

THE TEMPORAL PROPERTIES OF THE HUMAN SHORT-WAVE PHOTORECEPTORS AND THEIR ASSOCIATED PATHWAYS

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Abstract—Flicker modulation sensitivity measurements made on high intensity orange steady backgrounds indicate that signals from short-wavelength sensitive cones (*S*-cones) have access to two pathways. At low *S*-cone adaptation levels the frequency response falls quickly with increasing frequency, but at higher adaptation levels it extends to much higher frequencies. At these higher *S*-cone adaptation levels, the following procedures can selectively expose either a process sensitive to low frequencies or one more sensitive to higher frequencies: (1) at high flicker frequencies, the *S*-cone signal can be nulled by a long-wavelength sensitive cone (*L*-cone) signal of suitable amplitude and phase, but at low frequencies a residual flicker persists; the modulation sensitivity for the residual flicker is lowpass in shape with a rapid decline in sensitivity with increasing flicker frequency; (2) sensitivity to flicker in the presence of a 17 Hz *S*- or *L*-cone mask is also lowpass with a similarly steep loss of high frequency sensitivity; yet (3) sensitivity to flicker during transient stimulation of the *S*-cones at 0.5 Hz is comparatively wideband (and slightly bandpass) in shape. The *S*-cone signal produced by the high frequency process is almost as well-maintained towards high frequencies as *M*- and *L*-cone signals. Furthermore, it is capable of participating in flicker photometric nulls with *M*- and *L*-cone signals. At low frequencies, however, when the low frequency *S*-cone signal is also present, satisfactory nulls can not be found. From these and phenomenological considerations, we identify the low and high frequency *S*-cone processes as *S*-cone inputs to the chromatic and luminance pathways, respectively. The phase adjustments needed to optimize flicker photometric nulls reveal that the *S*-cone input to the luminance pathway is actually *inverted*, but this is demonstrable only at relatively low frequencies: at medium or high frequencies the *S*-cone influence can be synergistic with that of the other cone types because of a delay in the transmission of *S*-cone signals.

Color vision Short-wavelength sensitive cones Blue cones Flicker sensitivity Phase lags
Luminance

INTRODUCTION

In this paper we will be concerned mainly with the dynamics of the visual response to flickering lights detected only by the short-wavelength sensitive (*S*) cones.

Vision that relies upon signals from the *S*-cones is strikingly impoverished. In the temporal domain subjects exhibit a lower c.f.f. or critical flicker fusion frequency (Brindley, du Croz & Rushton, 1966; Marks & Bornstein, 1973), and a rapid decline in modulation sensitivity with increasing temporal frequency (Kelly, 1974; Wisowaty & Boynton, 1980). These deficits could plausibly be attributed to an idiosyncrasy of the *S*-cones themselves, or of the post-receptoral pathways through which the *S*-cone signals pass.

The signals from the three cone types are thought to be either differenced and conveyed through *chromatic* pathways or added together

and conveyed through the *luminance* pathway. The recoding of photoreceptor signals into chromatic and luminance signals was first proposed on psychophysical grounds (Donders, 1981), and it is still the psychophysical evidence that supports it most clearly (see the General Discussion below). For example, at low frequencies the alternation of differently colored lights is subjectively registered as a fluctuation in both color and luminance, but as the frequency is increased the chromatic component subjectively drops out leaving only achromatic flicker (Ives, 1912). This is taken as evidence that the chromatic pathway is unable to follow rapid flicker. The luminance flicker that remains at high frequencies can be cancelled or *nulled* simply by adjusting the relative intensity of the two alternating lights (Ives, 1912). The fact that these nulls can be set independently of the color of the alternating lights is consistent with a model in which high frequency flicker is detected only by one single,

color blind "luminance" channel or pathway that simply adds together cone signals.

It has always been assumed that the *S*-cones contribute little to the luminance pathway, and many psychophysical theorists have thought their contribution to be zero (Schrödinger, 1925; Luther, 1927; Guth, Alexander, Chumby, Gillman & Patterson, 1968; Smith & Pokorny, 1975). In support of this position, there is evidence that *S*-cone signals do not contribute to flicker nulls or the related minimum-motion nulls (Smith & Pokorny, 1975; Eisner & MacLeod, 1980; Cavanagh, MacLeod & Anstis, 1987), both of which are supposed to reflect the cancellation of signals within the luminance pathway. If *S*-cone signals are confined to chromatic pathways, their sluggishness (a term we use to denote their longer persistence and their associated inability to track rapid flicker) may reflect a sluggishness of that type of pathway, rather than a sluggishness of the *S*-cone response itself (Mollon & Krauskopf, 1973; Smith, Bowen & Pokorny, 1984). And some evidence does suggest that *S*-cone signals do pass along a pathway with distinctive properties, at least in the earliest postreceptoral stages (Moreland, 1969; Valeton & Van Norren, 1979; Pugh & Mollon, 1979; Mariani, 1984).

Using very intense long wavelength steady backgrounds to suppress selectively the sensitivities of the *M*- and *L*-cones, we have been able to follow the temporal sensitivity of the *S*-cones at higher luminances and flicker frequencies than has been possible before. The results suggest that *S*-cone signals can be registered through either a brisk or a sluggish pathway. The different properties of these two pathways, in particular the fact that the brisk *S*-cone signal can contribute to flicker photometric nulls, make them plausibly identifiable with the above-mentioned luminance and chromatic pathways.

The modulation sensitivity for *S*-cone flicker detection using the brisk pathway is almost as well-maintained toward high flicker frequencies as that of the *M*- and *L*-cones. The marked loss of high frequency *S*-cone sensitivity found under more typical adaptation conditions must therefore be imposed by the pathways through which the *S*-cone signal travels rather than by the *S*-cones themselves.

To null *M*- or *L*-cone flicker with *S*-cone flicker often requires substantial adjustments in temporal phase. These adjustments reveal not only a large delay of the *S*-cone signal,

but also an unexpected feature of the *S*-cone contribution to luminance: it is negative.

GENERAL METHODS

Apparatus

The optical apparatus used in these experiments was a four-channel, Maxwellian-view system. The light source was a 1000-W xenon arc lamp. There were four achromatic lenses in the optical path of each of the four channels: two collimating and two condensing. In three of the channels the first image of the arc was focussed onto an aperture stop that restricted the diameter of the image of the arc at the pupil to less than 2 mm (no stop was needed in the fourth channel since the pupillary image was already smaller than 2 mm). The sizes of the test and field stimuli were defined by circular field stops. Shutters were placed close to the first image of the arc. They were small, mechanical shutters (Uniblitz, 6 mm aperture, Model no. 26L), which have rise and fall times of 0.6 and 0.9 msec, respectively, and are rated for frequencies up to 100 Hz. Each was run independently by separate shutter drivers connected to frequency generators (Wavetek or Heathkit). With this arrangement we could obtain reliable square-waves up to the highest frequency that we required (about 30 Hz). The optical waveforms so produced were monitored periodically using a Pin-10 photodiode (United Detector Technology) and oscilloscope. The position of the observer's head was maintained by a dental wax impression rigidly mounted on adjustable cross slides taken from a milling machine.

Test and field wavelengths were selected by use of 3-cavity, blocked interference filters with half maximum bandwidths of between 7 and 11 nm. Infra-red radiation was minimized by heat absorbing glass placed early in each beam, and a u.v. filter was placed in the intense background beam. Fixed neutral density filters (Inconel) were placed in the beams as required, and less frequently thin gelatin neutral density filters (Wratten) were used. Variable neutral density wedges were positioned in two of the test beams. These were mounted on stepping motors, and their position could be controlled by either the subject or the experimenter.

For modulation sensitivity measurements, fixed and adjustable polarizers were placed in two of the test beams. The adjustable polarizers were antagonistically yoked, so that increasing

the steady component reduced the flickering component, and vice versa. We could thus exchange a steady light with a flickering light and maintain the same time-averaged intensity.

Procedures

To desensitize selectively the *M*- and *L*-cones, we superimposed all our test stimuli, except where noted otherwise, on a steady 617 nm background providing $10^{12.04}$ quanta sec $^{-1}$ deg $^{-2}$ at the cornea, a visual illuminance of $10^{5.52}$ phot. td. The observer fixated the center of the fields. The test fields were 3 deg in diameter, and the background field was 5.8 deg in diameter. All subjects light adapted to test and background fields for at least 2 min prior to any data collection. Details of the various experimental procedures are given below.

Calibration

The radiant fluxes of test and background fields were measured at the plane of the observer's entrance pupil with an EG&G Radiometer that had been cross-calibrated with an independently-calibrated Pin-10 silicon photodiode and linear operational amplifier. The measured energy values were converted to quantal values. Photopic troland values, where given, were obtained by applying the appropriate formula to the quantal values. Neutral density filters, fixed and variable, were calibrated *in situ* for all test and field wavelengths used. Particular care was taken in calibrating the interference filters: a spectroradiometer (E,G & G) was used to check for any side-band leaks, and to measure the center wavelength and the bandwidth at half amplitude of each interference filter *in situ*. The spectroradiometer was calibrated against a reference mercury lamp, and a calibrated light source.

Subjects

Four male observers (AS, DD, DM and PY) were used in these experiments: the authors (AS, DM and DD), and an undergraduate (PY) who remained naive as to the purposes of these experiments during early runs. Observer DM is deuteranomalous. The other three subjects enjoyed normal color vision. AS and DD are emmetropic. DM is slightly hypermetropic, but required no correction lens. PY was myopic, and wore colorless contact lenses during the experiments.

RESULTS AND DISCUSSION

Experiment I: *Flicker Sensitivity Measurements*

To isolate the responses of the *S*-cones, we present violet test lights in the center of a very intense orange background field. To assess the extent of *S*-cone isolation under these conditions, we measured flicker detection sensitivity, flicker photometric sensitivity and critical flicker fusion frequency at different test wavelengths. The change in sensitivity with test wavelength should be consistent with an *S*-cone spectral sensitivity, if *S*-cones do mediate detection.

Methods

For flicker detection spectral sensitivity measurements, a 3 deg diameter test field of variable wavelength, flickering at either 5, 12.5 or 20 Hz, was presented in the center of the $10^{12.04}$ quanta sec $^{-1}$ deg $^{-2}$, 5.8 deg diameter 617 nm background. The subject set the radiance of the flickering test light so that the flicker was at threshold.

For flicker photometric measurements, an additional 561 nm, flickering test field was added, and was set by the subject to be just above flicker threshold (usually about 0.2 log units above threshold) or four times flicker threshold. The standard test field and the variable test field were flickered out-of-phase at 16 Hz. At each test wavelength, the subject varied the radiance of the variable-wavelength test field until it nulled the flicker of the standard.

For c.f.f. measurements, 437 or 468 nm test fields were presented in the center of 617 nm background fields. At each test field intensity the subject adjusted the flicker frequency of the test light until the flicker was just at threshold (see the inset of Fig. 2).

Data points shown in Figs 1 and 2 are averaged from four settings made during each of two separate sessions.

Results

Figure 1(a) shows flicker-detection spectral sensitivities measured on the standard orange background at 5 Hz (squares), 12.5 Hz (circles) and 20 Hz (triangles) for subject AS. DD and PY gave similar results. The spectral sensitivity at short wavelengths is consistent with that of the *S*-cones as exemplified by Stiles' π_3 sensitivity (Stiles, 1978; continuous curves, our Fig. 1). Sensitivity is determined by the *S*-cones up to nearly 543 nm at 5 Hz, and up to 500 nm at 20 Hz. Under these conditions, the fitted cone

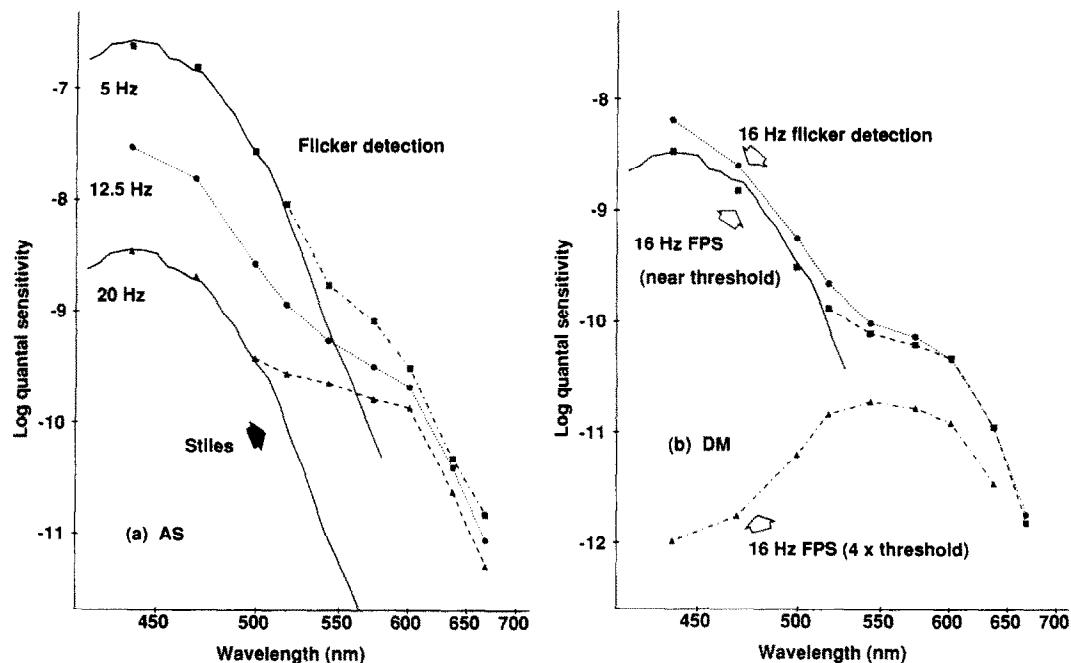


Fig. 1. (a) Flicker spectral sensitivities measured at frequencies of 5 (■), 12.5 (●) and 20 Hz (▲) for subject AS. The two solid lines represent Stiles' π_3 aligned vertically to fit the 5 and 20 Hz data points at short-wavelengths. (b) Comparison of 16 Hz flicker detection spectral sensitivity (●) with 16 Hz flicker photometric sensitivity obtained using a 561 nm standard of a radiance either close to flicker threshold (■) or four times above threshold (▲). The solid line represents part of Stiles' π_3 aligned vertically to fit the near-threshold FPS data.

spectral sensitivity templates suggest that the *S*-cones are more than 1000 times more sensitive to 5 Hz, 437 nm flicker than the *M*- or *L*-cones and more than 100 times more sensitive to 20 Hz flicker. 25 Hz, 437 nm flicker is also detected by the *S*-cones, but conventional threshold intensity measurements at that frequency are impractical.

From the c.f.f. data shown in Fig. 2 (below), it can be seen that 25 Hz is seen over only a limited range of test radiances and that increasing or decreasing the test radiance could bring the 25 Hz flicker to threshold. The c.f.f. measurements, reported below, confirm that frequencies up to 26 Hz are detected by the *S*-cones.

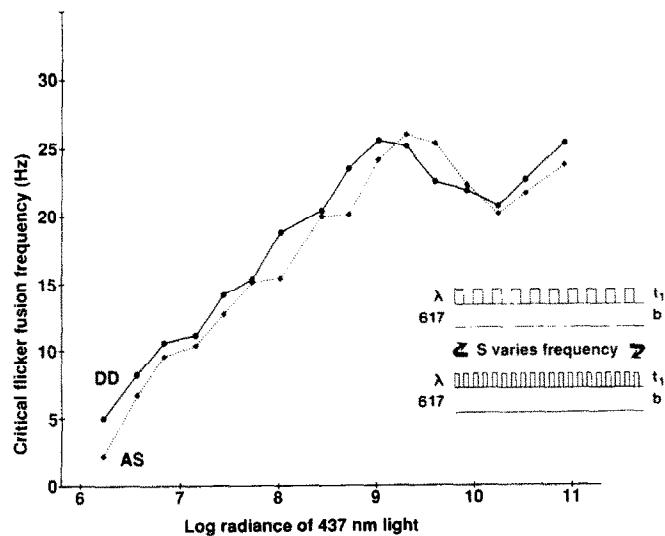


Fig. 2. Critical flicker fusion frequencies for AS (◆) and DD (●) measured using a 437 nm test light at a 617 nm background radiance of $10^{12.04}$ quanta sec $^{-1}$ deg $^{-2}$. Inset. Procedure: the subject varies the frequency of a single test light to find the highest at which the flickering light can be seen to flicker.

Thus the *S*-cones are capable of following frequencies that are too high to be conveyed by the type of sluggish chromatic pathway suggested by psychophysical experiments (Truss, 1957; De Lange, 1958; Wisowaty, 1981). If the high frequency *S*-cone signal is conveyed instead by a luminance pathway, the signal should be capable of cancelling *M*- and *L*-cone signals if its amplitude (and perhaps its phase) is suitably adjusted. Using a 16 Hz flicker photometric standard of 561 nm that was just above flicker threshold (the wavelength of the standard is not critical—574 and 637 nm lights were also used), we were able to make quite well-defined nulls using the radiance adjustment only. The results are shown in Fig. 1(b). The resulting spectral sensitivity (squares) follow the flicker threshold spectral sensitivity (circles) very closely, including the prominent short-wavelength peak. The *S*-cone null is dependent on the relative phase of the *S*- and *M*- or *L*-cone stimuli (see expt VII below). Furthermore, the *S*-cone stimulus can bias a null already established between *L*- and *M*-cone stimuli (Stockman & MacLeod, 1986). These properties suggest a true null, reflecting independent additive or subtractive contributions from the three cone types to a single signal or channel (according to conventional wisdom, the “luminance” channel: see General Discussion below), rather than some highly nonlinear suppressive interaction between different cone types.

If the standard 561 nm stimulus is increased further above flicker threshold, the *S*-cone influence on flicker photometric sensitivity rapidly becomes negligible, yielding a spectral sensitivity lacking the short wavelength peak (triangles). *S*-cone signals, thus, appear to be capable of cancelling *M*- and *L*-cone signals only if the *M*- and *L*-cone signals are kept within about two times threshold. Apparently the *S*-cone signal, unlike *M*- and *L*-cone signals, is—for reasons that we do not fully understand—limited to a near-threshold level. Comparable flicker photometric spectral sensitivity measurements were also obtained at 8 and 20 Hz, with essentially similar results. Flicker photometric nulls could be completed between *S*-cone lights and *M*- and *L*-cone lights at a variety of frequencies and *S*-cone adaptation levels. Commonly, the relative phase of the *S*-cone and *M*- and *L*-cone

lights had to be adjusted to complete the null. These adjustments are described in expt VII, below.

To extend our flicker sensitivity measurements to the limits of *S*-cone flicker detection and to higher 437 nm radiances, we measured critical flicker fusion frequency as a function of 437 nm test radiance on the standard orange field. The results for AS (diamonds) and DD (circles) are shown in Fig. 2. The two c.f.f. functions rise slowly to a shallow maximum at about 26 Hz, but thereafter drop slightly reaching a minimum at about 20 Hz, before rising again at the highest test radiances. For AS the c.f.f. function was measured at other test wavelengths and at other orange background radiances. These measurements show that the c.f.f. function shown in Fig. 2, including the downturn or saturation, has an *S*-cone spectral sensitivity. Only the final rise in c.f.f. has a spectral sensitivity consistent with detection by *M*-cones. At lower orange background radiances, the transition from *S*-cone to *M*-cone flicker detection is accompanied by a sharp change in the slope of the c.f.f. function, which occurs at increasingly high test radiances as the orange background radiance is increased. On our standard orange background (Fig. 2), the c.f.f. data do not show evidence of this transition until the 437 nm radiance approaches $10^{10.5}$ quanta sec⁻¹ deg⁻², well above the highest 437 nm radiance used in the following experiments.*

Experiment II: *S-Cone Modulation Sensitivities*

Square-wave *S*-cone modulation sensitivities were measured for all subjects.

Methods

To measure *S*-cone modulation sensitivity, two 437 nm test beams were used. One provided the *steady* component of the test light and the other the *flickering* component. Their radiances were set so that, as the subject varied *S*-cone modulation by moving the position of the rotating polarizers, the time-averaged 437 nm radiance remained constant (see General Methods). The subject's task was to adjust the modulation to find modulation threshold. Unless otherwise stated, the modulation sensitivities plotted in Fig. 3 and in subsequent figures are the average of four settings made during each of four (AS and DD) or three (DM and PY) separate sessions. We used square-wave modulation produced by mechanical shutters throughout.

*Although the standard orange background was sufficiently intense to saturate the rod mechanism (Aguilar & Stiles, 1954), as a control for rod intrusion we measured the asymptote of the *S*-cone c.f.f. during the rod recovery of dark adaptation. There was no change in c.f.f.

The insertion of additional fixed and rotating polarizers to produce sinusoidal modulation would have restricted our measurements to lower, and less interesting, short-wavelength test radiances (see the inset of Fig. 3).

Modulation is defined as:

$$\frac{I_{\max} - I_{\min}}{I_{\max} + I_{\min}} \quad (1)$$

where I_{\max} is the maximum cone excitation and I_{\min} the minimum.

We were careful not to expose subjects to unnecessarily high modulations of low temporal frequencies, since we found, particularly for

inexperienced subjects who tended to make large excursions above threshold, that such exposure could elevate subsequent threshold settings.

We used time-averaged 437 nm radiances of $10^{7.25}$, $10^{8.13}$ and $10^{9.09}$ quanta sec $^{-1}$ deg $^{-2}$. We will refer to these levels in the text and figures as "low", "medium", "high" and "saturating" S-cone adaptation levels. S-cone modulation sensitivity functions at these four levels were measured on the standard orange background. For AS and DD only, modulation sensitivities at the low S-cone level were also measured on a less intense ($10^{10.35}$ quanta sec $^{-1}$ deg $^{-2}$) orange background field.

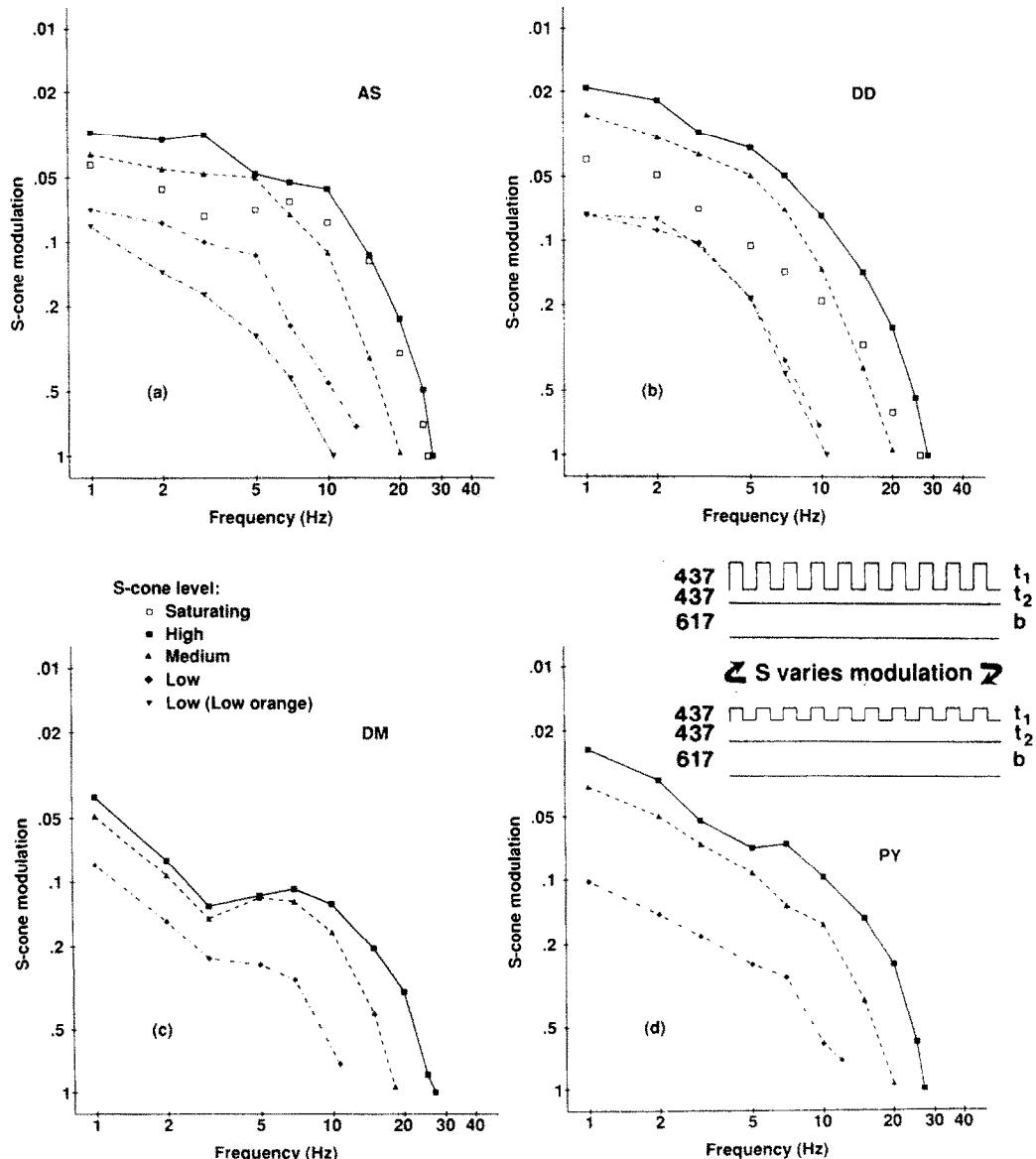


Fig. 3. Temporal modulation sensitivities for AS (a), DD (b), DM (c) and PY (d) obtained at 437 nm radiances of $10^{7.25}$ (◆), $10^{8.13}$ (▲) and $10^{9.09}$ (■) quanta sec $^{-1}$ deg $^{-2}$. (▼) (a, b) comparable to (◆) but with a dimmer ($10^{10.35}$ quanta sec $^{-1}$ deg $^{-2}$) orange background. Inset. Procedure: the subject varies the modulation at constant time-averaged radiance to find the modulation threshold for each of a range of flicker frequencies.

In our figures we plot "S-cone modulation". To calculate this we took into account the direct effect of the 617 nm background on the S-cones. An extrapolation to 617 nm of Stiles' short-wavelength π_3 field sensitivity function yields a difference of about $10^{5.05}$ (using the steepest part of the long-wavelength π_3 slope) between 437 and 617 nm. Another method is to fit the standard rod sensitivity function, corrected for lens and macular pigment absorption, to the entire Stiles π_3 function by transposing it on a wavenumber axis. This gives less weight to longer wavelengths where S-cone isolation is more difficult to maintain, and yields a sensitivity difference of about $10^{5.50}$. Direct measurements of monkey cone spectral sensitivities, corrected for pre-retinal absorption and self-screening (Baylor, Nunn & Schnapf, 1987, Fig. 6), yield a value of about $10^{5.05}$, but this figure is strongly dependent on the choice of correction factors. We have chosen an intermediate value of $10^{5.20}$ as the sensitivity difference between 437 and 617 nm. Thus our $10^{12.04}$ quanta sec $^{-1}$ deg $^{-2}$ 617 nm background is assumed equivalent in its direct effects on the S-cones to a 437 nm field of $10^{6.84}$ quanta sec $^{-1}$ deg $^{-2}$. When our dimmest test field is presented against our most intense background, allowance for the background's reduction of the S-cone modulation displaces the modulation sensitivities vertically upwards by 0.14 log units; this displacement has been made in the appropriate figures (under other conditions the correction is negligible).

Results

Figure 3 shows temporal modulation sensitivities as AS (a), DD (b), DM (c) and PY (d) measured at low (diamonds), medium (triangles) and high (squares) S-cone adaptation levels. For AS and DD two additional functions are shown. One (open squares) is measured at the saturating S-cone level. The other (inverted triangles) is measured at the low S-cone level, but on the low intensity orange background.

As the S-cone adaptation level is increased, there is a relative improvement in modulation sensitivity to higher frequencies, as well as an overall improvement in sensitivity. At the lowest S-cone levels (inverted triangles and diamonds), sensitivity falls off so rapidly that sensitivity cannot be measured beyond about 10 Hz. These functions are similar in shape to chromatic M- and L-cone temporal sensitivity functions (DeLange, 1958; Wisowaty, 1981), and S-cone functions measured by Wisowaty and Boynton

(1980). At the high S-cone level (squares), sensitivity can be measured up to nearly 28 Hz in experienced subjects, and is quite unlike the low level functions, being more extended to high frequencies.

At the saturating S-cone adaptation level (open squares) corresponding to the dip in the c.f.f. vs log I curves of Fig. 2, the modulation sensitivities for AS and DD are depressed by about 0.2 log unit across the whole frequency range, compared to the next lowest level (squares). A saturation of the short-wave mechanism has also been reported at comparable adaptation levels (Mollon & Polden, 1977a; Stromeyer, Kronauer & Madsen, 1978) for flash detection.

All of our subjects reported that at higher S-cone adaptation levels there is a change in the mode of detection as the frequency is increased. Between 1 and 3 Hz flicker is seen as a periodic yellowing or blueing of the test field at the flicker frequency, whereas above 7 Hz flicker was seen as a disturbance of the field without any definite color change (i.e. it was similar in appearance to high flicker frequencies detected by M- and L-cones). These subjective impressions suggest a change from a chromatic mode of detection at low frequencies, to an achromatic mode of detection. Despite the phenomenological evidence, there is little support for two modes of detection in the shapes of the higher level modulation sensitivity functions for AS, DD or PY, except for the slight inflection in the high level data for PY. But our deuter-anomalous observer, DM, shows a pronounced inflection in his data at all low, medium and high S-cone levels.

Experiment III: Modulation Sensitivities Measured in the Presence of Masking Stimuli

S-Cone modulation sensitivities

If there are two S-cone processes with markedly different temporal properties, corresponding perhaps to S-cone inputs to chromatic and luminance pathways, then it may be possible to favor detection by one of them by adding a masking stimulus of a frequency that selectively stimulates the other process. Consistent with this prediction, we find that 17 Hz masks can significantly reduce S-cone sensitivity to higher temporal frequencies, while having a much smaller effect at lower frequencies.

Methods. S-Cone modulation sensitivities were

measured in the presence of flickering *S*-cone or, more commonly, *L*-cone masks. All of these measurements were made on the standard orange adapting field.

To produce the *S*-cone mask the formerly steady component of the 437 nm test field was doubled in intensity and flickered at 17 Hz (thus maintaining its time-averaged intensity). Thus at the high *S*-cone level the amplitude of the mask was $10^{9.39}$ quanta sec $^{-1}$ deg $^{-2}$ or less. This arrangement causes the amplitude of the flickering mask to decrease as the test frequency modulation is increased, but in the results shown here the mask was always more than 70% of the total 437 nm light [see inset (a) of Fig. 4].

To produce the *L*-cone mask, a third 637 nm test field was added to the steady and flickering 437 nm test fields and was flickered at 17 Hz. The amplitude of the mask was set for each subject by flicker photometrically equating it with the 437 nm, *S*-cone mask (set to an amplitude $10^{9.39}$ quanta sec $^{-1}$ deg $^{-2}$). The 637 nm mask was about two times flicker threshold. For details see the inset (b) of Fig. 4.

Whichever mask was used, the subject's task was to set the 437 nm modulation, seen in the presence of the mask, to threshold. As the test frequency approached the mask frequency, the subject was able to detect the presence of the test by the beat frequency produced by test and masking lights. The test frequency was therefore kept at or below 10 Hz.

Results. Figure 4 shows the results of an experiment in which both 17 Hz *S*-cone (circles) and *L*-cone (squares) masks were used. The *S*-cone and *L*-cone masks were also combined out-of-phase (diamonds). Since they had been flicker-photometrically equated, this nulled the masking flicker. Finally, the continuous curve in Fig. 4 is the unmasked sensitivity (Fig. 3a, squares).

Both the *S*-cone and *L*-cone masks produce a sensitivity loss that *increases with frequency*, resulting in modulation sensitivity functions that are lowpass in shape. The main difference between the two functions is that the *S*-cone mask produces an additional sensitivity loss that is independent of frequency. The *L*-cone mask, at its chosen near-threshold amplitude, has little effect on *S*-cone modulation sensitivity at 1 Hz, but has a surprisingly large suppressive effect at high frequencies (compare continuous line with squares). We propose that these lowpass functions reflect the sensitivity of the low frequency *S*-cone process, which is revealed here because the masks selectively suppress a second process more sensitive to high frequency flicker.

As this interpretation might suggest, presenting the two masks together in cancellation phase partially restores sensitivity to intermediate frequencies (diamonds). The reappearance of a shoulder in the data probably reflects the re-emergence of the high frequency *S*-cone process. Since cancellation of the masking flicker does not

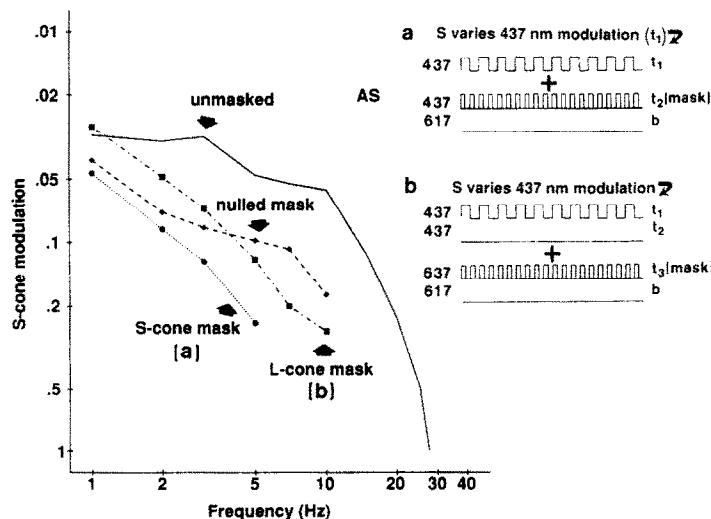


Fig. 4. Modulation sensitivities for AS measured in the presence of a 17 Hz, 437 nm mask (●), in the presence of a 17 Hz, 637 nm mask (■), and in the presence of both masks presented out of phase so that the masking flicker was nulled (◆). The 437 nm time-average radiance was $10^{9.09}$ quanta sec $^{-1}$ deg $^{-2}$ (for details, see text). The continuous curve represents conventional modulation sensitivities for AS measured at the same level (Fig. 3a, ■). *Inset.* Procedure: the subject varies modulation to find modulation threshold, but the settings are made in the presence of a 17 Hz mask, stimulating *S*-cones (a) or *L*-cones (b).

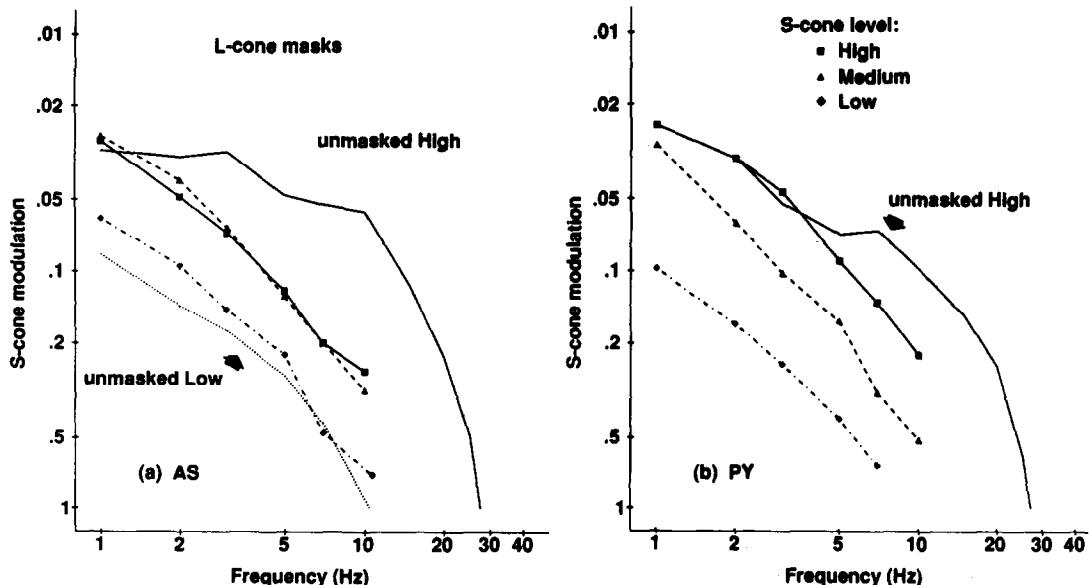


Fig. 5. Modulation sensitivities for AS (a) and PY (b) in the presence of a 17 Hz, 637 nm mask at 437 nm radiances of $10^{7.25}$ (\blacklozenge), $10^{8.13}$ (\blacktriangle) and $10^{9.09}$ (\blacksquare) quanta sec $^{-1}$ deg $^{-2}$. The curves without symbols are taken from Fig. 3. The dotted curve for AS represents conventional (unmasked) modulation sensitivities measured at the low 437 nm radiance ($10^{7.25}$ quanta sec $^{-1}$ deg $^{-2}$) on the less intense orange background ($10^{10.35}$ quanta sec $^{-1}$ deg $^{-2}$, 617 nm). The solid curves represent conventional modulation sensitivities at the high 437 nm radiance ($10^{9.09}$ quanta sec $^{-1}$ deg $^{-2}$) on the intense orange field.

restore the additional low frequency sensitivity loss caused by the *S*-cone mask, that loss presumably takes effect at an early site before the signals from the *L*-cone and *S*-cone masks come together.

In the remainder of the masking experiments, only the *L*-cone mask was used. Figure 5 shows the masked modulation sensitivities for AS (a) and PY (b) obtained at low (diamonds), medium (triangles) and high (squares) *S*-cone adaptation levels on the standard orange field. The dotted curve in Fig. 5a is the unmasked low *S*-cone level modulation sensitivity function measured on the dim orange background (inverted triangles, Fig. 3a), and the continuous curves are the high *S*-cone level functions measured on the standard background (Fig. 3a, d, squares).

The six masked sensitivity functions shown in Fig. 5 are similar in shape despite large changes in the *S*-cone adaptation level. This invariance of shape suggests that light adaptation changes the gain of the low frequency *S*-cone process, with little change in its temporal response properties. This intensity-invariance is in marked contrast to the intensity-dependence we observe (for instance, in Fig. 3) when no masking light is present and both low and high frequency *S*-cone processes are presumably involved. Moreover, the masked sensitivity functions are quite similar in shape to those modulation

sensitivity functions measured *without* a mask at the lowest level that we used (dotted curve, Fig. 5a). Evidently, then, the low frequency *S*-cone process dominates at low adaptation levels, while at higher levels the high frequency process becomes increasingly influential.

L-Cone modulation sensitivities

No frequency-selective suppression of comparable magnitude was found when *L*-cone test and masking stimuli are used. Not surprisingly, perhaps, the near-threshold, 17 Hz *L*-cone mask has only a relatively small effect on *L*-cone sensitivity below 10 Hz.

L-Cone modulation sensitivity was measured by replacing the 437 nm test lights with a 637 nm test light (see the Methods section of expt VI for more information).

Figure 6 shows conventional *L*-cone modulation sensitivities (squares) and those measured in the presence of the 17 Hz *L*-cone mask (circles) for AS (a) and DD (b).

For DD and AS, the near-threshold *L*-cone mask does comparatively little to distort the *L*-cone modulation sensitivity function, even though a similar mask caused *S*-cone sensitivity to fall precipitously in the same range of frequencies. DD shows no loss of sensitivity over the entire range of frequencies shown in the figure. AS does show a slight loss of sensitivity,

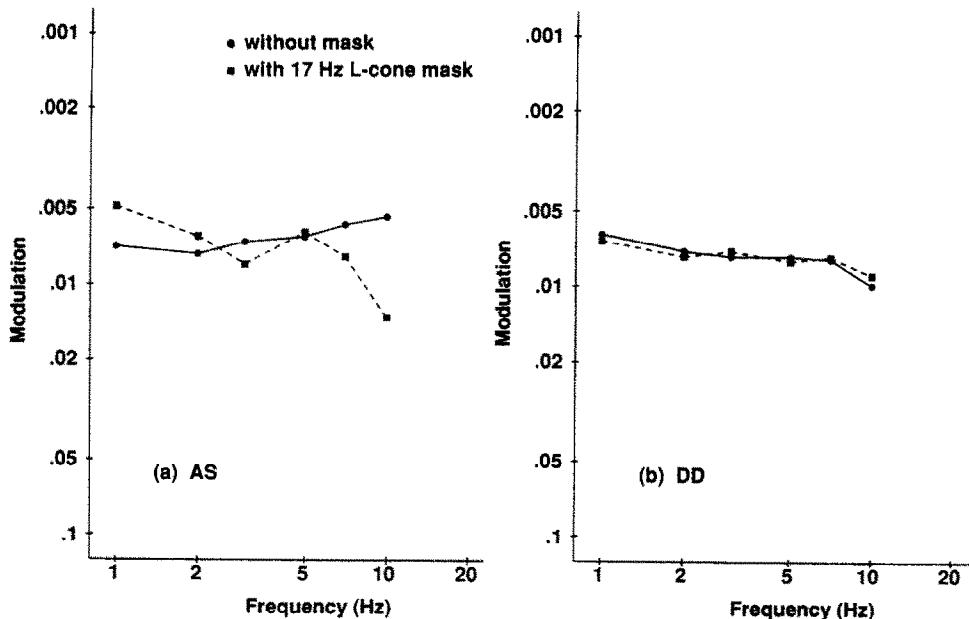


Fig. 6. Modulation sensitivities for AS (a) and DD (b) measured using a 637 nm light instead of a 437 nm light. The circles represent conventional modulation sensitivities, and the squares modulation sensitivities obtained in the presence of a 656 nm, 17 Hz mask.

but it is not substantial until about 10 Hz, which is in contrast to his *S*-cone modulation sensitivities that already show a four-fold loss of sensitivity by 7 Hz (see Fig. 5a).

Although it is tempting to take the greater elevation of *S*-cone threshold in these experiments as evidence for a suppression that acts selectively on *S*-cone signals, another interpretation seems equally likely: it might be a consequence of the above-noted failure of the brisk *S*-cone signals to grow very much above their (unmasked) threshold strength, despite substantial increases in stimulus amplitude. As a result, the *S*-cone flicker signal may never sufficiently increase as stimulus modulation increases to compensate for a relatively small masking effect of the *L*-cone flicker. The continued presence of the *S*-cone flicker signal—albeit below threshold—is suggested by easily detectable beats between the 17 Hz *L*-cone mask and *S*-cone flicker of nearby frequency.

Whatever the cause of the masking effect of near-threshold *L*-cone flicker, it is largely unique to *S*-cone mediated detection. Thus, the distortions are unlikely to be the result of a simple frequency-selective masking within a single pathway, in which the masking effect declines as the test frequency is made higher or lower than the masking frequency. Together, our results suggest that the suppressive effect of the *L*-cone masks is exerted mainly on the high

frequency *S*-cone process, the low frequency one being spared.

Subjectively, the effect of the rapidly flickering *L*-cone mask in the *S*-cone detection task was to enforce reliance on chromatic *S*-cone flicker, which could be easily distinguished from the colorless masking flicker. In other observations, we have used a two-alternative temporal forced-choice procedure in which the subject had to distinguish between an *S*-cone flicker pulse and a steady light of the same time-average intensity. In these experiments the *L*-cone mask seemed to be much less effective in raising *S*-cone threshold, but the reason for this was not because of an enhanced detectability of the *S*-cone flicker *per se*, rather it was because the flicker pulse appeared less bluish than the steady field. The subject was able to distinguish between the two alternatives on the basis of the color change. This cue was not as salient in the self-setting adjustment task, where the *S*-cone flicker was continuously present; hence the self-adjusted thresholds may actually be a truer reflection of the observers' sensitivity to flicker as such.

Experiment IV: *S*-Cone Modulation Sensitivities for Residual Flicker after Nulling by *L*-Cone Stimuli

In the previous experiment we showed that 17 Hz *L*-cone masking flicker can cause a disproportionately large loss of *S*-cone sensitivity

to high frequency flicker. We interpret this as showing that 17 Hz flicker can mask the response of an *S*-cone process more sensitive to higher frequencies, while leaving a lower frequency process relatively unaffected. In this experiment we use an alternative method to estimate the sensitivity and frequency response of the low frequency *S*-cone process.

The results of expts I and VI (below) show that *S*-cone flicker can cancel *L*- (or *M*-)cone flicker so as to produce a subjective flicker null. With suitable adjustments of relative phase and amplitude, near-perfect flicker cancellation can be achieved from medium frequencies up to the highest frequencies that the *S*-cones can follow, but good cancellation becomes difficult or impossible to obtain at low frequencies. Such a breakdown of flicker cancellation is consistent with our two process model, since the *S*-cone signals produced by the two processes are likely to require *L*-cone signals of different amplitude and phase for cancellation (particularly if, as we have suggested, the two processes correspond to *S*-cone inputs to chromatic and luminance pathways). Consequently, poor flicker nulls should be found at lower frequencies whenever the *S*-cone signals from both processes exceed threshold: some residual flicker should remain in one or other pathway whatever the relative amplitude and phase of the cancelling *S*- and *L*-cone lights. As the frequency is decreased from the c.f.f. of the high frequency *S*-cone process, perfect nulls without residual flicker should be possible until the c.f.f. of the low frequency *S*-cone process is reached, whereupon the nulls should deteriorate markedly in quality. By finding this transition frequency at various *S*-cone modulation levels, we can estimate the modulation sensitivity function of the low frequency *S*-cone process.

Methods

All measurements were made at a time-averaged 437 nm radiance of $10^{9.09}$ quanta sec $^{-1}$ deg $^{-2}$ on the standard orange adapting field. The *S*-cone modulation was fixed and the flicker frequency was reduced in 2 Hz steps from a value close to the *S*-cone c.f.f. at that particular modulation. At each frequency, the subject varied the relative phase and the intensity of a superimposed 637 nm light in an attempt to null the 437 nm flicker (see also the Methods section of expt VII). The frequency was reduced until it was no longer possible to satisfactorily null the *S*-cone flicker, there remaining clear residual

flicker even at those relative phase and intensity settings at which the subjective flicker was minimized. At each *S*-cone modulation level, we obtained an upper and lower estimate of this transition frequency. The upper limit was a frequency at which flicker cancellation was complete, and the lower limit one at which clear residual flicker remained. This procedure was repeated at a series of *S*-cone modulations down to the lowest at which reliable settings could be made. The relative phases of the *S*- and *L*-cone lights that gave rise to the best nulls in this experiment agree with those obtained in expt VII (Fig. 10).

Results

In Fig. 7, the right hand diamond of each linked pair shows the lowest frequency at which near-perfect nulls could be attained by adjusting the relative phase and amplitude of *S*- and *L*-cone lights, and the left hand diamond shows the highest frequency at which clear residual flicker was seen. The dashed line joining the mid-point of each linked pair is our estimate of the sensitivity of the low frequency *S*-cone process obtained using the "nulling" method. For comparison, the triangles show the 17 Hz "masked" *S*-cone modulation

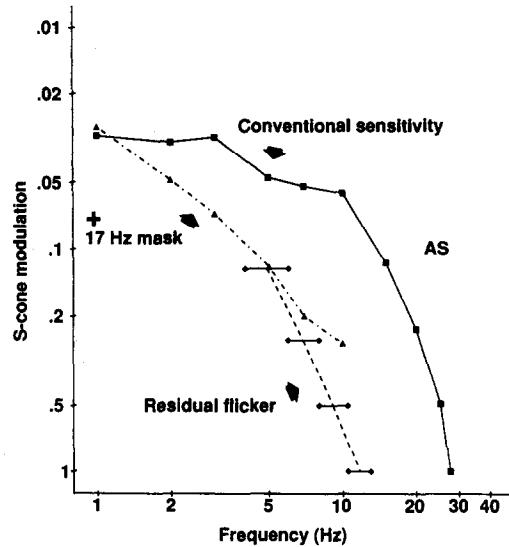


Fig. 7. The left hand diamond of each linked pair shows the highest frequency at which residual flicker could not be eliminated by varying the relative phase and amplitude of 437 nm and 637 nm lights. The right hand diamond shows the lowest frequency at which near-perfect nulls could be obtained. Measurements were made at the high *S*-cone level on the standard orange background. (■)—conventional modulation sensitivities (Fig. 3a, ■); (▲)—17 Hz masked modulation sensitivities (Fig. 5, ■).

sensitivities from Fig. 5 and the squares the conventional sensitivities from Fig. 3.

The failure to obtain good nulls using slow flicker does not by itself imply that both the fast and the slow pathways are involved, but if our two process interpretation is correct, the sensitivities defined by the masking and nulling methods should be those of the same low frequency S-cone process. And, indeed, the two estimates in Fig. 7 show rough agreement in shape and in sensitivity level. The divergence at higher frequencies may reflect the re-emergence of the high frequency S-cone process in the masked data.

We believe that the inner envelope of the masked and nulled sensitivities is a good representation of the modulation sensitivity function of the low frequency S-cone process under these conditions. The sensitivity of this process is comparable to the conventional S-cone sensitivity (squares) only at the very lowest frequency. At higher frequencies it shows a precipitous decline in sensitivity, culminating in a c.f.f. at 100% modulation of about 12 Hz, less than half the normal S-cone c.f.f. In fact, by 12 Hz the loss of sensitivity is more than 15 times greater for the low frequency S-cone process than for the conventional modulation sensitivity. The process that detects residual flicker after nulling responds very poorly to rapid flicker.

Apparently, the process that usually detects rapid flicker can be either suppressed (expt III) or nulled (expt IV) by L-cone flicker, revealing a second process. We believe this sluggish process to be chromatic, but this contention is based mainly on phenomenology. When a modulated S-cone stimulus falls outside the region bounded roughly by the triangles and diamonds of Fig. 7, the modulation appears as an achromatic disturbance with no recognizable chromatic component, whereas if it falls within this region the modulation is also seen as a chromatic alternation between shades of yellow or blue.

Chromatic modulation sensitivity for luminance-equated, red-green flicker was also measured under the same conditions of adaptation, and likewise showed a rapid loss of high frequency sensitivity—only slightly shallower than for S-cone flicker—with a c.f.f. for very bright test lights of just under 20 Hz (data not shown). Thus the limited high frequency sensitivity may be a characteristic of chromatic signals in general. The differences, in shape as well as in absolute sensitivity, between these chromatic functions and our S-cone modu-

lation sensitivity functions at high frequencies make it unlikely that chromatic pathways *per se* can be responsible for the extended high frequency S-cone sensitivity that we report here.

Experiment V: Modulation Sensitivities Measured under Transient Adaptation Conditions

We propose that the conventional modulation sensitivity functions reflect the combined sensitivities of two S-cone processes. The temporal sensitivity of the low frequency process can be revealed using either the nulling or masking methods, as demonstrated above. In this experiment, we show that the sensitivity of the high frequency process can be revealed by using slow, transient S-cone adaptation that selectively suppresses the low frequency process.

Methods

The procedure for these measurements is similar to that for the earlier modulation sensitivity measurements, described above, except that both the steady and flickering components of the 437 nm stimulus were pulsed at 0.5 Hz (1 sec ON and 1 sec OFF). The subject's task was to set modulation threshold during the one second 437 nm pulses (see the inset of Fig. 8). Measurements were made on the standard orange field.

For the pulsed measurements the stated 437 nm refers to the average 437 nm radiance during the 1 sec ON cycle. Time averaging the radiance over the OFF and ON cycles would reduce the given radiances for the pulsed conditions by 0.3 log units. We have included pulsed sensitivities at 1 Hz in these figures, but only one complete 1 Hz cycle could be viewed during each 0.5 Hz pulsed cycle. We phase-locked the cycles so that the 1 Hz test pulse occurred in the middle of the 1 sec, 0.5 Hz pulse. Thus, the 1 Hz data are not strictly comparable with data at other frequencies.

Results

Figure 8 shows as circles the square-wave modulation sensitivities measured using the pulsed-field procedure at the high S-cone adaptation level for AS (a), DD (b), DM (c) and PY (d). For comparison, the squares show the steady state modulation sensitivities (from Fig. 3), and the triangles the 17 Hz flicker masked sensitivities (from Fig. 5).

Compared to the conventional modulation

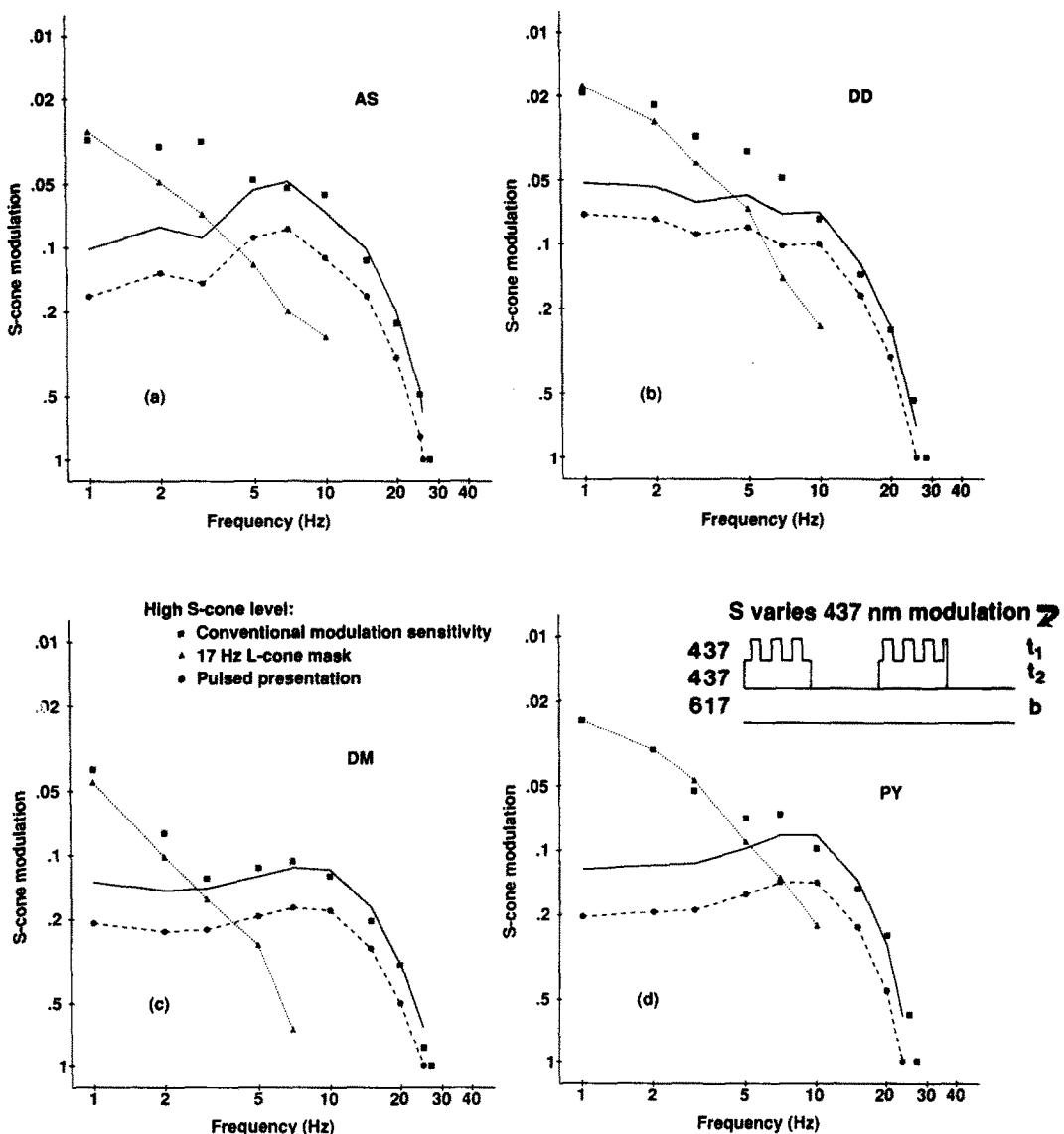


Fig. 8. Pulsed modulation sensitivities (●), 17 Hz, 637 nm mask modulation sensitivities (▲), and conventional modulation sensitivities (■) for AS (a), DD (b), DM (c) and PY (d) obtained at a 437 nm test field radiance of $10^{9.09}$ quanta sec $^{-1}$ deg $^{-2}$. The continuous line in each panel represents the pulsed modulation sensitivity function shifted upwards to align it with the conventional modulation sensitivity function at higher frequencies (see text for details). *Inset.* Pulsed modulation sensitivity procedure: the subject sets the modulation threshold with the 437 nm test stimulus pulsed at 0.5 Hz.

sensitivities, the pulsed presentation of the *S*-cone test lights produces a large loss of sensitivity at low frequencies for each subject. The loss of sensitivity at higher frequencies, on the other hand, is relatively slight.

These data, then, suggest that pulsing the *S*-cone stimulus suppresses the low frequency

S-cone process, exposing the high frequency process over a considerable range of frequencies. The temporal response of the higher frequency process so revealed is slightly bandpass in nature (despite our use of square-wave modulation).

A straightforward combination of the shapes of the masking (triangles) and pulsed (circles) functions provides a reasonable description of the conventional modulation sensitivity functions (squares) for all four subjects, but a better fit is achieved by shifting the pulsed functions upwards by small amounts, as shown by the continuous lines in Fig. 8.*

*Such a shift could be justified on the grounds that the subject adopts a higher criterion in the pulsed procedure, because the response interval is restricted to 1 sec windows. Alternatively, a pulsed field may simply be more effective than a steady field of the same intensity in raising the threshold of the high frequency *S*-cone process.

The consistency in shape of the *L*-cone masking sensitivity function across our four subjects is quite striking. Similarly, the shape of the pulsed sensitivity function is relatively invariant. Thus Fig. 8 suggests that many of the differences between the conventional modulation sensitivities can be explained by individual differences in the relative contributions of the underlying low and high frequency processes to the temporal sensitivity envelope. One clear difference between our four subjects is that the low frequency process is much more prominent for PY and DD than it is for AS and DM.

Experiment VI: Comparison Between S-, M- and L-Cone Modulation Sensitivities

The pulsed procedure apparently makes it possible to monitor *S*-cone signals through a pathway capable of following rapid flicker. The experiments with flicker photometry (Fig. 1b) and with luminance-nulled masks (Fig. 4), and other experiments to be discussed below (expt VII) suggest that this pathway is a single channel that receives input from all cone types. If so, it is of interest to compare *S*-cone modulation sensitivities with *M*- or *L*-cone sensitivities under conditions where all cones make use of this one postreceptoral pathway.

Methods

To measure *M*- or *L*-cone modulation sensitivities a flickering 574 or 637 nm test light was used, presented in the center of the standard 617 nm background. The subject set the intensity of the flickering test light, so that the flicker was at threshold. It was possible to vary the *M*- and *L*-cone modulation simply by varying the test field intensity, because the intensity of the background was much higher than that of the test fields. Thus, varying the intensity of the test field has only a small effect on the overall time-averaged intensity. (By referring to the functions as "M-" and "L-" cone functions we do not claim perfect isolation in either case, although the differences between the two do suggest that they are dominated by different mechanisms, probably deriving from different cone types.)

The modulations plotted in Fig. 9 are *M*-cone and *L*-cone modulations, calculated by taking into account the cone sensitivities to the test and background wavelengths (using Smith-Pokorny *L* and *M* sensitivity functions; Smith & Pokorny, 1975). (The *S*-cone function in the figure has

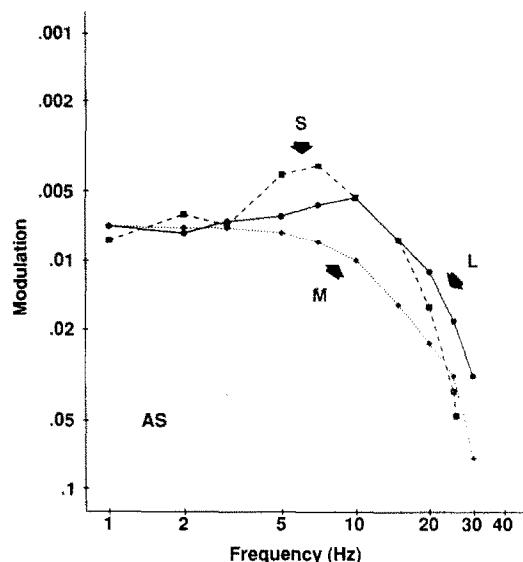


Fig. 9. Modulation sensitivities for AS measured using a 637 nm test light to favor *L*-cones (●), or a 574 nm test light to favor *M*-cones (◆). (■) show the pulsed *S*-cone modulation sensitivity function shown in Fig. 8a (■).

been displaced vertically with respect to the ordinate.)

Results

Figure 9 shows *M*-cone (diamonds) and *L*-cone (circles) modulation sensitivities for AS obtained on the standard orange field used for *S*-cone measurements. The squares show the pulsed *S*-cone modulation sensitivity shown previously as circles in Fig. 8.

Some differences between the shapes of the three functions should be expected simply because of the different adaptive states of the three cone types. The fact that there are differences between the shapes of the *M*-cone and *L*-cone functions (and differences in phase discussed below) does suggest that distinct cones are responsible for detection of the 574 and 637 nm test lights on the 617 nm field.

Despite the different states of cone adaptation, the shapes of the functions are quite similar. The *S*-cone function is slightly steeper at the highest frequencies than either the *M*- or *L*-cone functions, but the overall differences are not great. The similarities between the *S*-cone function and those of the other two cone types—particularly at higher frequencies—suggests that the steep high frequency loss of sensitivity normally associated with the *S*-cone response under less extreme conditions is likely to be introduced mainly by the *S*-cone pathways, not by the receptors.

Experiment VII:
Flicker Nulls and Phase Lags

At some frequencies and radiances, flicker photometric nulls between *S*-, *M*- and *L*-cone can be made without adjusting the relative phases of the lights, but, more typically, phase adjustments are required to secure a compelling null (Stockman & MacLeod, 1986, 1987). Such experiments, which are reported in this section reveal some unusual properties of *S*-cone flicker cancellation.

Methods

To vary the relative phase of two flickering lights, we used two frequency generators: one set to the frequency of interest, and a second, a phase-lockable generator, phase-locked to the signal from the first. The outputs of the two generators were used to drive shutters in two different test channels. Thus by adjusting the variable phase delay of the phase-locked generator, the subject could adjust the relative phase of two flickering test lights. The subject was instructed to minimize or null the flicker produced by the two flickering lights by varying their relative phase and modulation. Generally, the subject (i) made an approximate setting of the point of minimum flicker by adjusting phase, then (ii) made fine adjustments of the modulation of the *S*-cone stimulus or of the *M*- or *L*-cone stimulus to improve the minimum, and finally (iii) made the final phase settings. At each frequency four (AS) or three (DD) phase settings

were made during each of four experimental settings. By means of a switch on the phase-lockable generator that inverted its output signal, the subject was easily able to compare the subjective flicker produced by phases separated by 180 deg. The measurements reported here, then, are essentially flicker photometric nulls with the additional requirement that phase must be optimized.

For the majority of measurements, an *S*-cone (437 nm) and an *L*-cone (637 nm) light were used. The time-averaged 437 nm radiance was varied, as was temporal frequency. The 637 nm light was kept just above threshold (below about two times flicker threshold).

At the high *S*-cone level ($10^{9.09}$ quanta sec⁻¹ deg⁻²), phase lags were measured between *S* (437 nm), *M* (574 nm) and *L* (637 nm) lights. The amplitudes of the 574 and 637 nm lights were kept just above threshold. We assume that the 437, 574 and 637 nm lights were detected by *S*-, *M*- and *L*-cones, respectively. All measurements were made on the standard orange background.

Results

Figure 10 shows phase lags for subject AS (a) and DD (b) measured as a function of frequency at seven *S*-cone adaptation levels, four of which correspond to the low, medium, high and saturating levels of previous experiments. Data for a third subject (PY) are very similar. The data, taken as a whole, are approximately fan-like, if the lines are extrapolated to 0 Hz, they cross the

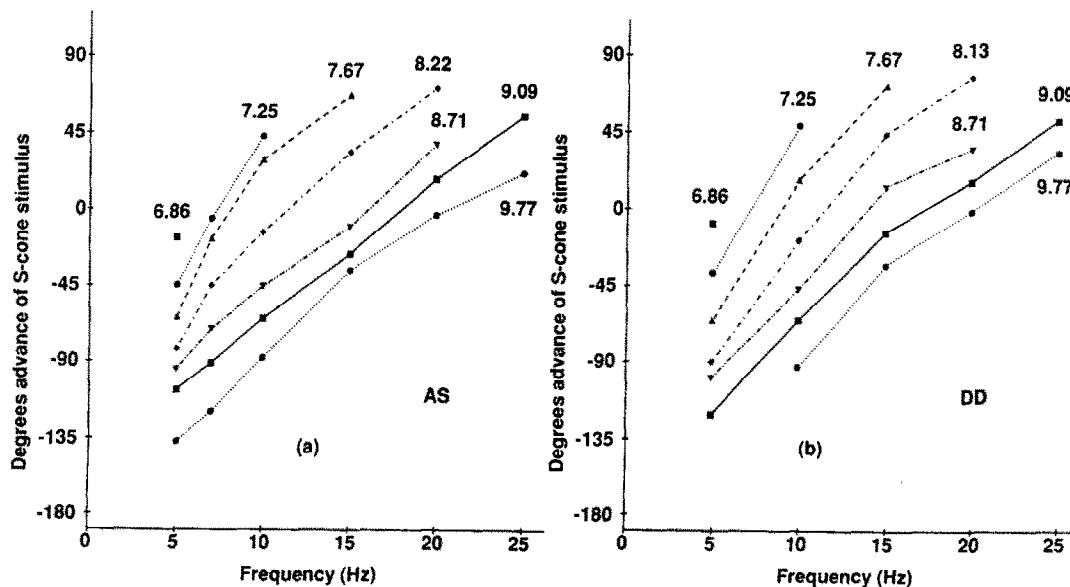


Fig. 10. Phase lags for AS (a) and DD (b), given in terms of the degrees advance of the 437 nm stimulus required to null a 637 nm light, plotted as a function of frequency with radiance as a parameter.

ordinate between about 140 and 180 deg. These data, therefore, suggest that the *S*-cone input to the achromatic channel is *inverted* in sign, relative to the inputs from the other cones. If the high frequency *S*-cone process represents an input to the luminance channel, then that input is negative.

From Fig. 10 it can be seen that at most frequencies there is a radiance of the 437 nm light at which the phase lag is close to 0 deg. At those radiances and frequencies it is possible to set flicker photometric nulls without adjusting phase (as was the case, for instance, at 16 Hz in expt I). The simplicity of this situation is deceptive (Stockman & MacLeod, 1987): as the data of Fig. 10 reveal, the *S* cones are neither as fast as the others nor synergistic with them. Rather, their apparent synergism is due to a half cycle delay of an antagonistic signal.

No data are shown in Fig. 10 below 5 Hz. This is because nulls proved to be impossible for our trichromatic observers at frequencies below 5 Hz. Some flicker always remained whatever the relative phase and intensity of the 437 and 637 nm lights, suggesting that another process comes into play at low frequencies. This second process may be the low frequency *S*-cone process revealed by the masking measurements (Fig. 5) and the residual flicker measurements (Fig. 7).

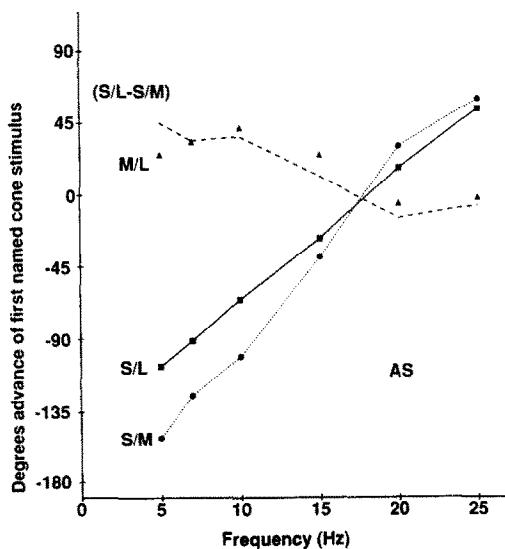


Fig. 11. Phase lags for AS set between 574 and 637 nm lights (\blacktriangle), 437 and 637 nm lights (\blacksquare), and 437 and 574 nm lights (\bullet). The time-averaged 437 nm radiance was $10^{9.09}$ quanta sec $^{-1}$ deg $^{-2}$. The dashed line represents phase lags predicted on the basis of transitivity from the lags measured between the 437 and 574, and the 437 and 637 nm lights.

The inferred antagonistic influence of *S*-cones and *L*-cones makes it desirable to investigate similarly the phase relation between *S*-cone and *M*-cone signals. Figure 11 shows *M/L* (triangles), *S/M* (circles) and *S/L* (squares) phase lags obtained at the high *S*-cone adaptation level on the standard orange field.

The *S/L* and *S/M* phase lags suggest that there is a sizeable phase lag between the *M*- and *L*-cone signals under intense orange adaptation. The *M/L* phase lags predicted, assuming phase additivity, from the difference between the *S/M* and *S/L* phase lags are shown in the dashed line in Fig. 11. The measured *M/L* phase lags (triangles) fall close to the predicted line. Thus, the phase lags between signals from the three cone types are approximately transitive. Although the signals from the *M*-cones are nearly 40 deg slower than those from the *L*-cones at lower frequencies, they become slightly faster at higher frequencies (see also Swanson, Pokorny & Smith, 1986).

GENERAL DISCUSSION

In summary, our findings are consistent with the notion that signals from the *S*-cone have access to two pathways. One pathway may correspond to the sluggishly updated chromatic system, and the other to a faster, but color blind, luminance system; this is supported by the subjective appearance of flickering lights under the relevant conditions, and the fact that *S*-cone signals through the brisk pathway can flicker photometrically null *M*- and *L*-cone signals. The *S*-cone input to the luminance channel is inverted. The *S*-cones themselves are relatively similar to other cones in their frequency response, but show a large phase lag that reaches 180 deg within the visible range of frequency, making their signals effectively synergistic with those of other cones when this happens.

Relationship to Earlier Psychophysical Measurements

Some aspects of our results are foreshadowed in earlier reports. Our maximum *S*-cone c.f.f. of 28 Hz is only slightly higher than earlier estimates of 18 Hz (Brindley et al., 1966), 20 or 24 Hz depending upon the subject (Green, 1969) and 24 Hz (Marks & Bornstein, 1973). Our measurements benefit from a more extended range of intensities within which we can maintain *S*-cone isolation. Modulation sensitivity

functions measured at moderate or low adaptation levels (Kelly, 1974; Wisowaty & Boynton, 1980) resemble our masked S-cone modulation functions in shape, whereas those measured at high levels (Green, 1969) are more similar to our pulsed modulation sensitivity functions.

One aspect of our results that is not foreseen in earlier reports is that we find an unmistakable S-cone contribution to flicker photometry. Eisner and MacLeod (1980) looked for an S-cone contribution at 2, 5 and 10 Hz and found no measurable effect, and Verdon and Adams (1987) found no evidence of an S-cone contribution to mesopic or photopic luminance at 2 Hz. But there may be no conflict between these findings and our own. The earlier measurements were made under much less extreme adaptation levels than those used in our studies, levels at which the high frequency S-cone signal (which we think contributes to luminance flicker) may be negligible. Indeed, we have no evidence that a negative S-cone input to luminance is important or measurable under ordinary adaptation conditions.

S-cone vision is subject to a number of well-documented adaptational anomalies (e.g. Stiles, 1978; Mollon & Polden, 1977b; Augenstein & Pugh, 1977; Mollon, Stockman & Polden, 1987). Many of these phenomena suggest that S-cone signals pass through a "second site" where they can be attenuated by signals from the other cone types (e.g. Pugh & Mollon, 1979). Since this second site is chromatically opponent, the weak S-cone input to luminance may well bypass it. But the finding that the *b*-wave of the S-cone ERG is subject to one of the adaptational anomalies, transient tritanopia (Valeton & Van Norren, 1979) suggests that the second site is very early in the visual system, perhaps earlier than the bifurcation of the S-cone signal into brisk and sluggish pathways. The latter possibility is made plausible by an incidental observation that under conditions where the brisk pathway is relevant, S-cone temporal resolution is increased (to a c.f.f. of 33 Hz for DM) a few seconds after the onset of the adapting and test fields; this has parallels with the transient improvement in S-cone sensitivity for flashes found by Mollon and Polden (1980) following the onset of combined yellow and violet fields. Likewise, Lee and Stromeier (1989) have evidence of transient tritanopia affecting the S-cone input to motion.

What are the Two S-Cone Pathways?

Our results are consistent with the idea that S-cone have access to two pathways under the extreme conditions of our experiment. But, what might these two pathways be?

We have only limited evidence about the low frequency S-cone pathway, although its properties do clearly distinguish it from the high frequency pathway. When the low frequency pathway signals flicker, the flicker appears as a color fluctuation and flicker photometric nulls become difficult to make. These phenomena and the steep loss of high frequency sensitivity found in the low frequency S-cone temporal sensitivity functions (obtained using either the masking or nulling methods)—which is comparable in slope to other chromatic modulation sensitivity functions (e.g. Truss, 1957; Wisowaty, 1981)—suggest to us that the low frequency S-cone pathway is a *chromatic* pathway. A steep loss of high frequency sensitivity seems to be a general property of chromatic detection that changes little with adaptation level. Even under the high intensity conditions of our experiment, we find a rapid loss of high frequency sensitivity for red-green chromatic detection as well as for S-cone detection (see expt IV). Furthermore, the steepness of the "chromatic" S-cone function remains invariant with intensity despite changes in test radiance of nearly $2 \log_{10}$ units (Fig. 5). An invariance of chromatic S-cone temporal sensitivity is consistent with reports that the critical durations for Stiles' π_1 and π_3 are not substantially reduced by light adaptation (Krauskopf & Mollon, 1971; Friedman, Yim & Pugh, 1984).

We have more evidence about the high frequency S-cone pathway. First and most importantly, the signals conveyed by it can participate in flicker photometric nulls with *M*- and *L*-cone signals up to moderately high temporal frequencies. That such nulls are possible tells us that the high frequency S-cone signal appears in a *single, color-blind* channel shared by signals from all three cone types. Second, the frequency response of the S-cones through this pathway is not very different from that of the *M*- and *L*-cones. Third, phenomenally, the high frequency S-cone flicker looks achromatic, as does its *M*- and *L*-cone counterpart. But there are other characteristics of the high frequency S-cone signal that would not be expected of a simple input to the luminance pathway. First, the S-cone flicker signal never

rises far above threshold and saturates at high intensities. Second, the signal is inverted with respect to the signals from the other cones. Third, it has a large phase delay that can be more than half a cycle at some frequencies. The properties suggest the possibility that the *S*-cone input to luminance is comparatively indirect and may be significantly modified before it participates in flicker photometric nulls.

In a sense the brisk high frequency channel is color opponent by virtue of its weak inverted *S*-cone input. Nevertheless, the feasibility of flicker nulls identifies the operative pathway as the luminance pathway of flicker photometry: if the *S*-cone signal under these conditions were in a different channel, such nulls would be precluded. Instead of that, as Fig. 1 illustrates, near-threshold *S*- and *L*-cone signals can subjectively cancel, and such cancellation occurs at frequencies spanning the flicker photometric range (Fig. 7). The pathway's frequency response, and its relative sensitivity to *M*- and *L*-cone inputs, support that identification. The possibility that chromatically opponent *neurons* at, say, the LGN level might provide input to this psychophysically defined luminance pathway is discussed below.

Physiological Considerations

If the *S*-cone input to the high frequency pathway is always near-threshold, it may be difficult to detect it physiologically even under optimal conditions. Thus, it might be hard to find consistencies between our psychophysical results and physiological data. One thing that is clear, however, is that *S*-cones can sustain the high frequency flicker rates required by our psychophysical results (e.g. Van Norren & Padmos, 1973; Zrenner & Gouras, 1981; Derrington & Lennie, 1984; Baylor, 1987, see p. 42).

Our results show that *S*-cones have access to a high frequency pathway that, on the basis of flicker nulls and other phenomena, we have identified with the so-called "luminance" channel. Any physiological study, in which a cell known to be a part of that channel was found to have an *S*-cone input, would provide some support for our conclusion.

The existence of two distinct streams in the retinostriate pathway of the primate—the *M* (or P_s) ganglion cells projecting to the magnocellular LGN and the *P* (or P_β) ganglion cells to the parvocellular LGN—has led to speculation that the two streams may correspond to the luminance and chromatic channels, respectively.

Consistent with this view is the fact that cells in the magnocellular stream have a higher temporal resolution and weaker color opponency than those in the parvocellular stream (see, for instance, Schiller & Malpeli, 1977; Kaplan & Shapley, 1982; Hicks, Lee & Vidyasagar, 1983; Derrington & Lennie, 1984; Derrington, Krauskopf & Lennie, 1984). There are, however, strong arguments against such a simple correspondence. First, the chromatic and temporal differences between cells in the two streams are much less than might be expected from the relative psychophysical detectability of luminance modulated flicker and isoluminant chromatic flicker. Parvocellular LGN cells have been found that respond to temporal frequencies of up to 40 Hz and beyond (e.g. Hicks et al., 1983; Derrington & Lennie, 1984). Clearly, the extreme sluggishness of chromatic vision is not a characteristic of chromatic cells of the parvocellular LGN. Second, the magnocellular stream appears to lack the smallness and density of receptive fields, particularly in the foveal projection, needed to support the high visual acuity of primates for patterns having only luminance contrast (Derrington & Lennie, 1984), and this high acuity is severely compromised by selective damage to *P* cells (Merigan & Eskin, 1986).

These and other problems have led some to suppose that the magnocellular stream cannot be the substrate of the luminance pathway (e.g. Lennie, 1984; Lennie & D'Zmura, 1988). Rather they adopt the assumption that chromatically opponent cells can be double-duty and carry luminance as well as chromatic information (e.g. Wiesel & Hubel, 1966; DeValois, Snodderly, Yund & Hepler, 1977; Ingling & Martinez, 1983), suggesting that the parvocellular chromatic cells are the substrate of the psychophysical luminance and chromatic channels—the two being segregated at a later stage than the LGN. According to this view, we should look for an *S*-cone luminance contribution in cells of the parvocellular stream. And many of those cells do have a clear *S*-cone input (e.g. De Monasterio, Gouras & Tolhurst, 1975; Derrington et al., 1984), with temporal resolution as high as 40 Hz or more at the ganglion cell level (Zrenner & Gouras, 1981).

It may be premature, however, to discount the magnocellular stream as at least part of the substrate of the luminance channel, particularly in the case of high frequency flicker and flicker photometric nulls. To do so would require that higher frequency flicker detected by cells of the

magnocellular stream should not contribute to perception. Lee, Martin and Valberg (1987) report that the equivalent of heterochromatic flicker nulls can be obtained in magnocellular cells when the relative intensities of the two lights correspond to the V_λ function. If the magnocellular cells do contribute to luminance flicker, it is for these cells that our results imply an *S*-cone input. This, too, is physiologically observed (De Monasterio, 1978; Derrington et al., 1984), although the polarity of the *S*-cone influence varies from cell to cell.

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