The S-cone contribution to luminance depends on the M- and L-cone adaptation levels: Silent surrounds?

Caterina Ripamonti   Institute of Ophthalmology, University College London, London, UK

Wen Ling Woo   Institute of Ophthalmology, University College London, London, UK

Elizabeth Crowther   Institute of Ophthalmology, University College London, London, UK

Andrew Stockman   Institute of Ophthalmology, University College London, London, UK

Under dim background conditions, the S-cones make little or no contribution to luminance (A. Eisner & D. I. MacLeod, 1980; W. Verdon & A. J. Adams, 1987), yet under conditions of intense long-wavelength adaptation, a small but robust contribution to luminance—as defined by heterochromatic flicker photometry (A. Stockman, D. I. MacLeod, & D. D. DePriest, 1987, 1991) or motion (J. Lee & C. F. Stromeyer, 1989)—can be found. Here, by using selective adaptation and/or tritanopic metamers to isolate the S-cone response, we investigate the dependence of the S-cone luminance input on changes in background wavelength and radiance. Interestingly, the S-cone luminance input disappears completely when no adapting background is present, even though the same S-cone stimulus makes a clear contribution to luminance when a background is present. The dependence of the S-cone luminance input on the wavelength and radiance of the adapting background is surprising. We find that the S-cone signal can be measured on fields of 491 nm and longer wavelengths that exceed a criterion background radiance. These criterion radiances roughly follow an L + M spectral sensitivity, which suggests that the S-cone luminance input is silent unless the L- and M-cones are excited above a certain level. We hypothesize that the L + M cone signals produced by the steady adapting backgrounds somehow "gate" the S-cone luminance signals, perhaps by being modulated by them.

Keywords: S-cones, M-cones, luminance, color vision, adaptation, heterochromatic flicker photometry, silent surrounds

Introduction

The appearance of temporally alternating lights that differ in luminance and chromaticity changes as their frequency of alternation increases. At low frequencies, the lights appear to fluctuate in both luminance and color, but at high frequencies they appear to fluctuate only in luminance (Ives, 1912). This has been taken as evidence that the pathways that signal color are relatively sluggish and unable to follow fast flicker (De Lange, 1958; Kelly & van Norren, 1977; King-Smith & Carden, 1976; Noorlander, Heuts, & Koenderink, 1981; Regan & Tyler, 1971; Smith, Bowen, & Pokorny, 1984; Sternheim, Stromeyer, & Khoo, 1979; Tolhurst, 1977). Moreover, the luminance flicker that remains at higher frequencies has the important property that it can be cancelled or "nulled" simply by adjusting the relative intensity of the two alternating lights, which can be of any chromaticity (Ives, 1912). This suggests that fast luminance flicker is mediated by a single, univariant, color-blind channel or pathway that simply sums the cone signals it receives.

The perceptual dissociation of color and luminance has led to models in which the photoreceptor signals from the three types of cones [short (S)-, middle (M)-, and long (L)-wavelength-sensitive] are transformed after the photoreceptors into separate chromatic and luminance signals (Donders, 1881). Traditionally, the more sluggish chromatic signals are assumed to be generated by the opposition of cone signals: L − M and S − [L + M], and the luminance signal by the addition of signals from just two of the three cone types: L + M (Boynton, 1979; De Lange, 1958; Eisner & MacLeod, 1980; Guth, Alexander, Chumbly, Gillman, & Patterson, 1968; Luther, 1927; Schrödinger, 1925; Smith & Pokorny, 1975; Walls, 1955). This psychophysical model has some physiological and anatomical support (see Physiological and anatomical considerations section).

The lack of an S-cone contribution to luminance has been contentious, but it is clear that S-cone signals can make a small luminance contribution when the S-cone response is isolated by intense long-wavelength adaptation. Under such conditions, the S-cone luminance input is negative but also substantially delayed, so that at moderate frequencies (15–20 Hz, depending on the S-cone adapting level) the S-cone flicker adds to luminance but at low frequencies subtracts from it (see Figures 3, 4, and 5, and Drum, 1983; Lee & Stromeyer, 1989; Stockman, MacLeod, & DePriest, 1987, 1991). Under some conditions, however, an S-cone contribution to luminance has not been found (Cavanagh, MacLeod, & Anstis, 1987; Eisner & MacLeod, 1980; Verdon & Adams, 1987). A goal of this work was to reconcile these contradictory findings.

Any psychophysical investigation of S-cones and luminance has two main experimental requirements. The first is that the psychophysical task should depend predominantly on the response of the univariant luminance channel. Tasks that favor the response of the luminance channel typically involve the use of moderate to high temporal and/or spatial frequencies to which chromatic channels are insensitive (e.g., De Lange, 1958; Kelly & van Norren, 1977; King-Smith & Carden, 1976; Noorlander et al., 1981; Regan & Tyler, 1971; Smith et al., 1984; Sternheim et al., 1979; Tolhurst, 1977). In this paper, we use a version of flicker photometry, in which the observer is asked to adjust the luminances of two sinusoidally alternating lights in order to null the perception of flicker. If the two lights produce only univariant signals in the luminance channel, then it should be possible to null those lights regardless of the cone type from which the signals originated. One caveat, however, is that the S-cone luminance input is delayed and inverted with respect to the L- and M-cone inputs (Lee & Stromeyer, 1989; Stockman et al., 1987, 1991). Consequently, the observer must also adjust the relative phase of the two lights in order to complete the nulls.

The second experimental requirement is that one of the flickering stimuli should produce a strong S-cone response. We accomplished this by using one or both of two standard techniques used in previous papers whose findings we are re-examining here: selective chromatic adaptation and silent substitution. Chromatic adaptation relies on an adapting background that selectively suppresses the M- and L-cones but has little direct effect on the S-cones (such as one of 610 nm, see Figure 1, top). A superimposed target to which the S-cones are relatively sensitive (such as one of 436 nm) is then detected primarily by the S-cones. Although chromatic adaptation is quite effective at isolating the S-cone response, silent substitution has the advantage that an adapting background is not required. It relies on the alternation of pairs of targets (such as 436 nm and c. 490 nm, see Figure 1, bottom) that is invisible both to the L- and to the M-cones. When these "tritanopic metamers" are alternated at

Chromatic adaptation

L+M cone-detected 620-nm flickering 3.5° diam. target

S-cone-detected 436-nm flickering 3.5° diam. target

Intense 610-nm 8.5° diam. background light

Silent substitution (tritan pairs)

L+M cone-detected 620-nm flickering 3.5° diam. target

S-cone-detected 436/c.490-nm luminance-equated alternating tritan pair of 3.5° diam. targets
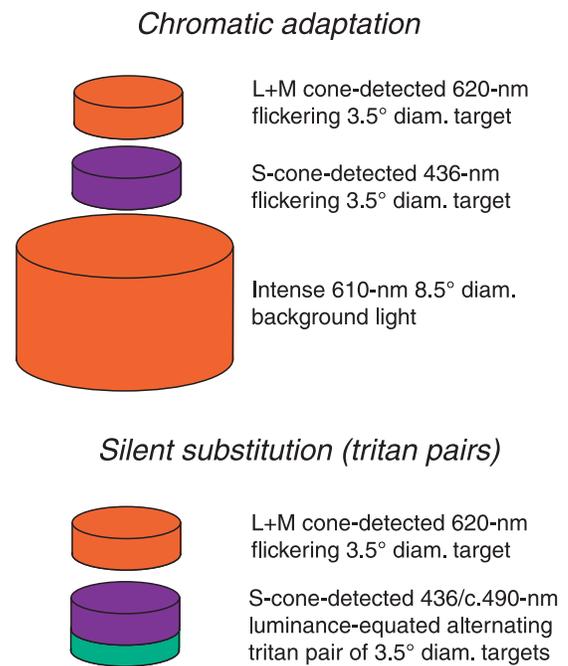
Figure 1. S-cone isolation techniques. For details, see text.

equiluminance, the alternation should be invisible to both the L- and the M-cones and detected only by the S-cones. These metamers should therefore be indistinguishable to a tritanope, an observer lacking S-cones.

We have introduced methodology in the Introduction section because the principal difference between experiments like those of Stockman et al. (1991), who found an S-cone luminance input, and experiments like those of Eisner and MacLeod (1980), who found none, is that the former used selective chromatic adaptation to isolate the S-cone response, whereas the latter relied on silent substitution (except for one experiment in which a 60-td, 563-nm background was used). Their conflicting results could be the result of some dependence of the S-cone luminance contribution upon chromatic adaptation. We investigated this possibility by monitoring the S-cone contribution to flicker photometry as a function of changes in background radiance and changes in background wavelength.

Methods

Observers

Two female observers (KR and WL) and one male observer (AS) participated in this study. KR and WL carried out all the experiments, AS only a subset of them. Their color vision was assessed by standard tests (Farnsworth-Munsell 100-hue, Rayleigh and Moreland anomaloscope matches, and Ishihara plates) and was found

to be normal. This study conformed to the standards set by the Declaration of Helsinki, and the procedures were approved by local ethics committees at the University College London.

Apparatus

The optical apparatus was a conventional five-channel Maxwellian-view optical system with a 2-mm exit pupil. Two light sources were used: A 75-W Xenon (Xe) arc lamp illuminated three channels, and a 100-W Mercury (Hg) arc lamp the remaining two. Test and field wavelengths were selected with interference filters with full-width at half-maximum (FWHM) bandwidths of between 7 and 11 nm (Ealing or Oriel), or by Jobin-Yvon H-10 monochromators with 0.5-nm slits, the spectral outputs of which were a triangular function of wavelength with an FWHM bandwidth of 4 nm. Infrared radiation was minimized by heat-absorbing glass (Oriel). The 436-nm Hg line, used to illuminate one member of the tritan pair, was isolated with an interference filter and had an FWHM bandwidth of 4 nm. The radiance of each beam could be varied by adding or removing fixed neutral-density filters or varied under computer control by rotating circular, variable neutral-density wedges mounted on stepping motors (Rolyn Optics). Sinusoidal modulation was produced by pulse-width modulating fast, liquid-crystal light shutters (Displaytech) around a carrier frequency of 400 Hz. Each shutter had rise and fall times of less than 50 μs and could produce sinusoidal modulations from 0% to 92%. The observer's head was stabilized by a dental wax impression. This system has been described in more detail elsewhere (Stockman & Sharpe, 2000b).

Stimuli

Heterochromatic flicker photometry and phase delays

The luminance contributions of the targets were measured by nulling flicker in a foveal heterochromatic flicker photometric procedure using sinusoidally flickering targets of 3.5° in visual diameter. They were presented alone or superimposed in the center of 8.5° diameter backgrounds. The background wavelengths were 491, 510, 543, 579, 610, 633, 658, or 678 nm. Flicker photometric nulls were set between an S-cone target and an L- and M-cone target (which we will refer to as the LM-cone target). The S-cone flickering target was either a single target of 436 nm or a tritanopic pair of luminance-equated sinusoidally alternating targets, one of which was also 436 nm. The 436-nm target radiance was fixed at 9.08 $\log_{10}$ quanta s^{-1} deg^{-2}. This radiance was chosen so that the S-cone luminance response could be measured up to about 20–25 Hz in most subjects (see Figures 1–3 of Stockman, Langendörfer, & Sharpe, 2007). The wavelength and radiance of the tritanopic pair to the 436-nm

target was determined experimentally for each subject (see Tritan measurements section). The wavelength of the LM-cone target, which was superimposed on the S-cone target, was as close to that of the background as our available interference filters allowed, so that it generated mainly achromatic flicker with respect to the background. The background/LM-target wavelength combinations were: 491/492, 510/500, 543/540, 579/578, 610/620, 633/630, 658/656, and 678/678 nm. The radiance of each LM-cone target was adjusted by the subject so that at the maximum *target* modulation of 92% the flicker was just visible at 20 Hz (the actual modulation produced by the target was, of course, reduced by the other targets and field). In this way, the LM-cone target was made just intense enough to perform the psychophysical task but was always much dimmer than the background. For instance, on the 610-nm backgrounds of 11.49 to 8.10 log quanta s^{-1} deg^{-2} used by WL, the time-averaged radiance of the 620-nm, LM target varied from 9.84 to 7.26 log quanta s^{-1} deg^{-2}, while on the 610-nm backgrounds of 11.40 to 9.22 log quanta s^{-1} deg^{-2} used by KR, it varied from 9.84 to 7.69 log quanta s^{-1} deg^{-2}. Comparable differences were found for other background and LM-target wavelength combinations. All the stated stimulus radiances are time-averaged. The targets were flickered at frequencies of between 5 and 25 Hz (phase settings could often be made at 25 Hz despite the S-cone flicker being slightly subthreshold—see Stockman, MacLeod, & LeBrun, 1993). The S-cone and LM-cone targets were initially presented in opposite phase, but their relative phase and modulation could be adjusted by the observer.

The spatial configuration of the background and target was not crucial to the results. Comparable findings were obtained when the background was removed and the radiance of the LM target increased to match that of the missing background.

Procedures

Subjects light-adapted to the target and background fields for at least three minutes 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 computer-generated tones.

We used a variation of heterochromatic flicker photometry in which the subject was allowed to vary the phase difference between the two flickering stimuli as well as their relative modulation in order to optimize the flicker null. In a typical run, the observer first 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 (c. 0.2 $\log_{10}$ above threshold). (If the flicker

was invisible, the observer set the modulation to maximum.) The observer then adjusted the phase difference between the two stimuli and their relative modulation to find the best flicker null. Subjects could also reverse the relative phase of the two stimuli by 180° to help them find the correct nulling phase. Flicker frequencies from 5 to 25 Hz in 5-Hz steps were used. After some practice, observers became very skilled at this task. In this work, we were concerned with the phase delays, because they are diagnostic of the presence or not of the S-cone luminance input (see below). Consequently, observers were instructed to pay more attention to finding the optimal relative phase for the null rather than the optimal modulation.

In general, the S-cone and LM-cone modulations at the null settings are near-threshold or a small multiple of threshold. This was partly by design, since we intentionally kept the radiance of the LM-cone target low, but also necessitated by the fact that the S-cone luminance signal can cancel LM-cone modulations that are no more than about 2 or 3 times above the LM-cone threshold modulation (see Figure 1 of Stockman et al., 1991). This was also the case here. For example, over the range of 610-nm backgrounds on which the S-cone luminance signal could be measured, the 10-Hz S-cone signal cancelled LM-cone modulations that ranged from just above threshold to 3 times threshold. In general, the S-cone signal that cancelled LM-cone flicker was usually suprathreshold, but at 25 Hz the S-cone signal could be subthreshold, as noted above. The restriction of the S-cone flicker signal to near-threshold levels is probably due in large part to S-cone saturation (see Stockman & Plummer, 1998).

Unless stated otherwise, all data points are averaged from three or four settings made on four separate runs. Further details of these methods can be found elsewhere (see Stockman & Plummer, 2005b; Stockman, Plummer, & Montag, 2005).

Tritan measurements

Pairs of target lights that differentially excite only S-cones when equiluminant (tritanopic matches) were determined individually for each subject using a color matching procedure. Foveal matches were made between two vertically bisected 3.5° diameter half targets that were juxtaposed to make a circular bipartite field. The bipartite field was superimposed in the center of a circular 8.5° diameter, 420-nm background field, the radiance of which was varied in steps during the experiment. One half field was illuminated by the 436-nm spectral line from the Hg arc lamp. The other half field, which was variable in wavelength, was illuminated by the Xe arc lamp. Its wavelength was varied under the observer's control using the Jobin-Yvon H-10 monochromator. For more details, see Stockman and Sharpe (2000b).

The tritan measurements followed the procedures of Stockman and Sharpe (2000b). To avoid S-cone detection of the test fields, we carried out the matches as close as possible to the contrast threshold of the 436-nm target. For reliable matches, this was 0.9 $\log_{10}$ unit above threshold. To set the 436-nm radiance, observers were first presented with the half-field illuminated by the 436-nm Hg line and were asked to adjust its radiance until it appeared to be just at contrast threshold. Each threshold setting was made three times and the results averaged. By the removal of a calibrated 0.9 $\log_{10}$ unit neutral-density filter, the half-field could be set to 0.9 $\log_{10}$ unit above its contrast threshold for the main experiment.

Observers were next presented with the second, variable wavelength half-field and were asked to adjust its wavelength and radiance to match the half-field illuminated by the Hg line. After each match, the observer was asked to report on the quality of the match. The task was challenging, because changes in radiance or wavelength could cause changes in both apparent color and apparent intensity, as a result of which subjects often had to readjust the radiance after each wavelength adjustment and vice versa. Nonetheless, after some practice, the observers could set repeatable, satisfactory matches between the two half-fields. When a range of wavelengths produced a match, observers were asked to set the middle of the range.

Observers made tritanopic matches on four 420-nm background radiances of 10.80, 11.11, 11.38, and 11.70 $\log_{10}$ quanta s^{-1} deg^{-2}. As the radiance increased, the match improved and reached an asymptotic wavelength. The mean asymptotic wavelength for the highest three radiances was taken as the wavelength for the tritan match to the 436-nm half-field. It was 489.0 nm for KR, 492.3 nm for WL, and 496.8 nm for AS. The radiance that matched the 436-nm target of 9.08 $\log_{10}$ quanta s^{-1} deg^{-2} used in the experiments was determined by averaging flicker photometric matches made without a background at 15, 20, and 25 Hz (the matches were independent of frequency).

The equiluminant tritan pairs used in the flicker experiments were 436 nm and 9.08 $\log_{10}$ quanta s^{-1} deg^{-2} paired with 489.0 nm and 8.08 $\log_{10}$ quanta s^{-1} deg^{-2} for KR, 492.3 nm and 7.99 $\log_{10}$ quanta s^{-1} deg^{-2} for WL, and 496.8 nm and 7.84 $\log_{10}$ quanta s^{-1} deg^{-2} for AS. When the tritan pairs are superimposed and alternated at equal luminance, the alternation should be invisible to the M- and L-cones.

Calibration

The radiant fluxes of test and background were measured at the plane of the observer's entrance pupil with a photodiode (Graseby Electronics), which had been cross-calibrated with comparable devices traceable to US and German national standards. Targets and backgrounds were spectrally calibrated in situ with a spectroradiometer (Gamma Scientific).

Results

S-cone luminance input depends on the presence of a background

In the first experiment, we investigated whether the S-cone luminance contribution found under long-wavelength adaptation survived the removal of the adapting background. First, we characterized the S-cone luminance response under long-wavelength adaptation, by replicating a subset of the measurements made by Stockman et al. (1991). The flickering S- and LM-cone targets were superimpose on an intense orange adapting background of 610 nm and 11.50 $\log_{10}$ quanta s^{-1} deg^{-2} (c. 5 $\log_{10}$ ph td). The optimal phase delays for the null are shown in Figures 2a and 2b for KR and AS, respectively, as orange triangles.

Next, we repeated the same measurements, but using a tritan pair as the S-cone stimulus instead of the single 436-nm light. The use of the S-cone isolating tritan pair on the long-wavelength background should be superfluous for S-cone isolation, since the S-cone response is already isolated by the background. Nonetheless, it is important for the comparison between the background and no background conditions that the same S-cone stimulus be used in the two cases. The observers were asked, as before, to null the S-cone and the LM-cone flicker by varying the relative modulation and phase. The results are shown in Figures 2a and 2b as blue circles. Not surprisingly, given that the long-wavelength background isolates the S-cone response, the S-cone phase delays measured with the tritan pair are nearly identical to those measured with the 436-nm target alone.

The S-cone phase delays found under long-wavelength adaptation are comparable to previous measurements (Lee
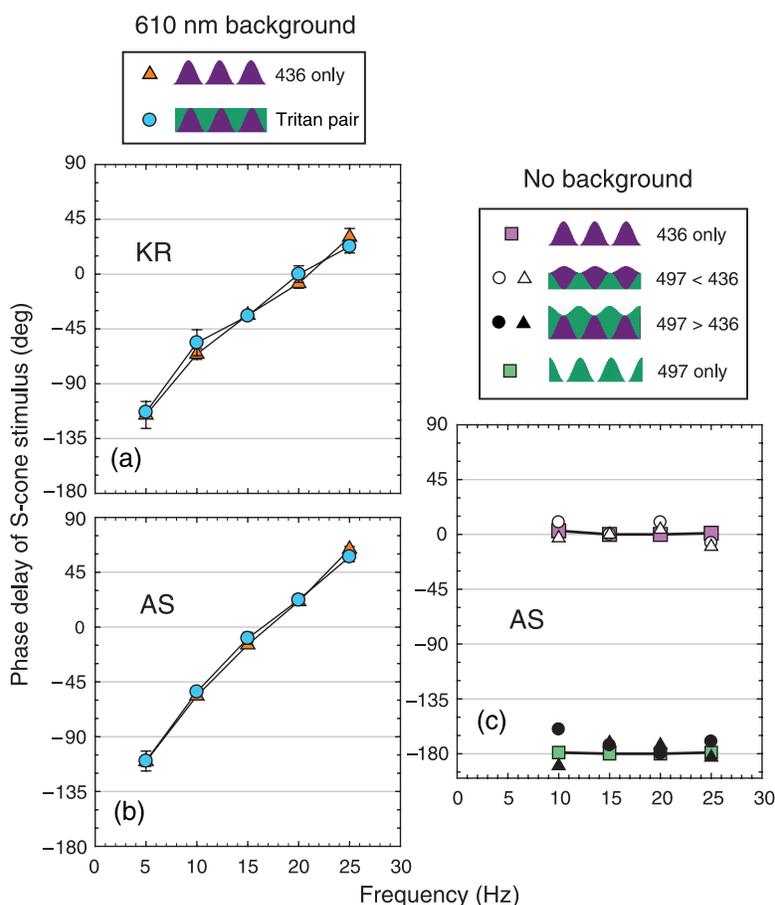

Figure 2. S-cone phase delays for (a) KR and (b) AS measured relative to an LM-cone target with either a single 436-nm flickering light (orange triangles) or with a tritan pair (blue circles) on an orange adapting background of 610 nm and 11.50 $\log_{10}$ quanta s^{-1} deg^{-2}. The radiance of 620 nm, LM-cone target, which was set by each subject so that 20-Hz flicker was just visible, was 10.15 and 10.24 $\log_{10}$ quanta s^{-1} deg^{-2} for KR and AS, respectively. (c) Phase delays obtained with no background for AS. Phase delays could not be set for the tritan pair and are therefore not shown. Slight offsets of −0.12 (open circles), −0.05 (open triangles), +0.05 (filled triangles), and +0.12 (filled circles) in the radiance of the 497-nm target away from equiluminance enabled phase delays to be measured again, but the results have the same delays as either the 436-nm target alone (pink squares) or the 497-nm target alone (green squares). Without the background, the 620-nm, LM-cone target radiance was set to 7.04 and 7.56 $\log_{10}$ quanta s^{-1} deg^{-2} for KR and AS, respectively.

& Stromeyer, 1989; Stockman et al., 1987, 1991). Two features of the results are characteristic signatures of the S-cone luminance signal so far reported. First, the phase delays increase with frequency, which means that S-cone luminance response is delayed relative to the L- or M-cone responses. Second, the phase delays tend towards $-180°$ as the frequency is decreased to 0 Hz (so that near 0 Hz the S-cone flicker must be *in phase* with the L- and M-cones in order to cancel it), which means that at low frequencies the S-cone signal has the opposite sign to the L- and M-cone signals.

Next, we measured phase delays between the tritan pair and 620-nm target without the 610-nm background and found that all three subjects were unable to set flicker nulls. This clearly indicates the absence of any measurable luminance component in the flickering tritan pair in the absence of the 610-nm background. These results are therefore consistent with those of Eisner and MacLeod (1980). They suggest that the presence of the S-cone luminance input depends strongly on the level of long-wavelength chromatic adaptation.

Although the removal of the 610-nm background has relatively little *direct* effect on the S-cones, it substantially reduces the excitation of the M- and L-cones. This increases the LM-cone modulation produced by the 620-nm target, which as a result must be decreased in radiance by roughly 3 $\log_{10}$ units to maintain 20-Hz LM-cone flicker just above threshold.

As a control, we varied the radiances of the tritan pair slightly away from L- and M-cone equalities as shown for subject AS in Figure 2c. Slight imbalances of just ±0.05 log unit away from the equiluminant radiances for AS or ±0.10 log unit for KR and WL (not shown) enabled phase settings to be made again. When the 436-nm component of the tritan pair is greater, the optimal phase delays for the null are near $0°$, whereas when the c. 490-nm component is greater, they are near $-180°$. These results are consistent with the flicker produced by each component of the "tritan" pair being generated by the same cone type(s) that detect the 620-nm target, because the phase delays are consistent with the physical delays between the stimuli. A phase delay of $0°$ is to be expected when the 436-nm component is greater, because at $0°$ that component is physically in opposite phase with the 620-nm flicker. In contrast, a phase delay of $180°$ is to be expected when the c. 490-nm component is greater, because at $180°$ that component is physically in opposite phase with the 620-nm flicker.

Dependence of the S-cone luminance input on background radiance

The apparent disappearance of the S-cone luminance signal when the 610-nm background is removed suggests that there might be some "critical" background radiance below which the S-cone luminance signal can no longer be measured. We estimated this "critical" radiance by decreasing the radiance of the 610-nm background in steps. At each step, we set phase delays for the optimal flicker cancellation between the S-cone and LM-cone flicker as a function of flicker frequency. If we can set phase delays on a given background, it suggests that some form of flicker cancellation and/or enhancement between S-cone and LM-cone flicker must be occurring.

Again, we used the tritan pair (see above) to isolate the S-cone response. The need for the tritan pair in maintaining S-cone isolation becomes more important as the 610-nm background radiance is decreased. The phase delays that could be measured are shown in the left panels of Figure 3. The background radiance was decreased in steps that were made smaller as the critical radiance at which an S-cone signal could no longer be measured was approached. The 620-nm target was initially 11.08 $\log_{10}$ quanta s^{-1} deg^{-2} on the brightest background, but was then decreased with background radiance so that the 20-Hz LM-cone flicker remained just visible. As shown in the figure, phase settings could be made on 610-nm fields with radiances of 9.22 $\log_{10}$ quanta s^{-1} deg^{-2} and above for subject KR, and 8.10 $\log_{10}$ quanta s^{-1} deg^{-2} and above for subject WL. Below those background radiances, phase settings could no longer be made. The lowest background levels for which phase data are shown in the left panels of Figure 3 (and in the panels of Figures 4 and 6) correspond to those critical background radiances below which S-cone phase delays could not be measured. It is important to note that all the phase delays that could be measured have the characteristics of the S-cone luminance signal, so that there is no evidence here for another S-cone signal, such as one that is synergistic with the L- and M-cones at low temporal frequencies.

It is instructive to measure the phase delays using just a 436-nm target instead of the tritan pair. With such a target S-cone isolation eventually fails as the 610-nm field radiance is decreased, and 436 nm is detected by M- (or L-) cones as the background radiance is decreased. As shown in the left panels of Figure 3, the radiance of the 610-nm background was decreased in steps from 11.5 to 6.5 $\log_{10}$ quanta s^{-1} deg^{-2}, and again the radiance of the 620-nm target was also decreased so that the 20-Hz LM-cone flicker remained just visible. The phase delays for KR and WL are shown in the right panels of Figure 3. The phase settings at the three highest background radiances show both the signal delay and the signal inversion that are characteristic of the S-cone luminance input. In contrast, at the lowest levels the phase settings are roughly $0°$, which suggests that there is no delay and no inversion between the 436-and 620-nm signals. No phase delays suggest that detection of both 436- and 620-nm flicker is mediated by the same fast M- or L-cone luminance mechanisms. The settings at 8.90 $\log_{10}$ quanta s^{-1} deg^{-2} are intermediate between the settings at lower and higher background radiances. They suggest that at this level the 436-nm flicker is detected by the S-cones and M-cones.
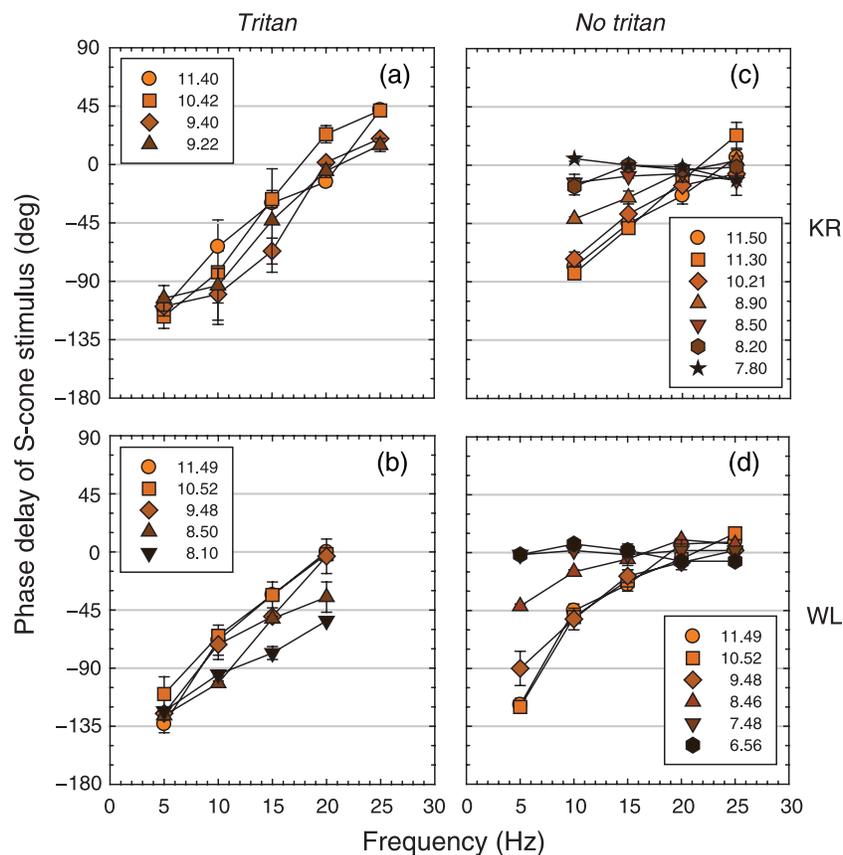
Figure 3. S-cone phase delays for (a) KR and (b) WL measured between a tritan pair and a 620-nm target on 610-nm backgrounds of various radiances. Note that these represent background levels at which S-cone phase delays could be measured. Phase delays could not be measured at levels lower than the ones shown, which is indicative of the lack of a measurable S-cone luminance contribution. Panels (c) for KR and (d) for WL show "S-cone" phase delays measured between a 436-nm and a 620-nm target on 610-nm backgrounds. At low radiances the phase delays become characteristic of the M- or L-cones, which is indicative of a failure of S-cone isolation. For background radiances and symbols, see panel keys. See text for other details.

In summary, S-cone phase delays can be measured, but only if the 610-nm background radiance meets or exceeds 9.22 or 8.10 $\log_{10}$ quanta s^{-1} deg^{-2} for KR or WL, respectively.

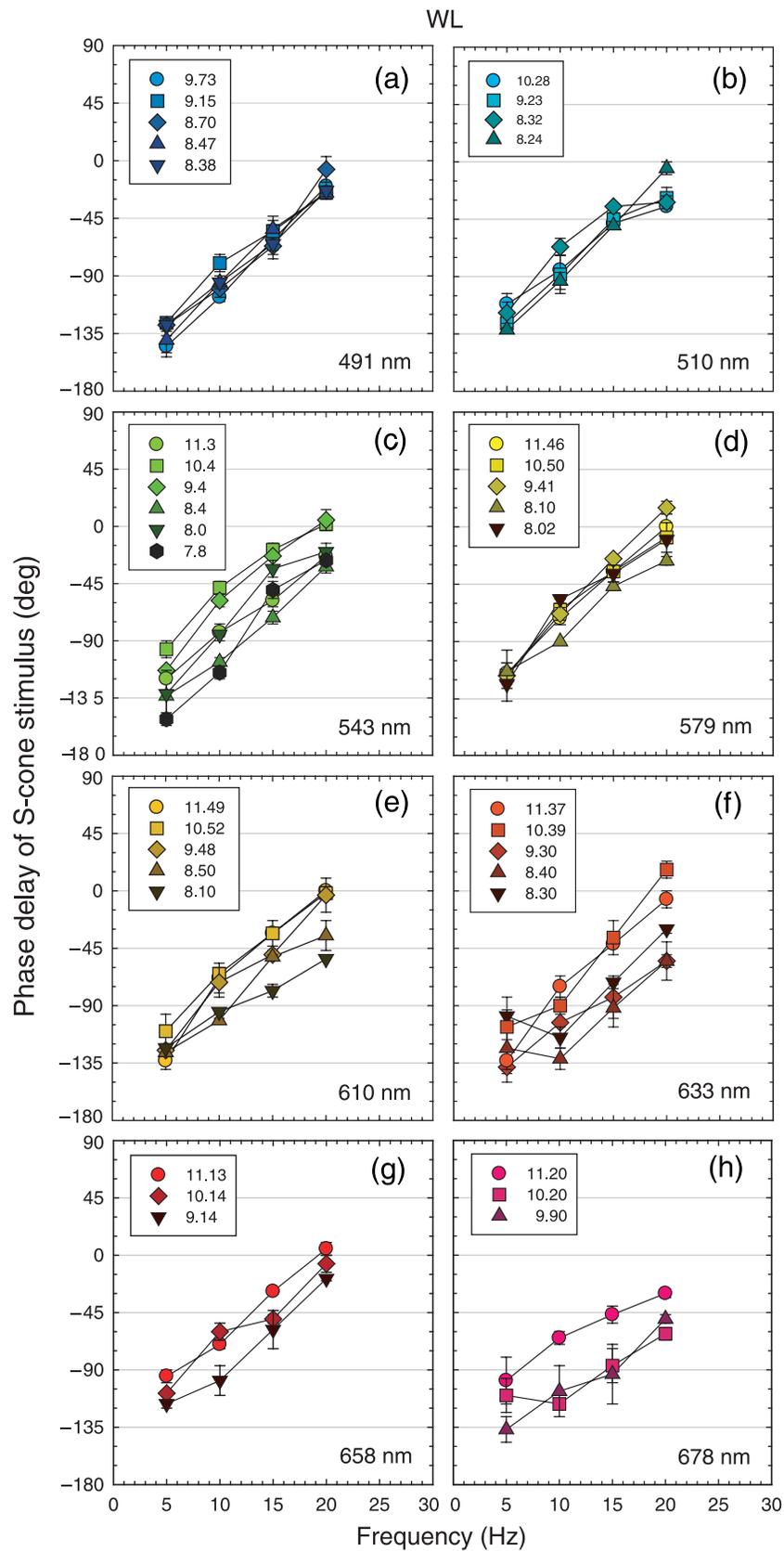## Dependence of the S-cone luminance input on background chromaticity

Spectral backgrounds

The results obtained with the 610-nm backgrounds suggest that the S-cone luminance contribution might be somehow "gated" by the L- and/or M-cone excitation produced by the 610-nm background. In the next experiment, we investigate the spectral properties of the gating mechanism by varying the background wavelength, and determining the critical radiance at each background wavelength for which the S-cone luminance input could just be measured.

We extended our study to include backgrounds of 491, 510, 543, 579, 633, 658, and 678 nm. Background wavelengths shorter than 491 nm were not used because

they reduce the S-cone modulation (and thus the visibility of S-cone flicker) by directly exciting the S-cones. At each background wavelength, the background radiance was decreased in steps until it was no longer possible to set flicker nulls. The flickering targets consisted of the tritan pair and an LM-cone target, the wavelength of which was as close to the background wavelength as our selection of interference filters allowed. These target wavelengths were 492, 500, 540, 578, 630, 656, and 678 nm. As before, the radiances of the LM-cone targets were adjusted for each background condition so that 20-Hz LM-cone flicker was just visible.

The phase delays required to null the LM-cone flicker are shown for WL in Figure 4. Data for the 610 nm shown previously in Figure 3 are also included. Comparable data (not shown) were obtained for KR, who carried out the same experiment as WL, and for AS, who carried out a more limited experiment in which the measurements were concentrated near the critical radiances. At all background wavelengths, observers were able to null the S-cone and LM-cone flicker provided that the background exceeded a critical radiance. Notice that as for the 610-nm background,

all the phase delays that can be measured have the characteristics of the S-cone luminance signal. There is a tendency for the phase delays to decrease with background radiance for WL, which is likely to be due to the slowing down of the L- and M-cone responses with decreasing light level (see, for example, Figure 5 of Stockman, Langendörfer, Smithson, & Sharpe, 2006).

Figure 5 shows the critical background radiances for all three subjects plotted as spectral sensitivities. We can estimate the cone inputs to the mechanism that might gate the S-cone luminance contribution from the shapes of the spectral sensitivity functions. Specifically, we fitted them with linear and non-linear combinations of the Stockman and Sharpe (2000a) M- (green lines) and L- (red lines) cone fundamentals. We found that the spectral sensitivities could be described very simply by an additive combination of the M- and L-cone spectral sensitivities as shown in Figure 5 by the black lines. The best-fitting ratios of L:M cone weights are 0.73, 1.61, and 2.05 for KR, WL, and AS, respectively. The peaks of the fitted functions are −8.92, −7.88, and −7.92 for KR, WL, and AS, respectively.

White backgrounds

Given the prevalent use of achromatic backgrounds in CRT-based vision research, we thought that it is important to determine whether the S-cone luminance input is also present on white backgrounds. The results from the previous section suggest that this should be the case if the M- and L-cone excitation level exceeds a criterion level consistent with the spectral sensitivities shown in Figure 5. However, a complication is that white fields will directly excite the S-cones, so reducing the S-cone modulation produced by the S-cone target. We produced achromatic fields by combining two complementary spectral fields. The wavelength of one field was fixed at 610 nm, while that of the other was selected by the observer. At each level of the 610-nm background, the observer adjusted the wavelength and radiance of the second background, so that the combined field appeared achromatic (or as nearly achromatic as could be achieved). Both observers consistently chose a complementary wavelength of 487 nm. The radiances of the 610/487 nm fields for the five levels used by KR in $\log_{10}$ quanta s^{-1} deg^{-2} were 9.88/10.58, 9.34/10.04, 9.16/10.26, 8.85/9.73, and 8.42/9.36, while those for the five levels

Figure 4. S-cone phase delays for WL measured between a tritan pair and an LM target on backgrounds of (a) 491 nm, (b) 510 nm, (c) 543 nm, (d) 579 nm, (e) 610 nm, (f) 633 nm, (g) 658 nm, and (h) 678 nm. Note that these represent background levels at which S-cone phase delays *could* be measured. Phase delays could not be measured at levels lower than the ones shown. For background radiances and symbols, see panel keys. The LM target wavelength was as close to the background wavelength as our available filters allowed (see text for details).
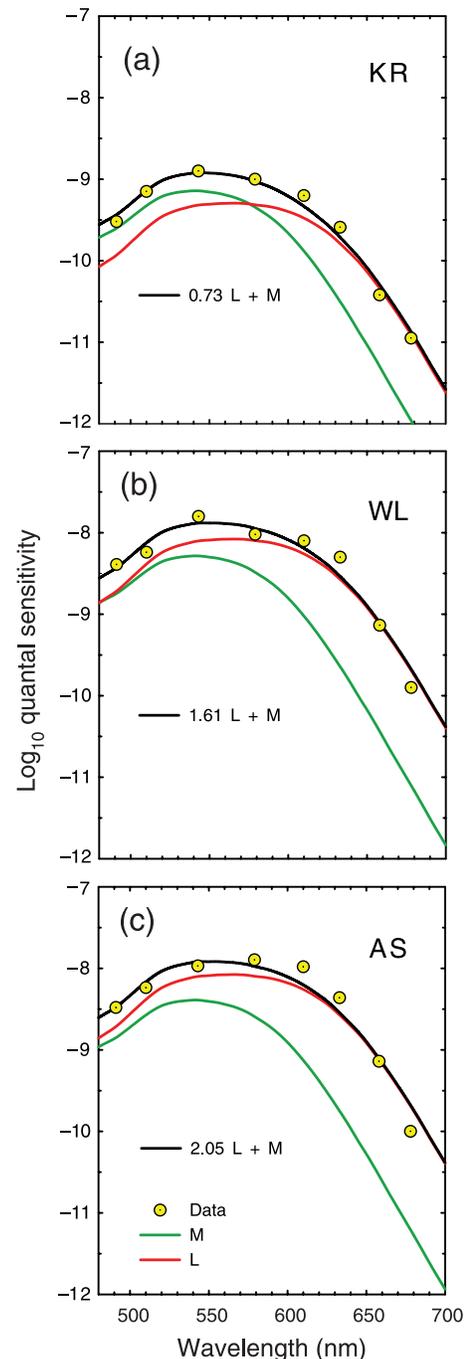

Figure 5. Minimum background radiances required to be able to measure S-cone phase delays for (a) KR, (b) WL, and (c) AS plotted as sensitivities and fitted with linear combinations (black lines) of the Stockman and Sharpe (2000a) M- (green lines) and L- (red lines) cone fundamentals.

used by WL were 9.88/10.53, 9.34/9.92, 8.85/9.41, 8.67/9.22, and 8.42/9.06. The LM-cone target used in these experiments was 563 nm on the grounds that it produces roughly the same relative quantal catches in the L- and M-cones as the white background. As with other LM-cone targets, its radiance was adjusted on each background so that 20-Hz flicker was just at threshold. The S-cone phase
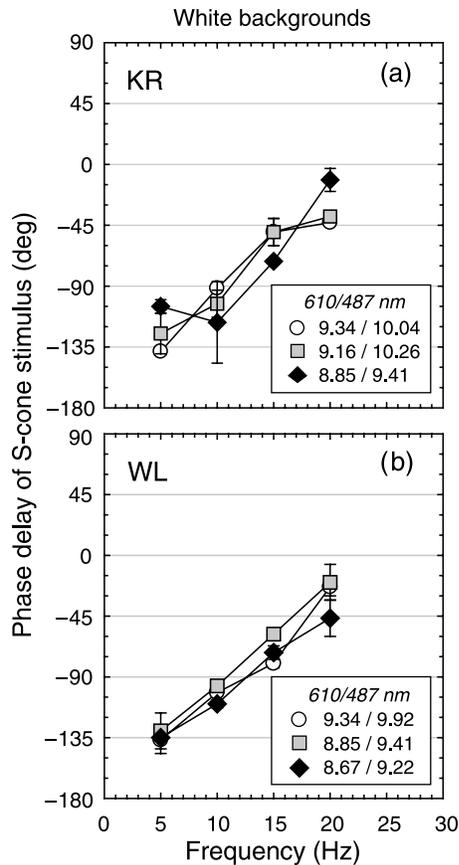
Figure 6. S-cone phase delays for (a) KR and (b) WL measured between a tritan pair and a 563-nm target on fields made up of bichromatic mixtures of 610 and 487 nm that appeared white. See panel keys for background radiances and symbols.

lags are shown in Figure 6. Characteristic S-cone phase lags were found at the three middle achromatic background levels. Nulls at the lowest and highest levels could not be set. The failure at the highest levels is due to the 487-nm component directly exciting the S-cones and reducing the S-cone modulation (see When is an S-cone luminance input found? section). The failure at the lowest levels is consistent with the total L- and M-cone excitation produced by the background component falling below the required criterion level consistent with the results found with other backgrounds.

Discussion

We have found evidence for a characteristic S-cone contribution to flicker photometry on backgrounds with wavelength between 491 and 678 nm and on achromatic backgrounds—provided that the backgrounds exceed a criterion level. These results agree with earlier work that found evidence for an S-cone contribution to luminance

(Lee & Stromeyer, 1989; Stockman et al., 1987, 1991). On backgrounds that fall short of the criterion level, however, we found no evidence for an S-cone contribution to flicker photometry. These results agree with earlier work that found no S-cone contribution to luminance (Cavanagh et al., 1987; Eisner & MacLeod, 1980; Verdon & Adams, 1987). Our findings therefore reconcile the conflicting results of previous studies. The presence of the S-cone luminance contribution depends on the level of excitation in the other cone types. The clear finding of an S-cone luminance contribution on white and spectral fields of modest radiance poses a problem for the myriad of experiments in which tritan modulations are used to isolate chromatic channels.

When is an S-cone luminance input found?

The first requirement for a viable S-cone luminance input is that the level of excitation in the M- and L-cones must exceed a criterion level. This level follows a roughly additive, $aL + M$ spectral sensitivity (see Figure 5). The L: M cone weights (a) were found to be 1.61 for WL and 2.05 for AS, which are close to the L:M cone ratio of roughly 2:1 typically assumed to be the mean or normal value for the relative L- and M-cone contributions to luminance (Albrecht, Jägle, Hood, & Sharpe, 2002; Carroll, McMahon, Neitz, & Neitz, 2000; Cicerone & Nerger, 1989; De Vries, 1948; Kremers, Scholl, Knau, Berendschot, & Sharpe, 2000; Sharpe, Stockman, Jagla, & Jägle, 2005). The low weight of 0.73 for KR is unusual but is not outside the normal range (Sharpe et al., 2005). More surprising is that the critical radiances for KR are about 10× higher than those for WL and AS. We have no explanation for this difference, but it suggests that substantial individual variability should be expected in the population.

The second requirement for a viable S-cone input (or, indeed, for detecting any S-cone flicker at all) is that the S-cone modulation must be high: for example, S-cone modulation thresholds as high as 15% and 30% are required to detect modulation at 10 and 15 Hz, respectively (see Figures 1–3 of Stockman et al., 2007). Because the thresholds are so high, the superposition of a steady background that *directly* excites the S-cones (and therefore reduces the S-cone modulation by adding a steady component to the flickering target) is likely to render the S-cone modulations produced by our targets invisible at higher temporal frequencies. Such backgrounds include the 10.53 and 10.58 log quanta s^{-1} deg^{-2} 487-nm components of the white fields upon which KR and WL, respectively, could not make phase settings. The direct effects of these fields on the S-cone modulation can be calculated straightforwardly using the S-cone spectral sensitivity (Stockman & Sharpe, 2000a).

The finding that the S-cone luminance contribution depends on the L- and M-cone excitation levels is reminiscent of the psychophysical model postulated by

Ingling and his co-workers (e.g., Ingling, 1977; Ingling, Russel, Rea, & Tsou, 1978) to explain several color phenomena attributed to the red–green cone-opponent mechanism. In their model, the S-cones can inhibit the M-cone signal, but only if an M-cone signal is present (and only to the extent that the M-cone signal exceeds the S-cone signal).

We hypothesize that some form of gating may also be involved here, but one that requires the joint L- and M-cone excitation to exceed some criterion level before the gating occurs. But by what mechanism might such gating operate? A simple gate would be one that opens whenever the level of excitation in the L- and M-cones exceeds some criterion level, thus allowing an inverted S-cone signal to contribute *directly* to luminance flicker. A more complex but perhaps more realistic gate would be one that allows the steady LM-cone signal generated by the background to be modulated by the S-cone signal whenever the LM-cone signal reaches a criterion level. The effect of S-cone signal on the LM-cone signal in this case is an *indirect* modulation. The modulation might reasonably result from a pooled gain control in which increases and decreases in the S-cone signal decreases and increases, respectively, the gain of the LM-cone signal. This type of scheme has the advantage that the S-cone modulation of the LM-cone signal will naturally be inverted, as we find. Moreover, it may also be consistent with the involvement of horizontal cells postulated in the Physiological and anatomical considerations section.

There are, of course, other possible explanations for the disappearance of the S-cone luminance signal at low L- and M-cone adaptation levels. It might be supposed, for example, that reducing the background luminance increases the saliency or strength of the LM-cone flicker signal so that it overwhelms the weaker S-cone signal. In these experiments, however, the LM-cone flicker signal was always kept near-threshold, which makes such an explanation unlikely. Alternatively, it might be supposed that the pathways through which the cone flicker signals travel change with adaptation level, and that the pathways at the different levels have different S-cone inputs. However, there seems to be no clear physiological support for such a scheme.

Sluggish, inverted M-cone signals

The inverted and delayed phase delays shown here are not confined to S-cone signals. M-cone phase delays with similar phase characteristics have been reported before under comparable conditions (Stockman & Plummer, 2005a, 2005b). Figure 7 shows such *M-cone* phase delays measured on the 610-nm background fields decreasing in steps from 10.41 $\log_{10}$ quanta s^{-1} deg^{-2} for KR and from 9.39 $\log_{10}$ quanta s^{-1} deg^{-2} for WL. The phase lags were measured between an M-cone-detected flicker target and the 620-nm flickering target. The M-cone target was
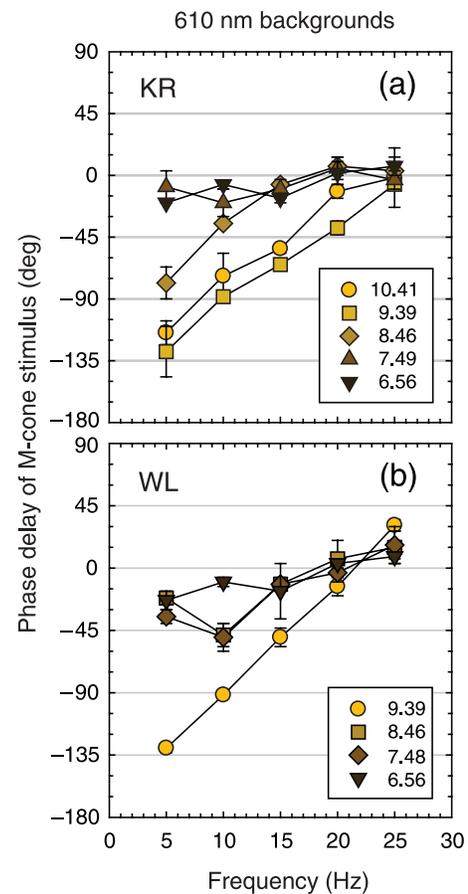

Figure 7. M-cone phase delays for (a) KR and (b) WL measured between an M-cone-detected stimulus (an L-cone-equated 620/579 nm pair of alternating lights) and a 620-nm target on 610-nm backgrounds of various radiances. For background radiances and symbols, see panel keys.

produced by alternating L-cone-equated 579- and 620-nm lights, the alternation of which should be invisible to L-cones—and also to the S-cones because of their insensitivity to the component wavelengths (Stockman & Sharpe, 2000a). The radiances of the targets were reduced with the 610-nm background radiance so that the 20-Hz modulation of each component remained just above threshold at its maximum modulation.

The phase delays in Figure 7 at the two highest background radiances for KR and the highest radiance for WL are consistent with the M-cone signal, like the S-cone signal, being delayed and inverted. This M-cone signal has been measured and modeled before and found to be consistent with the vector addition of a sluggish inverted M-cone signal and a faster non-inverted signal (Stockman & Plummer, 1994, 2005a, 2005b). As the 610-nm background radiance decreases, the results in Figure 7 suggest that the inverted M-cone signal declines leaving just the faster uninverted M-cone signal at the lowest radiances. The main difference between the M-cone phase delays shown in Figure 7 and the S-cone phase

delays shown in left panels of Figure 3 is that there is no faster uninverted S-cone signal, so that once the sluggish inverted S-cone signal disappears nothing is left. The phase delays in the right panels of Figure 3 reflect a mixture of S-cone phase delays at higher 610-nm background radiances and M-cone phase delays at lower radiances.

The marked similarities between the properties of the sluggish, inverted M-cone and S-cone signals are important because they suggest that they have a common physiological substrate.

Physiological and anatomical considerations

To the earlier evidence that the S-cones contribute to luminance flicker or motion perception with an inverted, delayed signal (Lee & Stromeyer, 1989; Stockman et al., 1987, 1991), we now add the caveat that the S-cone contribution depends upon the excitation of the L- and M-cones exceeding some critical level.

Given these unusual characteristics, we might expect that the signature of the S-cone luminance signal would be easily identifiable in physiological recordings. However, the optimal experimental conditions required for its generation may not be frequently encountered in modern physiological experiments, in which the range of intensities and chromaticities is often limited by display devices (such as CRTs), and then further limited by experimental design to modulations around an achromatic point. It is perhaps noteworthy that unusual combinations of cone signals, including S-OFF signals, were much more frequently encountered when spectral lights and adapting backgrounds were used rather than CRTs (e.g., De Monasterio, 1978; De Monasterio, Gouras, & Tolhurst, 1975a, 1975b; Zrenner & Gouras, 1981). Interestingly, Padmos and Norren (1975) in the LGN and De Monasterio et al. (1975a) in the retina both describe cells that require chromatic adaptation to reveal their color opponency.

If we were to encounter an S-cone luminance signal in physiological recordings, what might we expect to find and where might we expect to find it? Given that the S-cone signal we find is inverted with respect to the predominant M- and L-cone signals (but see Figure 7), we might expect the S-cone luminance signal to be an OFF signal. Yet the primary S-cone pathway through the retina is an ON pathway mediated by S-cone bipolar cells (Kouyama & Mashak, 1992; Mariani, 1984) and the distinctive bistratified "blue–yellow" ganglion cells (Calkins, Tsukamato, & Sterling, 1998; Dacey & Lee, 1994; Dacey & Packer, 2003; Herr, Klug, Sterling, & Schein, 2003) that project to the koniocellular layers of the LGN (Hendry & Reid, 2000; Martin, White, Goodchild, Wilder, & Sefton, 1997; Tailby, Solomon, & Lennie, 2008). Moreover, this pathway is usually associated with chromatic perception rather than luminance perception,

(e.g., Dacey & Lee, 1994). Other sparse but distinct populations of retinal ganglion cells with S-cone input have recently been identified—thanks to a new method using the retrograde tracer rhodamine-dextran injected into the LGN: one is a large-field bistratified cell with an S-ON input, and two are monostratified "giant" ganglion cells with S-OFF inputs, some of which are melanopsin-expressing and show intrinsic photosensitivity (Dacey et al., 2005; Dacey & Packer, 2003; Dacey, Peterson, Robinson, & Gamlin, 2003). These giant cells, although they have S-OFF inputs, also seem an unlikely substrate for the S-cone luminance signal given that there is no obvious mechanism by which they could null the L- and M-cone luminance signals typically assumed to be transmitted in the magnocellular stream. Despite the lack of a distinct anatomical substrate, S-OFF signals have been reported in recordings from some ganglion and/or LGN cells in the magnocellular (Derrington, Krauskopf, & Lennie, 1984), parvocellular (Derrington et al., 1984; Marrocco, 1976; Valberg, Lee, & Tigwell, 1986; Wiesel & Hubel, 1966), and koniocellular (Szmajda, Buzás, FitzGibbon, & Martin, 2006; Tailby et al., 2008) streams—see also De Monasterio and Gouras (1975), De Monasterio et al. (1975b), and Zrenner and Gouras (1981). Thus an S-OFF signal can potentially be found in any stream. The origin of S-OFF signals has been linked to contacts between S-cones and a class of midget S-OFF bipolar cells identified in anatomical reconstructions (Klug, Herr, Ngo, Sterling, & Schein, 2003), but these contacts have not been found in other studies (Lee, Telkes, & Grünert, 2005).

For the S-cone signals to cancel the L- and M-cone flicker signals suggests that at some stage in the visual system the signals must interact, and that the effects of that interaction or interactions must be transmitted to higher levels. If, for the sake of argument, we accept the idea, at least for luminance *flicker* perception, that the psychophysical luminance channel corresponds to activity in the magnocellular pathway (e.g., Kaplan, Lee, & Shapley, 1990; Lee, Martin, & Valberg, 1988; Lee, Pokorny, Smith, Martin, & Valberg, 1990; Livingstone & Hubel, 1987), then we might expect the effect of the S-cone luminance signal to appear as an S-OFF signal in the magnocellular stream. Such a signal, as well as an S-ON signal in some cells, has been reported in magnocellular LGN by Derrington et al. (1984). There remains, however, a good deal of controversy about S-cone inputs to magnocellular cells. While some authors find no S-cone contribution to such cells (Dacey & Lee, 1994; Lee et al., 1988; Sun, Smithson, Zaidi, & Lee, 2006), other authors find S-ON rather than S-OFF contributions (Chatterjee & Callaway, 2002; De Monasterio, 1978). Chatterjee and Callaway (2002), in particular, reported that the S-ON input to magnocellular cells was as high as 10% of the total cone input. Their finding, however, has been challenged by Sun et al. (2006), who reported that the S-cone stimulus used by Chatterjee and Callaway did not isolate the S-cone response.

The presence of an S-cone signal in magnocellular cells is consistent with the psychophysical evidence, but the observation that the signal is excitatory presents a difficulty. It should be noted, however, that at some temporal frequencies and intensities the S-OFF signal can be easily be mistaken for an S-ON signal because of its delay combined with its signal inversion. For example, at lower S-cone adaptation levels than those used here S-OFF signals as low as 6 Hz would can be synergistic with 6-Hz L- and M-cone signals (see Figures 1–3 of Stockman et al., 2007).

Can we infer anything else about the likely substrate of the S-cone luminance signal from our results? We believe that three findings are suggestive: First, the substantial delay of the S-cone signal suggests that the S-OFF signal is pooled over a relatively wide field. In terms of a time delay, our data suggest a signal delay of c. 25 ms, which is considerably more than that of typical center-surround delays in parvocellular cells of 8 ms or less (e.g., Benardete & Kaplan, 1999; Lee, Martin, & Valberg, 1989; Smith, Lee, Pokorny, Martin, & Valberg, 1992). Second, the S-cone contribution seems to be somehow gated by signals from the L- and M-cones, which suggests that the S-OFF signal may constitute a spatially extended inhibitory surround. Third, the S-cone luminance input is not unique, because an inverted M-cone signal is also found with very similar phase characteristics (see Figure 7 and Stockman & Plummer, 2005a, 2005b), which suggests that the mechanism of surround inhibition pools signals from other cone types.

We speculate that a plausible substrate for the sluggish S-cone luminance input (and its M-cone compatriot) might be horizontal cells. H1 and H2 horizontal cells both contact M- and L-cone pedicles, while 15% of H1 cells and 100% of H2 cells contact S-cone pedicles (Ahnelt & Kolb, 1994; Goodchild, Chan, & Grünert, 1996). Physiologically, the S-cone response was found only in H2 cells (Dacey, Lee, Stafford, Pokorny, & Smith, 1996), which suggests that they might be the substrate of the S-cone luminance contribution.

Conclusions

An S-cone luminance signal with a characteristic phase response can be identified in flicker photometric measurements made on adapting backgrounds from 491 nm to long wavelengths provided that the adapting background exceeds a criterion radiance. The change in criterion radiance with background wavelength can be described by a spectral sensitivity that is a linear combination of the L- and M-cone spectral sensitivities. We hypothesize that the criterion radiance reflects a gating of the S-cone luminance input, which remains silent unless the L- and M-cones are excited above a certain level. We hypothesize that the L- and M-cone signals produced by the steady adapting backgrounds somehow gate the S-cone

luminance signals. The modulation or gating of the L- and M-cone signals by the S-cone signals may be indirect and effected within, for example, a pooled gain control, with the result that increases and decreases in the S-cone signal cause decreases and increases, respectively, in the gain of the L- and M-cone signals (and thus the size of the signal generated by the steady background). A plausible substrate of this mechanism may be horizontal cell feedback.

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