*.

As well as interference, there is some selective suppression of the fast M-cone signal by deep-red backgrounds, which also contributes to the shift in spectral sensitivity towards L at higher temporal frequencies. This suppression is evident in the high slow/fast signal ratios (m) found for the M-cones at all long-wavelength background field radiances (see Fig. 2 legend, and see Stockman & Plummer, 2005*a*,*b*; Stockman et al., 2005). In contrast, the previously reported L-cone suppression by red fields, which was inferred from 15- and 22.5-Hz flicker spectral-sensitivity data (Eisner & MacLeod, 1981; Stromeyer et al., 1987, 1997), is probably largely due to destructive interference between the slow and fast cone signals.

Photopigment bleaching, which becomes significant at the highest field radiances, reduces the cone photopigment optical density and narrows the cone spectral-sensitivity functions (see, for example, Stockman & Sharpe, 1999), thus increasing the 520/650 nm sensitivity ratio. Photopigment bleaching, therefore, *reduces* the paradoxical shift toward L that we find at the highest levels.

An important feature of our model is the assumption that both pairs of slow spectrally opponent signals (+sM−sL and +sL−sM) coexist and that both contribute to luminance. Because the two pairs are in opposite phase and destructively interfere, one pair becomes prominent only when the other is relatively suppressed—by, for example, chromatic adaptation. On moderate intensity long-wavelength fields, we suppose that the +sM−sL pair is suppressed and +sL−sM revealed, whereas on short-wavelength fields the +sL−sM pair is suppressed and +sM−sL revealed (see also Stromeyer et al., 1997; Lee & Sun, 2004; Stockman & Plummer, in preparation). In contrast, on more neutral fields the two pairs of slow signals remain roughly balanced and largely cancel, so that luminance is dominated by the fast signals. The cancellation of the slow signals helps to explain why the sluggish spectrally opponent signals are relatively small under most conditions. This model was first described in abstract form (Stockman, 2001). Other evidence in support of this model and earlier work in this area are outlined in more detail in our previous papers (Stockman & Plummer, 2005*a*,*b*; Stockman et al., 2005).

Elsewhere we offer an explanation for the change in the polarity of the slow signals as the long-wavelength background intensity increases (Stockman & Plummer, 2005*b*). In brief, we hypothesize that the change occurs because at very high bleaching levels the red field becomes postreceptorally like a green field (and so relatively suppresses $+\mathrm{sL}-\mathrm{sM}$). This suggestion is supported by phenomenological observations, which indicate that at very high radiances the apparent color of long-wavelength fields changes from red to yellow and finally to green, which remains their "steady-state" appearance (Auerbach & Wald, 1955; Cornsweet et al., 1958; Stockman & Plummer, 2005*b*). It is also supported by several studies that show that bleaching actually falls below the predictions of first-order kinetics at low bleaching levels and above it at high levels (e.g., Smith et al., 1983; Burns & Elsner, 1985; 1989; Reeves et al., 1998; Mahroo & Lamb, 2004). The intense 658-nm background used here bleaches about 50% of the M-cone and 90% of the L-cone photopigment (Rushton & Henry, 1968; Stockman & Sharpe, 2000). First-order kinetics predicts a proportional loss of sensitivity with bleaching level at high levels that is consistent with Weber's Law. An additional loss of L-cone sensitivity *to the background* due to nonlinear bleaching kinetics could be sufficient to make the intense 658-nm field act postreceptorally more like a short- or middle-wavelength field, as our results suggest.

The effects of destructive and constructive interference are unlikely to be confined to long-wavelength background fields. Since the predominant slow signals on short-wavelength fields are $+\mathrm{sM}-\mathrm{sL}$ (Stromeyer et al., 1997; Stockman & Plummer, in preparation), we should expect comparable spectral-sensitivity shifts on short-wavelength fields to those we find on long-wavelength fields of high bleaching intensity (on which the slow signals are also $+\mathrm{sM}-\mathrm{sL}$). And, indeed, at moderate temporal frequencies, Eisner and MacLeod (1981) reported a much closer approach to an L-cone spectral sensitivity on shorter wavelength backgrounds than is predicted by Weber's Law.

Physiological and anatomical considerations are discussed in more detail in our earlier papers (Stockman & Plummer, 2005*a*,*b*; Stockman et al., 2005). In summary, the phase characteristics that we identify can be found in the responses of some macaque magnocellular (MC) ganglion cells (Smith et al., 1992), and in some macaque parvocellular (PC) ganglion or lateral geniculate nucleus (LGN) cells (Gouras & Zrenner, 1979; Lankheet et al., 1998), but some PC responses show smaller temporal-frequency-dependent effects than we find (Derrington et al., 1984; Lee et al., 1989, 1994; Smith et al., 1992; Benardete & Kaplan, 1997). Sizeable shifts in spectral sensitivity in the direction of selective chromatic adaptation have been reported in the responses of macaque MC cells (Pokorny et al., 2001). Moreover, Lee and Sun (2004) have reported that the phase response of macaque MC responses can depend on background chromaticity in a similar way to psychophysical data (Stromeyer et al., 1997). These findings point to a retinal origin for the phenomena reported here. However, a cortical origin also remains a possibility. Indeed, the delays that we find between slow and fast signals are comparable to transmission delays between parvocellular and magnocellular streams to the LGN (e.g., Schmolesky et al., 1998) which remain segregated until they reach V1, and color-luminance interactions are common in primary cortex (e.g., Hubel & Wiesel, 1968; Gouras, 1974; Lennie et al., 1990; Cottaris & De Valois, 1998; Conway, 2001; Vidyasagar et al., 2002; Johnson et al., 2004).

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References

Auerbach, E. & Wald, G. (1955). The participation of different types of cones in human light and dark adaptation. *American Journal of Ophthalmology* **39**, 24–40.

Benardete, E.A. & Kaplan, E. (1997). The receptive field of primate P retinal ganglion cell, I: Linear dynamics. *Visual Neuroscience* **14**, 169–185.

Boynton, R.M. (1979). *Human Color Vision*. New York: Holt, Rinehart and Winston.

Burns, S.A. & Elsner, A.E. (1985). Color matching at high luminances: The color-match-area effect and photopigment bleaching. *Journal of the Optical Society of America A* **2**, 698–704.

Burns, S.A. & Elsner, A.E., eds. (1989). *Localizing Color Vision Deficiencies in Eye Disease, Vol. IX*. Dordrecht: Kluwer Academic Publishers.

Cicerone, C.M. & Nerger, J.L. (1989). The relative numbers of long-wavelength-sensitive to middle-wavelength-sensitive cones in the human fovea centralis. *Vision Research* **29**, 115–128.

Conway, B.R. (2001). Spatial structure of cone inputs to color cells in alert macaque primary visual cortex (V-1). *Journal of Neuroscience* **21**, 2768–2783.

Cornsweet, T.N., Fowler, H., Rabedeau, R.G., Whalen, R.E. & Williams, D.R. (1958). Changes in the perceived color of very bright stimuli. *Science* **128**, 898–899.

Cottaris, N.P. & De Valois, R.L. (1998). Temporal dynamics of chromatic tuning in macaque primary visual cortex. *Nature* **395**, 896–900.

De Lange, H. (1958). Research into the dynamic nature of the human fovea-cortex systems with intermittent and modulated light. II. Phase shift in brightness and delay in color perception. *Journal of the Optical Society of America* **48**, 784–789.

Derrington, A.M., Krauskopf, J. & Lennie, P. (1984). Chromatic mechanisms in lateral geniculate nucleus of macaque. *Journal of Physiology* **357**, 241–265.

De Vries, H. (1948). The heredity of the relative numbers of red and green receptors in the human eye. *Genetica* **24**, 199–212.

Eisner, A. & MacLeod, D.I.A. (1980). Blue sensitive cones do not contribute to luminance. *Journal of the Optical Society of America* **70**, 121–123.

Eisner, A. & MacLeod, D.I.A. (1981). Flicker photometric study of chromatic adaptation: Selective suppression of cone inputs by colored backgrounds. *Journal of the Optical Society of America* **71**, 705–718.

Estévez, O. & Spekreijse, H. (1974). A spectral compensation method for determining the flicker characteristics of the human color mechanisms. *Vision Research* **14**, 823–830.

Gouras, P. (1974). Opponent-colour cells in different layers of foveal striate cortex. *Journal of Physiology* **238**, 583–602.

Gouras, P. & Zrenner, E. (1979). Enhancement of luminance flicker by color-opponent mechanisms. *Science* **205**, 587–589.

Guth, S.L., Alexander, J.V., Chumbly, J.I., Gillman, C.B. & Patterson, M.M. (1968). Factors affecting luminance additivity at threshold. *Vision Research* **8**, 913–928.

Hubel, D.H. & Wiesel, T.N. (1968). Receptive fields and functional architecture of monkey striate cortex. *Journal of Physiology* **195**, 215–243.

Johnson, E.N., Hawken, M.J. & Shapley, R. (2004). Cone inputs in macaque primary visual cortex. *Journal of Neurophysiology* **91**, 2501–2514.

Lankheet, M.J.M., Lennie, P. & Krauskopf, J. (1998). Temporal-chromatic interactions in LGN P-cells. *Visual Neuroscience* **15**, 47–54.

Lee, B.B., Martin, P.R. & Valberg, A. (1989). Sensitivity of macaque retinal ganglion cells to chromatic and luminance flicker. *Journal of Physiology* **414**, 223–243.

Lee, B.B., Pokorny, J., Smith, V.C. & Kremers, J. (1994). Responses to pulses and sinusoids in macaque ganglion cells. *Vision Research* **34**, 3081–3096.

Lee, B.B. & Sun, H. (2004). Chromatic input to cells of the magnocellular pathway: Mean chromaticity and the relative phase of modulated lights. *Visual Neuroscience* **21**, 309–314.

Lennie, P., Krauskopf, J. & Sclar, G. (1990). Chromatic mechanisms in striate cortex of macaque. *Journal of Neuroscience* **10**, 649–669.

Luther, R. (1927). Aus dem Gebiet der Farbreizmetrik. *Zeitschrift für technische Physik* **8**, 540–558.

MacLeod, D.I.A., Stockman, A. & Vivian, J.A. (1985). Flicker photometric approximations to cone sensitivities under bleaching and transient adaptation conditions. *Perception* **14**, A17.

Mahroo, O.A.R. & Lamb, T.D. (2004). Recovery of the human photopic electroretinogram after bleaching exposures: Estimation of pigment regeneration kinetics. *Journal of Physiology* **554**, 417–437.

Pokorny, J., Smith, V.C., Lee, B.B. & Yeh, T. (2001). Temporal sensitivity of macaque ganglion cells to lights of different chromaticity. *Color Research Applications* **26**, S140–S144.

Reeves, A., Wu, S. & Schirillo, J. (1998). The effect of photon noise on the detection of white flashes. *Vision Research* **38**, 691–703.

Rushton, W.A.H. & Henry, G.H. (1968). Bleaching and regeneration of cone pigments in man. *Vision Research* **8**, 617–631.

Rushton, W.A.H., Powell, D.S. & White, K.D. (1973). The spectral sensitivities of the "red" and "green" cones in the normal eye. *Vision Research* **13**, 2003–2015.

Schmolesky, M.T., Wang, Y., Hanes, D.P., Thompson, K.G., Leutgeb, S., Schall, J.D. & Leventhal, A.G. (1998). Signal timing across the macaque visual system. *Journal of Neurophysiology* **79**, 3272–3278.

Schrödinger, E. (1925). Über das Verhältnis der Vierfarben zur Dreifarbentheorie. *Sitzungberichte Abt 2a, Mathematik, Astronomie, Physik, Meteorologie und Mechanik Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Klasse* **134**, 471.

Sharpe, L.T., Stockman, A., Jagla, W. & Jägle, H. (2005). A luminous efficiency function, $V^*(l)$, for daylight adaptation. *Journal of Vision* **5**, 948–968.

Smith, V.C., Lee, B.B., Pokorny, J., Martin, P.R. & Valberg, A. (1992). Responses of macaque ganglion cells to the relative phase of heterochromatically modulated lights. *Journal of Physiology* **458**, 191–221.

Smith, V.C. & Pokorny, J. (1975). Spectral sensitivity of the foveal cone photopigments between 400 and 500 nm. *Vision Research* **15**, 161–171.

Smith, V.C, Pokorny, J. & van Norren, D. (1983). Densitometric measurement of human cone photopigment kinetics. *Vision Research* **23**, 517–524.

Stockman, A. (2001). Multiple cone inputs to luminance. *Investigative Ophthalmology and Visual Science* (Suppl.) **42**, S320.

Stockman, A., MacLeod, D.I.A. & DePriest, D.D. (1991*a*). The temporal properties of the human short-wave photoreceptors and their associated pathways. *Vision Research* **31**, 189–208.

Stockman, A., MacLeod, D.I.A. & Vivien, J.A. (1993). Isolation of the middle- and long-wavelength sensitive cones in normal trichromats. *Journal of the Optical Society of America A* **10**, 2471–2490.

Stockman, A., Montag, E.D. & MacLeod, D.I.A. (1991*b*). Large changes in phase delay on intense bleaching backgrounds. *Investigative Ophthalmology and Visual Science* (Suppl.) **32**, 841.

Stockman, A. & Plummer, D.J. (1994). The luminance channel can be opponent?? *Investigative Ophthalmology and Visual Science* (Suppl.) **35**, 1572.

Stockman, A. & Plummer, D.J. (2005*a*). Spectrally-opponent inputs to the human luminance pathway: Slow $+$L and $-$M cone inputs revealed by low to moderate long-wavelength adaptation. *Journal of Physiology* **566**, 77–91.

Stockman, A. & Plummer, D.J. (2005*b*). Long-wavelength adaptation reveals slow, spectrally-opponent inputs to the human luminance pathway. *Journal of Vision* **5**, 702–716.

Stockman, A., Plummer, D.J. & Montag, E.D. (2005). Spectrally-opponent inputs to the human luminance pathway: Slow $+$M and $-$L cone inputs revealed by intense long-wavelength adaptation. *Journal of Physiology* **566**, 61–76.

Stockman, A. & Sharpe, L.T. (1999). Cone spectral sensitivities and color matching. In *Color Vision: From Genes to Perception*, eds. Gegenfurtner, K. & Sharpe, L.T., pp. 53–87. Cambridge: Cambridge University Press.

Stockman, A. & Sharpe, L.T. (2000). Spectral sensitivities of the middle- and long-wavelength sensitive cones derived from measurements in observers of known genotype. *Vision Research* **40**, 1711–1737.

Stromeyer, C.F., III, Chaparro, A., Tolias, A.S. & Kronauer, R.E. (1997). Colour adaptation modifies the long-wave versus middle-wave cone weights and temporal phases in human luminance (but not red-green) mechanism. *Journal of Physiology* **499**, 227–254.

Stromeyer, C.F., III, Cole, G.R. & Kronauer, R.E. (1987). Chromatic suppression of cone inputs to the luminance flicker mechanisms. *Vision Research* **27**, 1113–1137.

Vidyasagar, T.R., Kulikowski, J.J., Lipnicki, D.M. & Dreher, B. (2002). Convergence of parvocellular and magnocellular information channels in the primary visual cortex of the macaque. *European Journal of Neuroscience* **16**, 945–956.

Vos, J.J. & Walraven, P.L. (1971). On the derivation of the foveal receptor primaries. *Vision Research* **11**, 799–818.

Walls, G.L. (1955). A branched-pathway schema for the color-vision system and some of the evidence for it. *American Journal of Ophthalmology* **39**, 8–23.

Walraven, P.L. (1974). A closer look at the tritanopic confusion point. *Vision Research* **14**, 1339–1343.