



ON and OFF S-cone pathways have different long-wave cone inputs

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Abstract

Three experiments compared thresholds for S-cone increments and decrements under steady and transient adaptation conditions, to investigate whether stimuli of both polarities are detected by the same cone-opponent psychophysical mechanism. The results could not be accounted for by a standard model of the S-cone detection pathway [Polden & Mollon (1980) *Proceedings of the Royal Society of London, B*, 210, 235–272]. In particular, a transient tritanopia detection paradigm that measured threshold elevation following the offset of long-wavelength fields produced different field sensitivities for S-cone increment and decrement tests. The decrement field sensitivity function was shifted to shorter wavelengths relative to the increment function. L-cone opponency is apparently stronger for S-cone increments than for decrements. The most plausible substrates of the two different psychophysical detection mechanisms are the ON and OFF channels. The results suggest that S-ON (bistratified) and S-OFF ganglion cells receive different relative amounts of L- and M-cone input. © 2000 Published by Elsevier Science Ltd.

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1. Introduction

Detection of S-cone signals is thought to be mediated primarily by a chromatic mechanism with two successive sites of sensitivity regulation: a first-site of cone-specific adaptation, and a second-site of cone-opponent interactions (Pugh & Mollon, 1979; Zaidi, Shapiro & Hood, 1992; Eskew, McLellan & Giulianini, 1999). Two classic examples of cone-opponent effects on S-cone increment detection are ‘combinative euchromatopsia’ (Polden & Mollon, 1980), and ‘transient tritanopia’ (Stiles, 1949; Mollon & Polden, 1977b). In combinative euchromatopsia, the addition of long-wavelength (yellow) light to a short-wavelength (violet) background field *reduces* the increment threshold for a short-wavelength test, compared to threshold on the short-wavelength field alone. In transient tritanopia, threshold for an S-cone-detected test is momentarily *elevated* following the offset of a long-wavelength

adapting field. The dependence of these effects on field wavelengths to which the S-cones themselves are relatively insensitive implicates the L- and M-cones in the regulation of S-cone sensitivity. The research reported here extends this earlier work on S-cone *increment detection* to explore the detection of S-cone *decrements*, and the relationships between increment and decrement sensitivities, using a model proposed by Pugh and Mollon (1979) and Polden and Mollon (1980) as a framework.

1.1. Working S-cone model

Fig. 1a shows a schematic diagram of the S-cone increment detection mechanism as described by Polden and Mollon (1980), based on the formal presentation of Pugh and Mollon (1979). Sensitivity is regulated at two sites. At the first site, sensitivity to transient signals is reduced by increasing the time-average S-cone quantal catch from the adapting field. At the second-site, sensitivity is controlled by a static, non-linear response to a cone-opponent signal, labeled Z , produced by subtracting some combination of L- and M-cone inputs from an S-cone input: $Z = S - f(L, M)$. Although this L- and

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M-cone combination is often assumed to be linear, this restriction is not necessary here.

Long-wavelength adapting fields that strongly stimulate the L- and M-cones but not the S-cones produce $Z < 0$, whereas short wavelength fields produce $Z > 0$, due to relatively greater stimulation of S-cones. The opponent site's response function, $R(Z)$, is sigmoidal: approximately linear through the origin and compressive for both positive and negative values of Z . As shown in Fig. 1b, threshold for an incremental change, $+\Delta Z$, requires a constant criterion change (k) in response (Adelson, 1982; Hayhoe, Benimoff & Hood, 1987). Due to response compression, sensitivity to $+\Delta Z$ is greatest when $Z \approx 0$. When the tonic opponent

signal is highly negative or positive, the site is said to be 'polarized,' toward blue when $Z > 0$ and toward yellow when $Z < 0$. Since we can know only the relative cone contributions to Z , we may assume a unit proportionality between S and Z with no loss of generality. Therefore, an S-cone-isolating increment test stimulus, $+\Delta S$, which causes no change in $f(L, M)$, is equivalent to $+\Delta Z$.

This model easily accounts for combinative euclimatopsia: the addition of yellow light to a blue adapting field increases the L- and M-cone signals at the opponent site, counteracting blue polarization caused by the strong S-cone signal from the blue field. Though there may be no change in S-cone first-site adaptation, overall sensitivity improves as the tonic opponent signal is neutralized.

To account for transient tritanopia, the model includes a 'restoring force', a slow subtractive adaptation process operating at the opponent site (Augenstein & Pugh, 1977; Pugh & Mollon, 1979). The restoring force counteracts the desensitizing effects of polarization by subtracting some function of the mechanism's output from the opponent signal, thus moving the site's operating point back toward the center of its response range. Because the restoring force responds slowly to changes in the adapting field, turning the field off causes a temporary *rebound* in polarization in the opposite direction, toward blue following yellow-field offset and toward yellow following blue field offset. Turning off a yellow field results in thresholds higher than when the field is on, but turning off a blue field is not likely to elevate threshold because of the concurrent recovery of the S-cone first site.

As shown in Fig. 1c, S-cone increments and decrements have opposite effects on the opponent signal, so to account for both increment and decrement detection, we modify the model such that threshold requires a constant change in the absolute value of R : $|\Delta R| = k$. The opponent response function is assumed to be approximately linear through the origin, so opponent-site sensitivities to increments and decrements will be equal during neutral adaptation and should therefore reveal the effects of cone-specific, first-site adaptation. We will also assume that first-site sensitivities to weak increments and decrements are roughly equal. Given these assumptions, if the same, single mechanism detects both S-cone increments and decrements, then polarizing adaptation conditions should cause the detection asymmetries outlined in Fig. 1c. Due to the curvature of the response function, blue polarization ($Z > 0$) will cause relatively greater threshold elevation for increments than for decrements, because the opponent signal must change by a greater amount in the positive direction than in the negative direction to produce the criterion

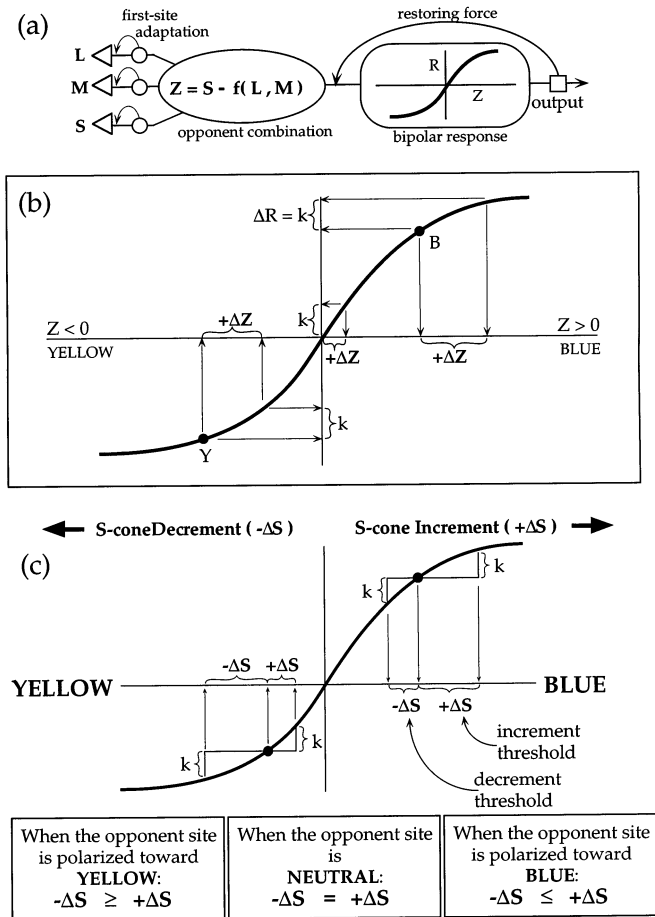


Fig. 1. (a) Model of the S-cone increment detection pathway as in Polden and Mollon (1980). An S-cone test stimulus produces a change in the opponent signal, Z . (b) To reach threshold, the test must produce a constant criterion change in response at the opponent site, $\Delta R = k$. Increment threshold is lowest when $Z \approx 0$, and increases as $|Z|$ increases (points B and Y). (c) Predictions for increment and decrement thresholds under different polarization conditions if stimuli of both polarities are detected by the same opponent mechanism. Threshold requires a criterion change in the absolute value of response: $|\Delta R| = k$. The predicted relationship between increment and decrement thresholds changes with the state of opponent polarization.

response change. Conversely, yellow polarization ($Z < 0$) will cause relatively higher decrement thresholds¹. Blue polarization occurs during adaptation to short-wavelength fields and following the offset of long-wavelength fields. Yellow polarization occurs during steady adaptation to long-wavelength fields and following the offset of short-wavelength fields.

Three experiments assess this single-mechanism working model by comparing the relative effects of chromatic adaptation on S-cone increment and decrement detection under steady-adaptation and field-offset conditions. The first experiment confirms that S-cone decrement detection is subject to the same hallmark opponent effects (transient tritanopia and combinative euchromatopsia) as increment detection. The second investigates the effects of opponency under adaptation to fields equated for their first-site effects upon S-cones. The third uses a transient tritanopia paradigm to examine the L- and M-cone signals that influence S-cone increment and decrement detection. Our results require two separate detection mechanisms, presumably S-ON and S-OFF pathways, having different opponent combinations of L- and M-cone inputs.

2. General methods

2.1. Apparatus

Test stimuli were created on a Macintosh computer and displayed on a Nanao T560i monitor by a standard video board with 8-bit digital-to-analog conversion. The monitor was seen in free-view via a two-lens relay optical system and produced a 110 Td white ($x = 0.309$, $y = 0.331$) background, 9.9° in diameter, which was continuously present during all experiments.

Two Maxwellian-view channels could be superimposed individually or together on the monitor image by means of a beamsplitter cube in the relay lens system. A tungsten light source and either narrow-band interference filters (~ 10 nm full bandwidth at half height) or a grating monochromator (Jobin-Yvon H-10, 2 mm slit, 17 nm full bandwidth at half-height) were used in these channels to produce chromatic adapting fields. With spectral centroids of 476 and 575 nm, the two channels could be combined to create a field with the same chromaticity (modified-Judd; Vos, 1978) as the white background produced by the monitor. An elec-

tronic shutter (Uniblitz) controlled by the computer could block the two Maxwellian-view fields but not the monitor background. An aperture image formed by the relay lenses created an optical pupil 2.4 mm in diameter in the observer's pupil plane. An achromatizing lens corrected for chromatic aberration. Observers' heads were stabilized with dental-impression bite bars. There was a small fixation spot at the center of the field.

2.2. Subjects

Four observers participated in different parts of these experiments. Three observers are color-normal as assessed by the FM-100 hue test (KKH, FG, PMK), and Rayleigh matches with a Nagel anomaloscope (PMK). One observer, JSM, is deuteranomalous with good discrimination as assessed by Rayleigh matches and the FM-100 hue test.

2.3. Calibration and stimuli

The monitor was spectroradiometrically calibrated at 1.05 nm intervals across the visible spectrum. The stimuli were two-dimensional circular Gaussian blobs with $\sigma = 0.5^\circ$, presented 0.75° away from fixation, for 200 ms. Stimulus strength for both incremental and decremental tests was defined as S-cone-contrast magnitude, $|\Delta S/S|$, calculated with respect to the *white monitor background alone*. Because the monitor background was always present, these units are proportional to the change in S-cone quantal catch produced by the test stimulus. The maximum S-cone contrast attainable on the monitor was 0.8. Gamma correction of the monitor output was achieved via software lookup tables.

2.4. S-Cone isolation

S-cone isolating stimuli were produced by changes in the monitor guns that were silent substitutions for both L- and M-cones: they caused either increments or decrements in S-cone quantal catch without altering the quantal catch rates of the other two cone classes. The short-wavelength cone isolating direction in the color space of our monitor primaries was determined by cross-multiplying the monitor gun spectra with the Smith and Pokorny (1975) cone fundamentals, interpolated to 1 nm intervals. For our primaries, the S-cone direction defined by the Stockman, MacLeod and Johnson (1993) 2°-from-10° fundamentals was identical except at the highest two test contrasts used, where it differed only trivially.

For one color normal observer (PMK) and the deuteranomalous observer (JSM), this nominal S-cone isolating direction was checked using a procedure similar to that employed by Webster, De Valois and Switkes (1990) and Webster and Mollon (1994). In the

¹The actual differences in increment and decrement threshold elevations depend upon the magnitude of the criterion response change, k , relative to the curvature of the response function. If first-site sensitivity were biased in favor of either increments or decrements, then by the principle of univariance, this bias would have to be constant across adapting field wavelengths. The predictions made here would then apply to threshold *elevations* above thresholds under neutral adaptation.

color space defined by our monitor primaries, we measured thresholds along the nominal S-cone direction and several nearby directions. We used a 610 Td 'white' background (476 and 575 nm mixture), and the same background plus an additional 430 nm field (4.5×10^8 quanta/deg²/sec). The short-wavelength field should elevate S-cone thresholds by diluting the contrast created in the S-cones, while having much less effect upon the L- and M-cones. For both observers, maximal elevation (blue field threshold divided by white field threshold) was along the nominal S-cone direction, indicating that the Smith–Pokorny (or Stockman et al., 1993) S-cone direction isolated the S-cones of our observers. McLellan (1997), Appendix A provides further details.

The monitor background was 2.44 log scotopic Td, which might be below rod saturation (Sharpe, Fach, Nordby & Stockman, 1989), and the maximum rod contrast produced by our test stimulus on this background was 0.52. Therefore, although rods are sparse close to the central fovea, these stimuli are potentially visible to rods. To test this possibility, two observers adapted for 20 min to the monitor background with its mean retinal illuminance reduced by use of neutral density filters to -1.9 log scotopic Td. Neither increments nor decrements were ever seen under these scotopic conditions. Assuming Weber's law holds over the range of -1.9 to 2.44 log scotopic Td (Sharpe et al., 1989), these S-cone tests should never have been detectable to rods in any of our experiments. In the main experiments, the appearance of the test was always consistent with it being seen by the S-cones (i.e. it was purple for increments, yellow–green for decrements).

2.5. Procedure

Detection thresholds were determined with a *spatial* 2AFC double adaptive staircase procedure. On each trial, the stimulus could appear 0.75° above or below the fixation spot, with equal probability. The observer's task was to indicate the stimulus location by button press, and feedback was provided after each trial. For each of two contrast staircases in each run, stimulus contrast was decreased by 0.1 log units after three consecutive correct responses and increased by the same amount after one incorrect response. The computer randomly chose the staircase for each trial. Staircase reversals were not used; instead, data from at least two runs were pooled, and thresholds (82% correct performance) were estimated by fitting Weibull functions to the frequency-of-seeing data using a maximum likelihood method. In some cases, runs from different days were pooled. Plotted error bars represent ± 1 SE of the mean, based upon between-run variability.

Thresholds were measured under steady adaptation and following adapting field offset. Observers adapted to all fields for 2 min before each run of 100 trials. In

field-offset runs, the monochromatic field was on for 4 s preceding each trial. The 200 ms test stimulus was presented 400 ms after the field was turned off. The field remained off for a total of 1 s. For the field-offset runs, the 2 min adaptation period consisted of 1 min of adaptation to the steady combination of white monitor background and monochromatic field followed by 1 min during which the monochromatic field was flickered as it was during the run: 4 s on followed by 1 s off. In steady adaptation runs, observers initiated trials themselves; in field-offset runs, trial timing was computer-controlled.

3. Experiment 1: neutral adaptation and opponent effects

The purpose of this experiment is to confirm that S-cone increment and decrement detection both exhibit the opponent effects of combinative euromatopsia and transient tritanopia, and also to determine whether a white field, hypothesized to be neutral in the working model, has equivalent effects on increment and decrement thresholds.

3.1. Methods

For two observers, S-cone increment and decrement thresholds were measured against the white monitor background to provide baseline neutral thresholds, and threshold-versus-radiance (TvR) functions for both test stimuli were measured under steady adaptation to four different fields that were added to the monitor background: (1) a 476 nm (blue) field; (2) a mixture of 476 and 575 nm (yellow) fields that produces a white of the same chromaticity as the monitor background; (3) a 476 nm field of fixed radiance (9.1 log quanta/deg² per s) and a 575 nm field of variable radiance; (4) a 575 nm field without the blue field present. TvRs were also measured following the offset of the 575 nm field.

3.2. Results

All thresholds for this and the following experiments are expressed in log S-cone contrast, $\log |\Delta S/S|$, relative to the white monitor background. Fig. 2a and b show TvR functions for the two observers. Open symbols represent increment thresholds, and filled symbols represent decrement thresholds. For both observers, the baseline thresholds (at left) are equal. The central portion shows TvRs for steady adaptation to the blue field (squares) and to the white field produced by a mixture of blue and yellow (diamonds). As the radiance is increased, both increment and decrement thresholds rise together, with no apparent differences between them at the radiances tested. At higher radiances,

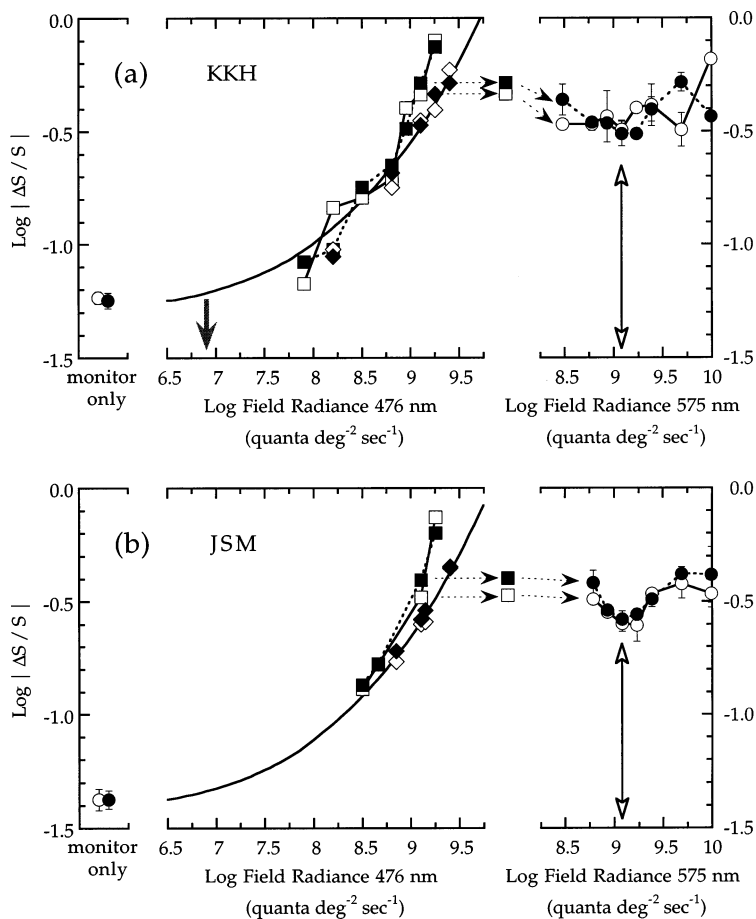


Fig. 2. Steady-field thresholds for S-cone increments (open symbols) and decrements (filled symbols) for two observers. Ordinate values are absolute S-cone contrast, calculated with respect to the monitor background field. The left-most points represent increment and decrement thresholds on the white monitor field alone. The middle portion shows TvRs on a 476 nm field (squares), and a white field mixture of 476 and 575 nm (diamonds), both plotted as a function of the 476 nm field radiance. The luminance of the brightest white field was 1800 Td. For the white field, the ratio of 575–476 nm radiances was fixed at 0.951. The white field data are fit with the Stiles ζ template (Wyszecki & Stiles, 1982). The right-hand portion shows thresholds as a function of radiance of a 575 nm field added to a fixed 476 nm field (9.1 log quanta/deg²/sec). To avoid clutter, error bars are not plotted in the middle portion. The solid arrow in (a) is discussed in Experiment 3.

adding yellow to the blue field (producing white) lowers the thresholds for both stimuli compared to the blue field alone (squares versus diamonds). This is an example of combinative euchromatopsia. The white-field TvRs are well-described by the standard ζ TvR template (Wyszecki & Stiles, 1982), showing that thresholds on white rise in accordance with Weber’s law. In contrast, the blue-field thresholds rise more steeply than Weber’s Law (Mollon & Polden, 1977a; Stromeyer, Kronauer & Madsen, 1978). Because the 476 nm light is strongly absorbed by the S-cones, the rise in threshold with increased radiance is partly the result of first-site processes, but the drop in threshold as the yellow light is added (to produce the white) implies that at least some of the threshold-elevating effect of the blue field can be attributed to an opponent site effect, as shown by Stromeyer, Kronauer and Madsen (1979) for increment detection. The right portions of Fig. 2a and b

show thresholds (circles) as a function of yellow-field radiance that is added to a fixed blue field radiance of 9.1 log quanta/deg²/sec. Thresholds for both increments and decrements show a wide trough, falling and then rising again as yellow radiance is increased, as shown by Polden and Mollon (1980) for increment stimuli. The double-headed arrows indicate the yellow radiance that is added to blue to produce a white field (3 log Td). Although the data are noisy for KKH, threshold minima for both subjects do occur near this mixture. These results indicate that the white field can be assumed to be approximately neutral for both increment and decrement detection.

According to Mollon and Estevez (1988), combinative euchromatopsia generally requires a blue field of high radiance (e.g. 9.7 log quanta/deg²/sec at 473 nm). The failure to elicit a strong effect from KKH may be the result of using a relatively low background radi-

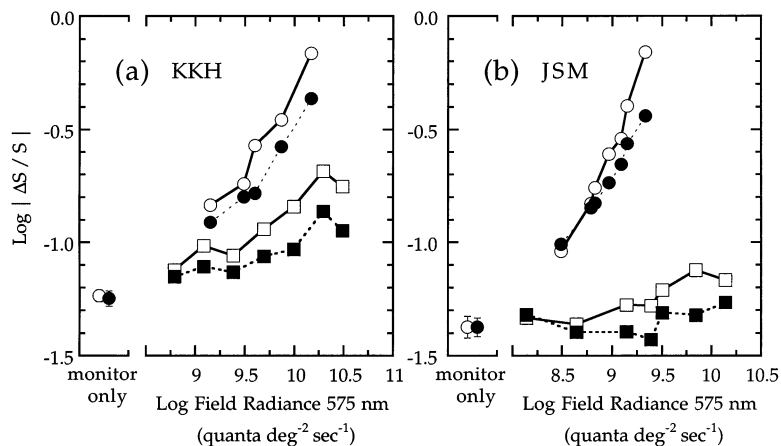


Fig. 3. S-cone increment (open symbols) and decrement (filled symbols) thresholds with a 575 nm adapting field under steady adaptation (squares) and field-offset (circles) conditions for two observers. The left-most points show thresholds on the monitor background alone; error bars are plotted for these points only.

ance; however, the stimulus contrast limitations of our monitor made it impossible to use higher adapting levels here.

Fig. 3 a and b show TvRs under steady adaptation (squares) and field-offset (circles) conditions with a field wavelength of 575 nm. The x -axis gives yellow field radiance during adaptation or prior to offset. Both subjects show very little threshold elevation for either stimulus on the steady yellow field; the slight rise must be ascribed to an opponent-site effect because the S-cones are quite insensitive to this wavelength. Both observers show the transient tritanopia effect for both increments and decrements: thresholds are higher following field offset than during steady adaptation to the field. According to the working model, the blue polarization resulting from yellow field offset will produce higher thresholds for increments than for decrements (see Fig. 1c), and this result is observed here. However, the steady field results are inconsistent with the model's prediction: a yellow steady field, producing the opponent signal $Z < 0$, should elevate decrement thresholds at least as much as increment thresholds, but both observers show the opposite result. Except for this last finding, these results are generally consistent with predictions of the working model. Both increment and decrement detection show combinative euchromatopsia and transient tritanopia, and a white field appears to be neutral for both.

4. Experiment 2: S-cone equated adapting fields

The results on different adapting fields in Experiment 1 show the influence of first site effects alone (white field), second-site effects alone (yellow field), and combined first- and second-site effects (blue field). In this experiment, opponent-site effects were isolated by fixing

the first-site adaptation state using 410–530 nm fields equated for S-cone quantal catch. In the context of the working model, if there is a chromatically neutral point within this spectral range, minimum thresholds should occur for both increments and decrements at this wavelength. Steady adaptation to fields shorter in wavelength than this neutral field should polarize the opponent site toward blue, resulting in higher increment thresholds than decrement thresholds (Fig. 1c), and turning off these fields should cause a rebound polarization toward yellow resulting in higher decrement thresholds. Field wavelengths longer than the neutral wavelength should produce the opposite polarizations and opposite results.

4.1. Methods

Fields of 410–530 nm were set to radiances that produced the same S-cone quantal catch according to the quantal 2-from-10° S-cone fundamental of Stockman et al. (1993). For JSM and KKH, field radiance was $8.48 \log \text{ quanta/deg}^2/\text{sec}$ at 440 nm and was greater at other wavelengths. For PMK, whose absolute sensitivity to the test stimuli was lower, the field radiance was threefold lower at each wavelength. Thresholds were measured under both steady-adaptation and field-offset conditions.

4.2. Results

In Fig. 4 a, b and c the squares represent thresholds under steady adaptation for three observers as a function of adapting wavelength. There is a broad trough in these threshold versus adapting wavelength functions, so there is no definite indication of a neutral wavelength, but thresholds generally rise at wavelengths longer and shorter than 500 nm (near unique green).

The broad trough suggests that the opponent polarization produced by some of these fields may not have been strong enough to move the opponent site much beyond the linear region of the response function. The use of more intense fields might have produced functions with sharper minima, but higher intensities would have made thresholds on the shortest wavelength fields unmeasurably high, given the limitations of the apparatus. (The field radiance used here was too high to allow KKH to measure a threshold on the 410 nm field.)

The rise in thresholds at the shorter wavelengths can be attributed to increasing second-site (blue) polarization. Increment and decrement thresholds are approximately equal on all short-wavelength fields for KKH and JSM, contradicting the working model's prediction of higher increment thresholds. For PMK there is a small difference in favor of decrements at all adapting wavelengths. Weak effects of increasing yellow polarization are suggested for all observers by the rise in thresholds at wavelengths longer than 500 nm. However, decrement thresholds are slightly lower than increment thresholds on these longer-wavelength fields, again inconsistent with the working model's prediction for yellow polarization.

The circles in Fig. 4 represent field-offset thresholds for these same S-cone equated fields. For the 500 nm field, increment and decrement thresholds are about

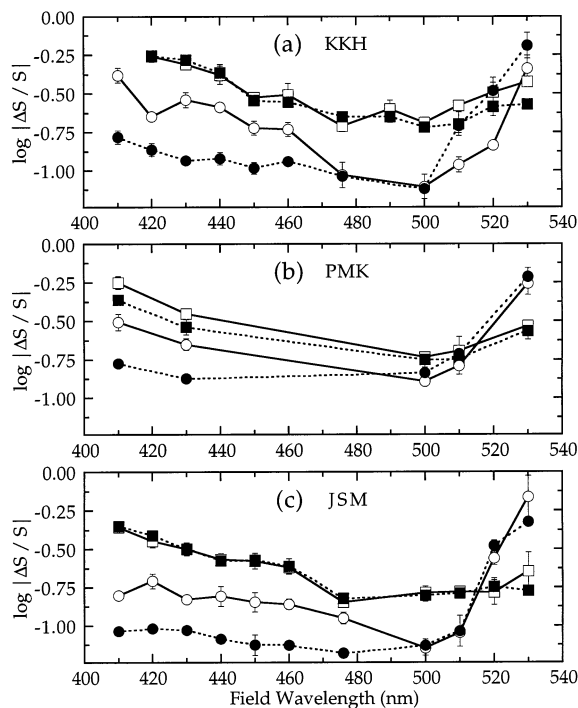


Fig. 4. S-cone increment (open) and decrement (filled) thresholds under steady adaptation (squares) and field-offset conditions (circles) for fields ranging from 410 to 530 nm. Adapting fields were equated for S-cone quantal catch.

equal at field offset. For increment thresholds especially, there is a sharp increase in thresholds at wavelengths both longer and shorter than 500 nm, consistent with a neutral point near this wavelength.

Following the offset of fields shorter than 500 nm, there are dramatic and unpredicted differences between increment and decrement thresholds. Because of the large change at the S-cone first-site with the offset of these fields, thresholds for both stimuli are expected to be lower at offset than during steady adaptation, which they are (squares and circles). However, contrary to the model's prediction, decrement thresholds are lower than increment thresholds, and the difference between them increases at shorter field wavelengths. These results agree qualitatively with those of Krauskopf, Williams, Mandler and Brown (1986), who found much greater threshold elevations for S-cone increments than decrements following the offset of a purple (S-cone increment) field step.

For adapting wavelengths longer than 500 nm, field-offset thresholds for both stimuli rise sharply. Transient tritanopia, indicated by field-offset thresholds that lie above steady-field thresholds, is observed for adapting wavelengths as short as 520 nm. Because this effect is associated with rebound blue polarization, thresholds should be relatively higher for increments than decrements, but KKH and PMK show the opposite relationship in these conditions.

5. Experiment 3: thresholds following long-wavelength field offset

The contradictions between the results of Experiment 2 and the model's predictions suggest that S-cone increments and decrements are detected by different mechanisms. However, the state of second-site polarization was free to vary in Experiment 2 because the L- and M-cone quantal catches varied with adapting wavelength (the L/M ratio varied by about twofold). Consequently, the results cannot be used to distinguish among a number of possible differences between the mechanisms, including differences in the opponent signals, the nonlinear response functions, the restoring forces, or a combination of these. Experiment 3 uses a transient tritanopia paradigm to investigate the first of these possibilities in further detail.

Long-wavelength adapting fields can produce substantial threshold elevation shortly after field-offset due to blue-polarization rebound, even at radiances too low to have a direct effect on the S-cone adaptive state. Since S-cone adaptation is held constant, the threshold elevation must result from the action of the L- and M-cone inputs to the opponent signals. In different runs, the radiance (prior to offset) of the long-wavelength field may be varied to attain a criterion threshold

elevation above the neutral-field baseline; for increment tests this radiance will be called the increment field point. Since threshold elevation is due to a second-site effect exclusively, the criterion elevation must correspond to a fixed operating point on the opponent response function for all field wavelengths, even though the radiance at the field points will differ with adapting wavelength. In the context of the working model, in which the same opponent signal regulates both increment and decrement detection, each wavelength's increment field point must in turn correspond to a constant degree of *decrement* threshold elevation because the operating point is fixed. Two different mechanisms with different long-wavelength inputs to their opponent signals would not obey this prediction because the degree of polarization in the two mechanisms would vary differently with wavelength.

The shapes of the increment and decrement TvRs are determined by the curvature of the response function. The single-pathway working model implies that TvRs will rise more steeply for increments than for decrements under blue polarizing conditions, but that the two TvR functions will maintain an invariant relationship across adapting wavelengths. Following the field displacement rule (Stiles, 1949; Enoch, 1972; Pugh & Kirk, 1986) the working model therefore implies that field sensitivities measured under opponent-site isolating conditions with increment and decrement tests will have the same shape, even though the TvR shapes themselves must differ.

5.1. Methods

For four observers, baseline S-cone increment and decrement thresholds were measured against the monitor background, and increment and decrement TvR functions were measured following adapting-field offset as a function of field radiance prior to offset. Adapting wavelengths ranged from 540 to 680 nm. Only a single field wavelength was used in any experimental session. The white monitor background was always present. Baseline thresholds and field-offset TvRs at 575 nm for KKH and JSM are taken from Experiment 1.

5.2. Results

Fig. 5 shows TvRs measured following the offset of long-wavelength fields for each of four observers. For each observer, monitor-only baseline thresholds (left-most points) are nearly equal. Increment and decrement field-offset TvRs for all observers rise with increasing field radiance at all adapting wavelengths, consistent with increasing opponent polarization following the offset of increasingly intense adapting fields.

For the three color-normal observers (top three panels), the Stiles ζ template provides a good fit to both the

increment and decrement TvRs. (The use of this template is not intended to imply any precise theoretical connection to Stiles' π mechanisms. However, the fact that the same template shape fits for different wavelengths is a good indication of shape invariance for increment TvRs and decrement TvRs over the range tested). The free parameter in these fits was the translation factor for each wavelength. The single mechanism model predicts that the relationship between increment and decrement TvRs should be constant across wavelengths, and this is clearly not the case for the color-normal observers. For example, for KKH and PMK (top two panels), decrement thresholds are consistently higher than increment thresholds following offset of 540 nm fields, but decrement thresholds are lower than increment thresholds for fields of 575 nm and longer. For FG (third panel), increment thresholds always exceed decrement thresholds, but the horizontal distance between the increment and decrement TvRs increases at longer field wavelengths.

For the deuteranomalous observer, the relationship between increment and decrement functions is much more nearly constant across wavelengths than for the color-normal observers. For this observer, decrement functions are fit with the Stiles template, but the increment functions rise more steeply, and are not adequately described by this template (see figure legend).

Fig. 6 summarizes the relationship between the increment and decrement functions, showing decrement thresholds obtained at the field points for criterion increment threshold elevation. With the assumption of shape-invariant TvRs, the choice of criterion elevation is arbitrary; 0.55 log units above baseline (mean of increment and decrement baselines) was chosen here because it falls within the range of increment thresholds measured for each observer, and occurs at relatively low field radiances, so that S-cone adaptation is undisturbed. The horizontal arrow in each panel of Fig. 5 shows the criterion elevation for each observer. In Fig. 6, the open symbols in each panel represent the constant increment thresholds at the increment field points. For PMK and KKH (top two panels) decrement thresholds are higher than increment thresholds on the shorter wavelength fields and lower on the longer fields. For FG (panel c) decrement thresholds never exceed increment thresholds, but they vary with wavelength in the same general way as in the top two panels. For the deuteranomalous observer (panel d) however, the difference between increment and decrement thresholds is negligible.

If there were a single S-cone detection mechanism, then the state of polarization of the mechanism would be independent of the test stimulus used to probe the system. Both increment and decrement tests would have to reveal the same underlying opponent process, and the relationship between increment and decrement

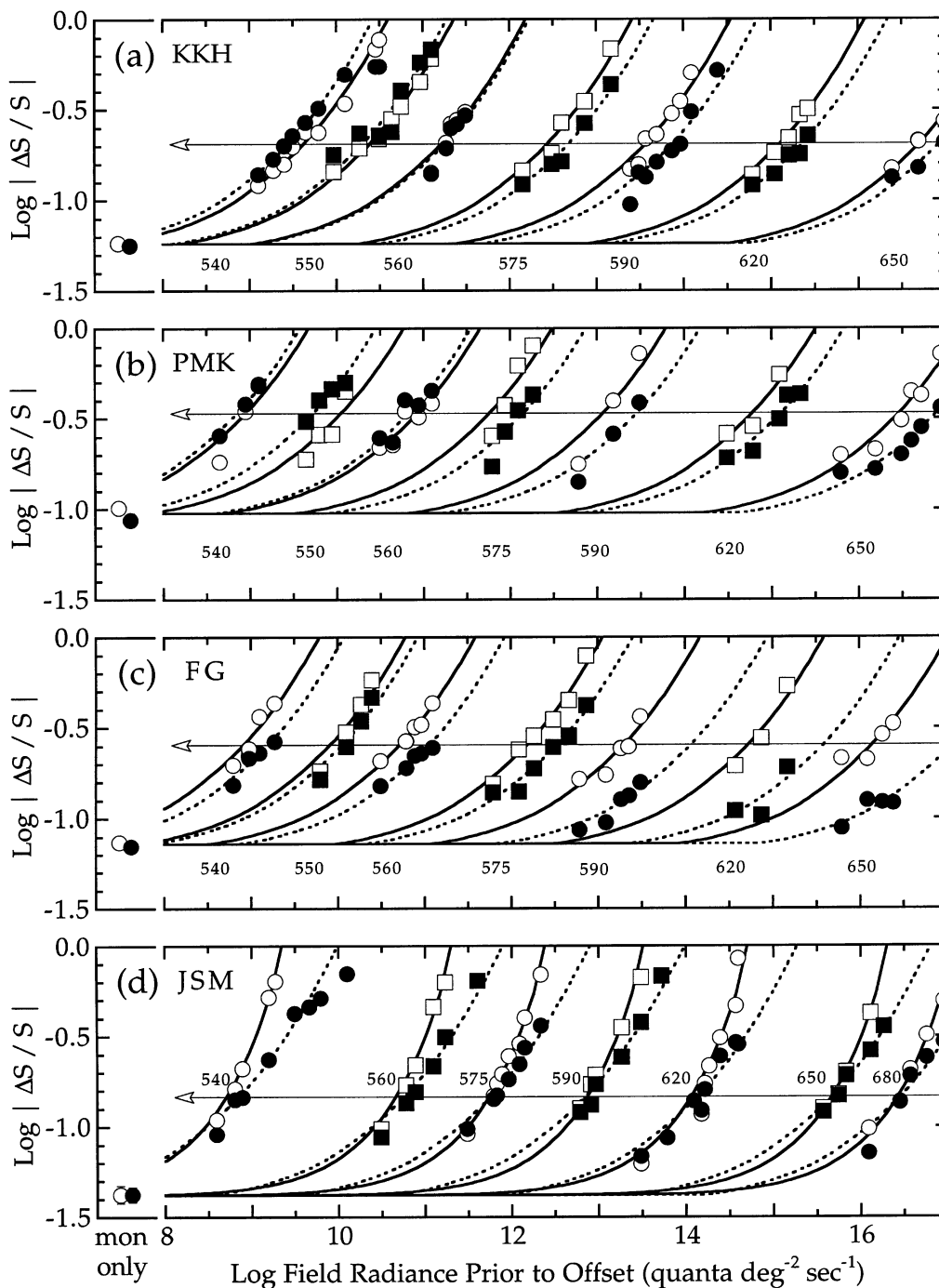


Fig. 5. TvRs for field offset of long-wavelength fields. Increment TvRs are represented by open symbols and solid curves, decrement TvRs by filled symbols and dashed curves. Data for 540 nm fields are shown at their correct radiance values on the x-axis. All other data are translated on the x-axis for clarity. Error bars are plotted for the left-most, monitor-only baseline thresholds. The horizontal arrow indicates a threshold elevation of 0.55 log units above the baseline thresholds (left-most points in each panel). All TvRs for color-normal observers, and decrements for the deuteranomalous observer JSM (panel d), were fit with the Stiles template (Wyszecki & Stiles, 1982). Because this template did not fit the increment functions for JSM well, a new template was derived to fit these data in log–log coordinates. First, a best-fitting power function of the form: $\log(\text{threshold}) = \log(\text{baseline threshold}) + a \{ \log(\text{radiance}) - T \}^b$ was fit to each TvR individually. The mean exponent, b , from these fits was then used to fit a new function to each TvR to determine the mean coefficient, a . The resulting template was translated on the x-axis to find the best fitting value of T for each function.

thresholds would have to be constant. For the color-normal observers, the results therefore imply distinct detection mechanisms for S-cone increments and decrements with different combinations of L- and M-cone inputs to their opponent signals.

5.3. Long-wavelength field sensitivities for S-cone increment and decrement detection

Field sensitivity functions, shown in Fig. 7, were determined by interpolating the field points for 0.55 log-unit threshold elevations from the increment and decrement TvR fits. FG (panel c) did not reach the criterion elevation for decrements on some of the fields, so these field points, (560, 590, 620, 650 nm) indicated by gray symbols, were extrapolated from the TvRs. For each of the color-normal observers, the decrement field sensitivity function (filled symbols) is shifted toward shorter wavelengths relative to the increment function (open symbols). Both the increment and decrement

functions have sharp peaks. For the deuteranomalous observer (lower right panel), the two functions are virtually identical to each other and are much broader than those of the color-normals. (Curve fits are described below.)

The long-wavelength input in the S-cone detection pathway, labeled $f(L, M)$ in Fig. 1, has been previously modeled as a sum of L- and M-cone sensitivities (Pugh & Mollon, 1979; Reeves, 1981b; Zaidi et al., 1992) or as a sum of an $(L + M)$ and an $|L - M|$ opponent term (Wisowaty, 1983). The narrow functions found here for the color-normal observers are not consistent with an additive combination of L and M , but instead suggest a subtractive or divisive influence from an $|L - M|$ input, since increases of both greenness and redness are associated with a relative reduction in sensitivity for both the increment and decrement functions.

The solid and broken curves in Fig. 7a, b, c represent fits of a function of the following form to the increment and decrement field sensitivity data:

$$f(L, M) = 10^{-k} \frac{\alpha L + M}{4|\gamma L - M| + 1} \quad (1)$$

L and M represent cone fundamentals from Stockman et al. (1993). Terms in the numerator may be interpreted as subtractive inhibition (since $f(L, M)$ is subtracted from the S-cone signal in the model), whereas terms in the denominator may be interpreted as divisive inhibition or gain control of the long-wavelength signal (perhaps via presynaptic inhibition). Larger values in the opponent term in the denominator result in less subtractive inhibition of the S-cone signal.

The best-fitting values of parameters k , α , and γ for each observer are given in Table 1. The constant 4 in the denominator was selected on the basis of preliminary analysis. The scale factor, 10^{-k} , was required to be the same for increments and decrements (the best-fitting values were quite similar to each other). PMK's increment function requires less total L-cone input than the other observers, but the three show very similar patterns. The decrement functions are all fit with a numerator L -coefficient, α , very close to 0.0. This is consistent with the findings of Valberg, Lee and Tigwell (1986) that the response of S-OFF cells in the macaque LGN can be modeled with little or no L-cone input. The value of the denominator L coefficient, γ , is about 20% higher for the decrement function than the increment function, reflecting the peak at a shorter wavelength for the decrements. According to this model, regulation of S-cone decrement sensitivity involves less L-cone inhibition, both directly (lower, perhaps zero, α) and indirectly (higher γ), than is true for S-cone increments. In other words, S-cone increments are effectively opposed by a greater L-cone signal than are S-cone decrements.

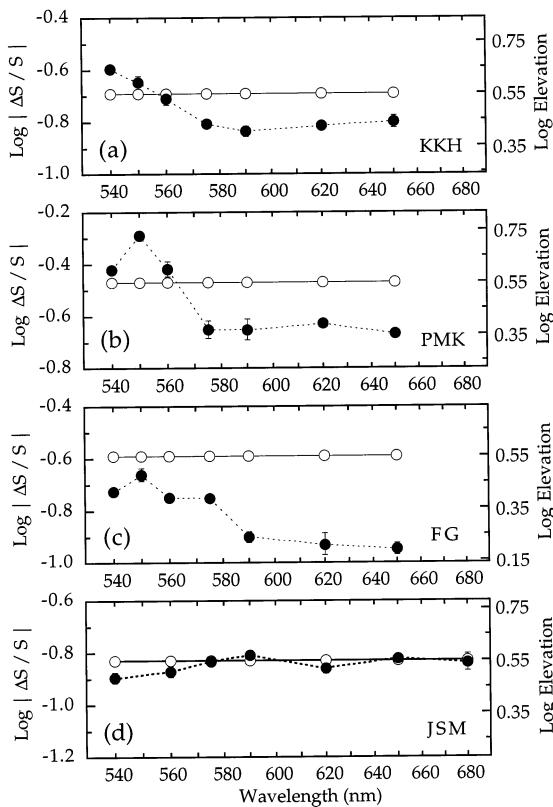


Fig. 6. Decrement threshold (filled symbols) at the increment field points for field-offset conditions. The criterion increment elevation is 0.55 log units above monitor-only baseline threshold. Constant criterion increment threshold is represented by the flat function (open symbols). For the color-normal observers (a–c), decrement thresholds are not a constant function of field wavelength. For the deuteranomalous observer (d) the decrement thresholds appear nearly constant at the increment field points. Error bars are plotted for all the decrement thresholds; these are based upon the error in the fit of the TvR template to the data of Fig. 5.

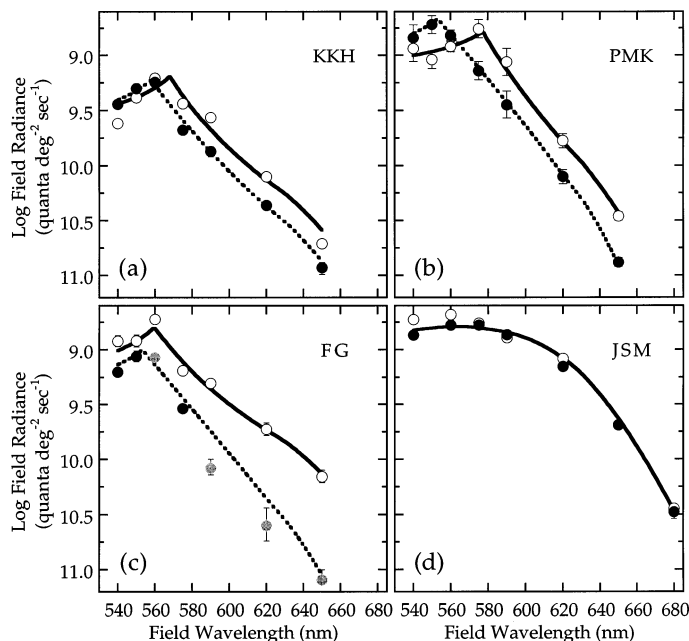


Fig. 7. Field sensitivity functions defined for S-cone increments (open symbols) and decrements (filled symbols). Increment functions are fit with solid curves and decrement functions with dashed curves. There is more influence of L cones on the S-cone increment function than the S-cone decrement function (see text). For FG (panel c), the gray symbols represent extrapolated points. Data from the deuteranomalous observer (panel d) are fit with the L-cone fundamental. Error bars, plotted for every point, are based upon fits of the TvR templates to the data in Fig. 5.

Two complications deserve mention. We cannot completely rule out a rod influence on either field sensitivity function. Rods can cause transient tritanopia in blue cone monochromats and perhaps contribute to it in normals to a small degree (Haegerstrom-Portnoy & Verdon, 1999). More importantly, there may be no unique action spectrum for transient tritanopia, as demonstrated by the background exchange experiment of Mollon and Polden (1979): the order in which the two background fields are presented (not simply their relative intensities) determines the degree of transient tritanopia at a given radiance. Nonetheless, the results in Fig. 7 show clear spectral differences for increments and decrements under the conditions in which we measured them.

The narrow shapes of these field sensitivities found here are not without precedent. The increment functions bear a strong similarity to the field sensitivity of the Π_2 mechanism identified by Stiles (1953), using an increment threshold paradigm. Fig. 8a shows the average model fit (line) for the S-cone increment functions (color normal observers only) along with Π_2 (circles). The π mechanisms are defined for steady adaptation conditions, but because Π_2 is revealed at low adapting intensities that have a negligible first-site effect on S-cones, it may provide a ‘purer’ indication of the L- and M-cone inputs into the S-cone increment pathway than Π_1 . Π_2 has a sharp dip in sensitivity at 580 nm that is not produced by our model, however. The increment field sensitivity functions for the color-nor-

mal are also similar to an action spectrum for combinative euchromatopsia described for one observer by Polden and Mollon (1980, Figs. 7 and 10). Fig. 8b shows these data (circles) with the same average increment function (line) from our model.

Both the increment and decrement field sensitivities for the deuteranomalous observer, JSM, closely resemble the L-cone fundamental (solid curve, Fig. 7d) and therefore appear to reflect a single $f(L, M)$ signal. The difference between these results and those of the color-normals are consistent with the influence of an $|L - M|$ input to the opponent signals for the color normals. Because JSM’s M-cone fundamental is shifted toward longer wavelengths, that is, toward the L-cone fundamental, the sum of L and M is similar to L alone, and the difference signal between L and M is relatively weak. Because this difference signal is weak, it would have less effect upon the field sensitivities for this observer than for the color normals.

Table 1
Best-fitting parameter values for Eq. (1)

Observer	k	Increment fit		Decrement fit	
		α	γ	α	γ
KKH	9.28	0.356	0.791	0.152	0.910
PMK	8.62	0.055	0.670	-0.036	0.959
FG	8.97	0.604	0.892	-0.003	0.958

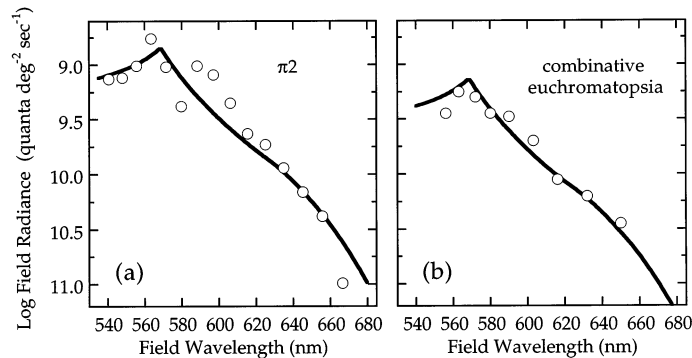


Fig. 8. The average increment field sensitivity function for the color-normal observers (solid curve) compared to (a) the π_2 field sensitivity function (circles) from Stiles (1953) and (b) the action spectrum for combinative euchromatopsia (circles) for one observer from Polden and Mollon (1980). In each case the average $f(L, M)$ increment function was slid vertically for best fit, with no horizontal adjustment.

The large differences in long-wavelength field sensitivities between JSM and the color-normal observers in this experiment stand in stark contrast to their very similar results on short-wavelength fields in Experiment 2 (Fig. 4). Because the S-cones would dominate the field sensitivities on short-wavelength backgrounds, differences in the long-wavelength signals to the opponent sites are likely to be unimportant under these conditions. Since some of JSM's results are inconsistent with the single-pathway model at short wavelengths, it seems likely that increment and decrement detection mechanisms must differ in several respects, not simply in the relative L- and M-cone inputs.

Fig. 6 shows that all observers have fairly constant differences between increment and decrement field points on the longest wavelength fields, with the differences occurring primarily at the shorter field wavelengths. Could this reflect changes in S-cone first-site adaptation rather than opponent-site differences — that is, is it incorrect to assume that all of these fields have a negligible effect on the S-cone first-site? While there is surely some S-cone quantal catch from these fields in the steady state, it is very unlikely that first-site effects have any influence on the field-offset thresholds. This fact can be illustrated by comparing the S-cone quantal catch produced by the 540 nm field to the S-cone quantal catch produced by a white field. For example, the increment field point for KKH at 540 nm produces a 23% increase in S-cone quantal catch relative to that produced by the monitor background alone. The thick gray arrow in Fig. 2a indicates the white field luminance (~ 6 Td) that would produce the same increase in S-cone quantal catch. This field luminance would produce only a negligible threshold elevation under steady adaptation and it is quite reasonable to assume that its effect would be unmeasurable 400 ms after field offset. The close agreement between the increment and decrement field sensitivities and the L-cone fundamental for the deuteranomalous observer argues against contamination of these results by S-cone first-site effects. Furthermore,

a first site effect could not explain the crossing of the increment and decrement TvRs for KKH and PMK from 540 to 575 nm. This result requires different long-wavelength opponent signals for increments and decrements.

6. General discussion

S-cone increment and decrement detection are subject to similar types of cone-opponent effects, but our results, taken as a whole, are not consistent with detection by a single mechanism of the kind described by Pugh and Mollon (1979). If their model is essentially correct for increment detection, then there must be an additional mechanism with different opponent characteristics that regulates decrement detection.

6.1. Two-pathway model

Fig. 9a schematizes a two-pathway model that can produce the kinds of results found here. Each pathway preserves the general form of the working model, but one responds to S-cone increment and the other to decrement tests. Each pathway employs a high-pass temporal filter and signal rectifier, explained below, to limit the response of the pathway to only one stimulus polarity.

In this model, tonic signals and transient signals of both incremental and decremental polarities flow to two different opponent sites. This is consistent with the responses of ON and OFF bipolar cells: despite their names, each of these cells responds to both stimulus polarities, but with depolarization to increments or decrements, respectively. In each pathway an S-cone increment increases the opponent signal and a decrement decreases it. The difference between the opponent signals in the two pathways is indicated by the two functions of L- and M-cone inputs, $f(L, M)$ and $f'(L, M)$. The two sites may also differ in response gain. Each site has a restoring force that causes rebound polarization following field offset (not shown).

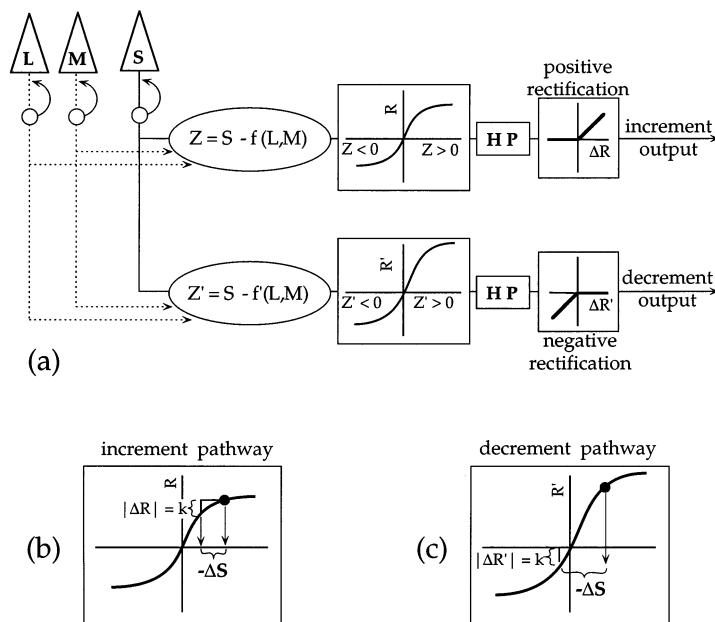


Fig. 9. (a) Two-pathway S-cone detection model. The increment pathway is above, the decrement pathway, below. HP is a high-pass filter. The details of the long-wave inputs f and f' are omitted for clarity. See text for details. (b) and (c) Without high-pass filtering, threshold for an S-cone decrement stimulus under blue polarization would be higher in the decrement pathway than in the increment pathway; a decrement stimulus would need to be large enough to produce a negative opponent signal, i.e. to produce a criterion $\Delta R'$ on the yellow limb of the decrement pathway.

If this were the entire model, then both mechanisms could detect both S-cone increments and decrements. The observed thresholds would be the result of probability summation between these two pathways; different adapting conditions might make one or the other more sensitive. The two pathways become distinct increment and decrement detectors through additional signal processing stages. In each pathway, the response of the opponent site is high-pass filtered and then half-wave rectified. The high-pass filters limit the signals arriving at the rectifiers to transients only, such that information about the state of polarization at the opponent sites is not transmitted to this later stage. The tonic opponent signal therefore maps to the origin at each rectifier. In the increment pathway (upper path in Fig. 9a), the filtered response is positively half-wave rectified, so positive changes in response are signaled, but negative changes are clipped. In the decrement pathway, the opposite rectification occurs, so only negative changes are signaled.²

Threshold in each pathway requires a change in opponent response large enough to produce a criterion

² The signs of incremental and decremental changes do not have to be opposite to each other in this two mechanism model. Both rectifiers could output positive values, in which case both increments and decrements would be signaled by increases in opponent signals at their respective opponent sites. Decrements are depicted as negative changes only to preserve the mnemonic convention of the terms 'blue' and 'yellow' polarization. This sign convention would allow the outputs of these pathways to be recombined at a later stage to produce a unitary yellow/blue hue mechanism.

change in the output of the rectifier. As in the working model, polarized conditions lead to higher thresholds than neutral conditions, but this two-pathway model can account for major features of our data not predicted by the working model because it does not constrain the relationships between increment and decrement thresholds under different adapting conditions. Most importantly, it allows differing field sensitivities for increments and decrements through different spectral combinations f and f' .

Without the high-pass filters, signal rectification could allow increment and decrement detection through the same pathway. Imagine, for example, a case of extreme blue polarization, as illustrated in Fig. 9b and c. The positive opponent signal would produce a positive output at the increment rectifier, and a zero output at the decrement rectifier. An increment stimulus would be detected as usual, as an increase in rectifier output in the increment pathway. To produce a response at the rectifier in the decrement pathway, a decrement stimulus would have to be large enough to make the opponent response negative (Fig. 9c). That is, the decrement stimulus would have to completely cancel the positive polarization before it could produce a decrement pathway response. In the increment pathway, a decrement stimulus would be detected when it caused a criterion change in the increment rectifier output (Fig. 9b); this would require a much smaller decrement than that needed to produce a response in the decrement pathway. A similar problem would occur for increment

detection under yellow polarization. Effectively then, without the high-pass filters, the increment pathway would detect all stimuli under blue polarization and the decrement pathway would detect all stimuli under yellow polarization.

6.2. Other psychophysical results

He and MacLeod (1998) found evidence for a local S-cone nonlinearity, presumably the effect of light adaptation in the cones themselves. They found Weber-like behavior (their Fig. 6) over a range spanning the S-cone adapting levels produced by our monitor alone (S-cone equivalent to a 43 Td, 457 nm background) and the monitor plus the S-cone equated fields in Experiment 2 (S-cone equivalent to a 236 Td 457 nm field). Their smoothly compressive early nonlinearity is consistent with the first-site sensitivity regulation incorporated in our model.

At slightly higher-S cone adapting levels than employed in any of our experiments, Stockman and Plummer (1998) also found evidence for a compressive S-cone nonlinearity, one that produces distortions in S-cone flicker by reducing peak responses compared to trough responses. In their model, the nonlinearity is hypothesized to be an abrupt ceiling. By clipping the S-cone signals, the ceiling would reduce or eliminate detectability of incremental S-cone tests. However, under no condition does their model predict that decrement thresholds will be higher than increment thresholds, as we found in several cases (Figs. 4 and 5), nor does this early nonlinearity offer a mechanism for different field sensitivities for incremental and decremental tests (Fig. 7). Stockman and Plummer (1998) used a very bright 620 nm field to suppress the L- and M-cones, and since our results indicate that relative increment and decrement S-cone sensitivity vary with background wavelength, it is possible that different nonlinear distortions would be observed on other backgrounds.

Shapiro and Zaidi (1992), using the ‘probe-flash’ paradigm, found less threshold elevation of both $+\Delta S$ and $-\Delta S$ tests when presented against a transient change in the background in the $-S$ direction, compared to the $+S$ direction. Vingrys and Mahon (1998), using the ‘test-pedestal’ paradigm, found no masking (only facilitation) of a $-\Delta S$ test on $-S$ pedestals, while the $+\Delta S$ test on $+S$ pedestals produced a conventional ‘dipper’ function with both facilitation and masking. Both of these results are consistent with there being two separate pathways for S-cone increment and decrement detection, with different nonlinear response functions and/or contrast gain control mechanisms.

The working model that guided this research was a simple extension of the model of Pugh and Mollon

(1979) for S-cone increment detection. That model is known to be wrong in some of its details. Its most controversial aspect may be the nature of the restoring force. As originally proposed, the restoring force was either a feed-forward or feedback linear subsystem with a long time constant. If this were correct, a fast flickering field would produce the same threshold as a steady field of the same time-average intensity; instead, flickering fields often produce no threshold elevation (Loomis, 1980; Reeves, 1981a). This failure of the working model is the major reason that we have not yet attempted to quantitatively fit our entire model to the data. In the context of the current experiments, however, any single detection mechanism will produce a constant relationship between increment and decrement thresholds at field offset, regardless of the precise form of the restoring force. Thus, although the Pugh and Mollon (1979) model is clearly not entirely correct, it seems unlikely that modifications of it designed to improve its prediction of restoring force effects would alter any of our conclusions. We have been unable to devise any plausible single-channel model that would account for the differences between our increment and decrement data.

The differing long-wavelength contributions to the S-cone increment and decrement detection pathways may be compatible with results indicating the existence of multiple, ‘higher-order’ or nonclassical color mechanisms (Krauskopf et al., 1986). The present findings might suggest there are two distinct ‘blue-yellow’-like pathways, with different long-wavelength sensitivities that might be revealed under conditions of chromatic adaptation (e.g. Webster & Mollon, 1994) or masking (e.g. D’Zmura & Knoblauch, 1998). When only the L- and M-cones are modulated, most experiments have found evidence for only the two, classical red-green and luminance mechanisms (Li & Lennie, 1997; Sankeralli & Mullen, 1997; Giulianini & Eskew, 1998; but see Gegenfurtner & Kiper, 1992), consistent with the idea that nonclassical color mechanisms might result from asymmetries in S-cone signal processing alone.

6.3. On and off pathways

If there are two separate detection mechanisms for S-cone increments and decrements, they are most likely the S-ON and S-OFF pathways. Despite arguments against the functional importance, and even the existence, of an excitatory response to S-OFF signals (Malpeli & Schiller, 1978; Zrenner & Gouras, 1981; Evers & Gouras, 1986), there is physiological (Derrington, Krauskopf & Lennie, 1984; Valberg et al., 1986; Lee, 1996) anatomical (Klug, Tsukamoto, Sterling & Schein, 1993; Calkins, 1999) and psychophysical (Smith, Harwerth, Crawford & Duncan, 1989) evidence in monkeys and psychophysical evidence in humans (Shinomori, Spillmann & Werner, 1999) that S-cone

signals travel through both ON and OFF pathways. Because the maintained firing rate of retinal ganglion cells is low, it is likely that decrement stimuli are usually detected through OFF pathways (Schiller, 1992).

The demonstration of differences between increment and decrement sensitivities is not new, nor is the idea of invoking ON and OFF channels to account for these differences. Detection asymmetries using either increment and decrement stimuli or rapid-on and rapid-off sawtooth test and habituation stimuli have been shown with both achromatic (Patel & Jones, 1968; Kelly & Savoie, 1978; Krauskopf, 1980; Bowen, Pokorny & Smith, 1989) and S-cone (Krauskopf, Williams & Heeley, 1982; Shinomori et al., 1999) stimuli. Such asymmetries have generally been interpreted in terms of ON and OFF channels (Krauskopf, 1980; Bowen et al., 1989; Shinomori et al., 1999). In these cases, the asymmetries themselves were taken to imply different detection mechanisms, with different response gains and/or different temporal adaptation characteristics.

However, we have shown that a single mechanism model predicts sensitivity asymmetries for increments and decrements under certain adaptation conditions, particularly those involving the offset of an adapting field. The results of Experiment 2 provide a qualitative rejection of the single mechanism model because the pattern of asymmetries across adapting wavelengths does not follow the model's predictions, and the results of Experiment 3 give a robust argument for separate mechanisms by demonstrating a changing relationship between increment and decrement sensitivities as a function of adapting wavelength. These results indicate that the signals must travel through different physiological pathways, with different opponent characteristics, and the most plausible pathways are the ON and OFF. Shinomori et al. (1999) also found that the pattern of threshold asymmetries for their rapid-on and rapid-off S-cone stimuli varied with habituation wavelength and concluded that the ON and OFF channels have different chromatic properties.

6.4. Anatomy

The bi-stratified ganglion cell (Dacey & Lee, 1994), which has been identified as a part of the S-ON pathway, receives excitatory input from S-ON bipolar cells and from L-OFF and M-OFF DB2 and DB3 bipolars (Calkins, Tsukamoto & Sterling, 1998; Calkins, 1999). S-OFF ganglion cells are believed to be more similar to the mid-ganglion cells, receiving excitatory input from bipolars and inhibitory input from amacrine and horizontal cells (Calkins, 1999; Klug et al., 1993). These differences could plausibly result in different long-wavelength field sensitivities as found here for increment and decrement detection. But they do not explain the narrow shape of these field sensitivities, modeled here as arising

from $|L - M|$ opponent inputs. It is conceivable that some of these interactions occur as late as the cortex, but transient tritanopia has been shown by ERG recordings to occur at the level of the bipolar cells (Valeton & van Norren, 1979). Inhibitory feedback could arise from axonal connections of HII horizontal cells to the S-cones (Ahnelt & Kolb, 1994), but because all cone inputs to horizontal cells are excitatory (Dacey, Lee, Stafford, Pokorny & Smith, 1996), HII cells could not be the seat of $|L - M|$ opponency. Furthermore, feedback directly on the S-cones themselves would not lead to qualitatively different results for increment and decrement detection.

7. Summary and conclusion

Sensitivities to both S-cone increments and decrements are regulated, in part, by inputs from other cone types. Both increments and decrements show transient tritanopia and combinative euchromatopsia, signatures of cone-opponent detection mechanisms. However, the pattern of threshold elevations produced by removing adapting fields is not consistent with the two polarities of S-cone stimulation being detected via a single pathway. After blue background fields are extinguished, increment thresholds are higher than decrement thresholds, but predictions of a single mechanism would suggest the reverse due to rebound, 'yellow' polarization in the channel. When the radiance of long-wavelength fields, fields that do not stimulate the S-cones, is varied to produce a criterion elevation in threshold upon offset, the relative sensitivity to these long-wave fields is different for the two S-cone polarities. The derived action spectrum is shifted to shorter wavelengths for the decrements. This is evidence of two distinct detection mechanisms, presumably ON and OFF pathways, with different cone-opponent characteristics.

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