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# Asymmetric high-contrast masking in S cone increment and decrement pathways

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ABSTRACT

Physiological, anatomical, and psychophysical evidence points to important differences between visual processing of short-wave cone increments and decrement (S+ and S−) stimuli. The present study uses the pedestal discrimination paradigm to investigate potential differences, using S+ and S− tests presented on (L)ong-wave, (M)edium-wave, S, L+M, L−M, and achromatic pedestals, of both contrast polarities. Results show that high contrast 'purplish' (S+ or −(L+M)) pedestals produce substantially more masking of both S+ and S− tests than 'yellowish' (S− or +(L+M)) pedestals do. The other pedestals produce no masking. These findings suggest greater nonlinearity – either a static nonlinearity or contrast gain control – in the mechanisms responsible for the 'purplish' polarity, likely the S ON pathway.

## 1. Introduction

### 1.1. S cone polarity differences

Like signals from L and M cones, S cone signals are split into ON and OFF channels early in the retina (Dacey, Crook, & Packer, 2014; Klug, Herr, Ngo, Sterling, & Schein, 2003). The ON pathways respond with excitation to increments in S cone quantal catch and the OFF pathways respond with excitation to decrements in S cone quantal catch.

Tailby, Solomon, and Lennie (2008) studied parafoveal LGN cells responding with excitation to both S increment and S decrement quantal catches in anesthetized macaques, and found a number of qualitative functional differences between them. S ON cells were more sensitive to contrast and saturated at high contrasts, whereas S OFF cells had lower maintained discharge, and were less sensitive and more linear. Unlike S OFF cells, S ON cells showed no contrast adaptation (habituation). Both cell types were found to combine cone signals linearly. S ON cells typically had the shortwave signal opposed to both L and M cone inputs, but in S OFF cells, the S signal and the M signal were more commonly jointly opposed to the L cone signal. Chatterjee and Callaway (2003) presented evidence that the S cone ON and OFF pathways are found in different laminae of V1, suggesting that the two pathways remain distinct until at least the early stages of cortical processing. Thus, differences seen in LGN activity between ON and OFF cells might also be reflected in behavior.

Psychophysical evidence supports the existence of qualitatively distinct S cone pathways for increments and decrements, which presumably reflects differences between the most sensitive S ON and S OFF cells. McLellan and Eskew (2000) found that transient tritanopia with S cone increments and decrements had different field sensitivities. Increment field sensitivities were shifted to longer wavelengths relative to decrement field sensitivities, suggesting greater L cone opponent influence on S + detection than for the S− detection—a result that seems inconsistent with the most frequently-occurring cells of Tailby et al. mentioned above. Recently, Wang, Richters, and Eskew (2014) showed that the identical masking noise raised S+ thresholds to a much greater degree than S− thresholds; this was true for all the noise chromaticities tested except achromatic noise, which produced equivalent (albeit weak) masking of S+ and S−. This latter result indicates that the difference between the mechanisms detecting S+ and S− involves cone opponent signals. However, unlike McLellan and Eskew (2000), Wang et al. did not find relative field spectral sensitivity differences. In a psychophysical study using both humans and monkeys, Gagin et al. (2014), like Wang et al., found higher S+ thresholds and more reduction with practice for S+ than S− tests (in the presence of achromatic noise). Other differences between S+ and S− physiology and psychophysics have been recently summarized by Smithson (2014).

The present experiments attempt to better characterize these increment and decrement pathways. These experiments study S cone increment and decrement sensitivity across a variety of contrast

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conditions, using a pedestal discrimination procedure (Graham, 1989).

### 1.2. Pedestal discrimination

In a temporal two-alternative forced choice version of the pedestal discrimination procedure, a "pedestal" stimulus of constant contrast and chromaticity is presented in both time intervals of a trial. A test is added to the pedestal in one of the two intervals, chosen randomly, and the observer must discriminate the pedestal plus test interval from the pedestal alone interval. In separate runs, pedestals of different contrasts are used to measure the relationship between test threshold and pedestal contrast (sometimes called a threshold vs. contrast or TvC function), for a given pedestal chromaticity (Chen, Foley, & Brainard, 2000; Foley & Legge, 1981; Nachmias & Kocher, 1970; Nachmias & Sansbury, 1974).

Different pedestal contrasts can raise (mask) the test threshold, reduce (facilitate) it, or have no effect on it. A lack of effect of a clearly-visible pedestal suggests that the mechanism(s) responding to the pedestal are independent of the mechanism(s) responding to the test. Masking may occur with high contrast pedestals, often thought to be the result of the pedestal engaging contrast gain control mechanisms to reduce contrast sensitivity (Mullen, Kim, & Gheiratmand, 2014; Wilson & Humanski, 1993). Masking is generally taken to imply that the same pathways respond to both test and pedestal (Cole, Stromeyer, & Kronauer, 1990; Webster, De Valois, & Switkes, 1990). Facilitation or negative masking (i.e., discrimination better than detection; Graham, 1989; Nachmias & Sansbury, 1974) may occur with low contrast pedestals. Low contrast facilitation may be interpreted to result from an accelerating nonlinearity at low contrasts, approximating subthreshold summation (Graham, 1989; Nachmias & Sansbury, 1974; Solomon, 2009), an interpretation that also assumes the pedestal and test act within the same mechanism. Facilitation might instead result from a higher-level interaction between two detection mechanisms, for example by channel uncertainty reduction (Pelli, 1985). However, Eskew, Stromeyer, Picotte, and Kronauer (1991) showed that uncertainty reduction could not account for facilitation of red or green chromatic tests by luminance pedestals; another higher-level process, modulation of filling-in effects by edges, might (Boynton, Hayhoe, & MacLeod, 1977; Eskew, 1989). Because the stimuli in the present experiments have blurred, rather than sharp edges, these edge effect are likely to be minimal here (Gowdy, Stromeyer, & Kronauer, 1999).

Several previous studies have measured chromatic pedestal effects with bipolar – grating – stimuli (Chen et al., 2000; De Valois & Switkes, 1983); their peaks produced equal and complimentary cone contrasts. Although Cao, Zele, Smith, and Pokorny (2008) used unipolar S cone stimuli (squares), they averaged opposing polarities together prior to reporting their results (Cao, personal communication). Mixing the two polarities would obscure potential polarity differences that are the focus of the present paper.

Vingrys and Mahon (1998) used a four-alternative forced choice task with unipolar (spot) stimuli, and cardinal axis color directions. Unlike the present experiment, however, the test and pedestal they used always had the same chromaticity. One of Vingrys and Mahon's results – an asymmetry for S+ and S− polarities – is replicated and extended here, as discussed later.

## 2. General methods

### 2.1. Apparatus

Stimuli were created on a Macintosh G4 computer and displayed on a Sony Trinitron Monitor by an ATI Radeon 7500 video card, with a driver verified to support 10-bit digital-to-analog conversion. A steady white background (x = 0.301, y = 0.309 and 51.5 cd/m$^2$) was used for all conditions. The observer's head position was stabilized using a chin and forehead rest. Viewing was monocular, at a distance of 68.5 cm. The monitor was calibrated using a PR-650 spectroradiometer. Correction for the intensity nonlinearity of the monitor was achieved by software look-up tables.

### 2.2. Subjects

After giving informed consent, six observers participated in different parts of these experiments: SHG (author), RTE (author), JG, RJG, SSM and DR. Except for RTE (who was 52 years old at the time of data collection), all observers were in their 20 s. All six had normal scores on the Munsell 100-hue test, and all were practiced observers. Northeastern University's institutional review board approved the research protocol, and the procedures conformed to the Declaration of Helsinki.

### 2.3. S cone isolation

The Stockman and Sharpe (2000) quantal cone fundamentals, interpolated to 1 nm intervals, were multiplied by the monitor's red, green, and blue primaries, and the product integrated over wavelengths, in order to find the isolating RGB direction for the short-wavelength cones. Changes along this isolating direction produced no modulation of the L and M cones for this standard observer, while incrementing or decrementing the quantal catch rates in the S cones.

The accuracy of this isolating direction was tested for some of our observers using the following method (McLellan & Eskew, 2000; Wang et al., 2014; Webster & Mollon, 1994). The monitor was viewed through a beamsplitter cube mounted near the eye. A circular field of 420 nm light of 17 td (as measured through the beamsplitter), from an optical channel arranged at right angles to the direction of gaze, was combined in the beamsplitter with the image of the monitor. This weak violet field, which overlaid the central region of the monitor image, reduces the cone contrasts generated by stimuli on the monitor, an effect that is about four times more powerful for the S than the L or M cones, so that it elevates S cone thresholds selectively.

Three observers (SHG, JG and RTE) measured their detection thresholds using the method of adjustment, viewing the monitor through the beamsplitter, with and without the 420 nm field. The nominal S cone isolating direction and nearby directions in the space of our monitor primaries, were used. The direction of maximal elevation was taken as the actual S cone isolating direction. For RTE and JG, this was the Stockman & Sharpe direction. For SHG, the estimated S cone direction was slightly different, and this new RGB direction was used for all SHG's S cone stimuli in the main experiment. For the other observers, the Stockman & Sharpe direction was assumed.

### 2.4. Stimuli

Test stimuli for each condition were S cone increments or decrements. The *pedestal* chromaticity varied from condition to condition. Pedestal conditions were S cone, L cone, M cone, equal L and M cone combination (of same sign, L+M, and of opposite sign, L−M), and increment and decrement achromatic, ± (L+M+S), where equality is in cone contrast units.

The stimuli, which are profiled in Fig. 1 and depicted in Wang et al. (2014), were radial raised Gabors, with a radial profile described by:

$$y(\rho) = Ck\, e^{-\frac{\rho^2}{2\sigma^2}}[1-Cos(2\pi f\rho)]$$

The eccentricity ρ is measured in degrees from the center of the display, the radial spatial frequency is f = 1/2 cpd and the Gaussian window had σ = 1°; *C* is the contrast, and k = 0.7584 normalizes to unit peak. This annular spatial profile peaks near 1 deg eccentricity, and increases the likelihood of test detection by the S cones, which are most dense near there (Curcio et al., 1991), and the hole in the middle decreases the likelihood of test detection by L or M cones, which are most

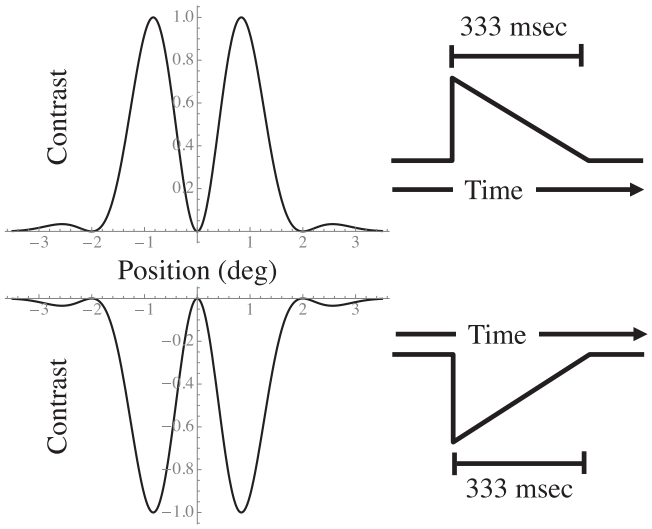


**Fig. 1. Stimuli.** Increment (top row) and decrement (bottom row) test and pedestal spatial and temporal profiles. The spatial profile of the stimuli (left column) shows peak contrast near 1° eccentricity and a contrast of zero in the center of each stimulus. All stimuli were presented using a rapid start temporal sawtooth waveform depicted in the right-hand column. All stimuli were displayed for a total time of 333 msec.

dense in the central fovea. The use of this test helps assure S cone isolation for the high-contrast S cone pedestals, where there might otherwise be small failures of silent substitution.

All stimuli were presented with a "rapid-start" sawtooth waveform. Rapid start sawtooth stimuli immediately jump to the extreme contrast (negative or positive for decrements or increments, respectively), and then gradually return to the mean field (over the next 333 ms), as shown on the right of Fig. 1. The rapid-start temporal profile, presented in two contrast polarities, is designed to differentially favor ON and OFF pathways, by avoiding an opposite polarity transient at the end of the stimulus presentation.

Pedestal contrasts were selected to be at multiples of their own thresholds. In some cases, thresholds for the two polarities (eg., +L and −L) were so similar that they were averaged before calculating the multiples; in other cases (e.g., +(L+M) and −(L+M)), they were not. Cone contrast values for the highest contrast pedestals are given in each figure panel.

For each observer, S+ and S− threshold multiples, for pedestals and tests, were calculated based upon the final, overall estimates of threshold without a pedestal (ie, based upon all the conditions in which a given observer participated). These no-pedestal threshold values are given in Table 1, below, in cone contrast units.

### 2.5. Procedure

Detection thresholds were measured by a temporal 2AFC double staircase procedure. Observers were adapted to the white background field for 90 s prior to each run of 100 trials. The observer initiated each trial and received feedback after each response. The pedestal contrast was fixed for a run. In each interval of a trial, the pedestal was presented using the rapid-start temporal profile (Fig. 1); the test was superimposed on the pedestal, with the same rapid-start time course, in one randomly-selected interval. In other words, the test contrast incremented the start of, and steepened, the sawtooth pedestal waveform (since the pedestal + test waveform returned to zero after 333 ms just as the pedestal alone waveform did). The test contrast was decreased by 0.1 log units after three consecutive correct responses and increased by the same amount after one incorrect response, converging on approximately 79% correct. Weibull functions were fit to the frequency-of-seeing data from each run using a maximum likelihood method (Watson, 1979) to estimate two parameters of the psychometric function for each stimulus: a threshold estimate corresponding to a detection rate of 82% and an estimate of the psychometric slope. Reported data points are the average of 3 to 5 threshold estimations for a given condition.

**Table 1**
Mean and (standard error) of S+ and S- thresholds, in cone contrast units. Standard errors are based on between-condition (ie, between pedestal chromaticity) variability for the observers who participated in more than one pedestal condition.

| Subject | S+ | S− | \|S+/S−\| |
|---|---|---|---|
| SHG | 0.053 | −0.038 | 1.40 |
| | (0.002) | (0.002) | |
| JG | 0.049 | −0.035 | 1.40 |
| | (0.002) | (0.001) | |
| RJG | 0.044 | −0.036 | 1.22 |
| | (0.006) | (0.004) | |
| RTE | 0.028 | −0.016 | 1.75 |
| SSM | 0.037 | −0.033 | 1.12 |

## 3. Results and discussion

### 3.1. No-pedestal thresholds

Each condition described below measures S cone increment and decrement tests. The thresholds for detecting S+ and S− alone were collected along with each condition for each subject. Table 1 summarizes these no-pedestal thresholds, which are based upon the entire dataset. These values were used to calculate test (and, for the S cone pedestal condition, pedestal) threshold multiples (Methods).

In each case, the S cone increment threshold is higher than the S cone decrement threshold (see also Wang et al., 2014, Table 1, and Gagin et al., 2014), with substantial individual differences; the more practiced observers (especially SHG and RTE, who had substantial experience in detecting S cone stimuli prior to the present study) tend to show greater asymmetries. Tailby et al. (2008) found even larger average differences in LGN cells: contrast gain was over twice as large in S ON compared to S OFF cells. However, maintained discharge differed by nearly the same factor in the same direction, suggesting that perhaps the signal/noise ratio was nearly the same for weak S+ and S− stimuli in these parafoveal cells.

### 3.2. S cone pedestals

Fig. 2 shows results from the use of S cone increment and decrement pedestals and tests. The origin, in the center of each panel, represents the constant gray background. S cone increment *pedestal* contrasts are plotted to the right and the decrement *pedestal* contrasts to the left in each plot, while S cone increment *test* contrasts are plotted in the top half and decrement *test* contrasts in the bottom half of each plot.

In Fig. 2 and the subsequent TvC plots, the S cone axes are scaled in threshold units, for each observer separately, using the threshold values given in Table 1. S+ and S− threshold units were applied separately, such that there are different pairs of scale factors in each of the four quadrants of Fig. 2.

As shown in this and subsequent figures, near-threshold as well as high-suprathreshold pedestal contrasts were used. The results with the weak pedestals turned out to be noisy, for all the pedestal chromaticities used. These data will be used to make a point about facilitation by some pedestal chromaticities, below, but the focus will be on high contrast pedestals.

More masking is found using high contrast S cone increment pedestals than with high contrast S cone decrement pedestals, regardless of the test polarity, as shown by comparing the left and right sides of each panel in Fig. 2. The asymmetry may initially seem paradoxical because the pedestal and test are the same chromaticity, suggesting there should be mirror symmetry in the TvCs. However, in the parts of the plots

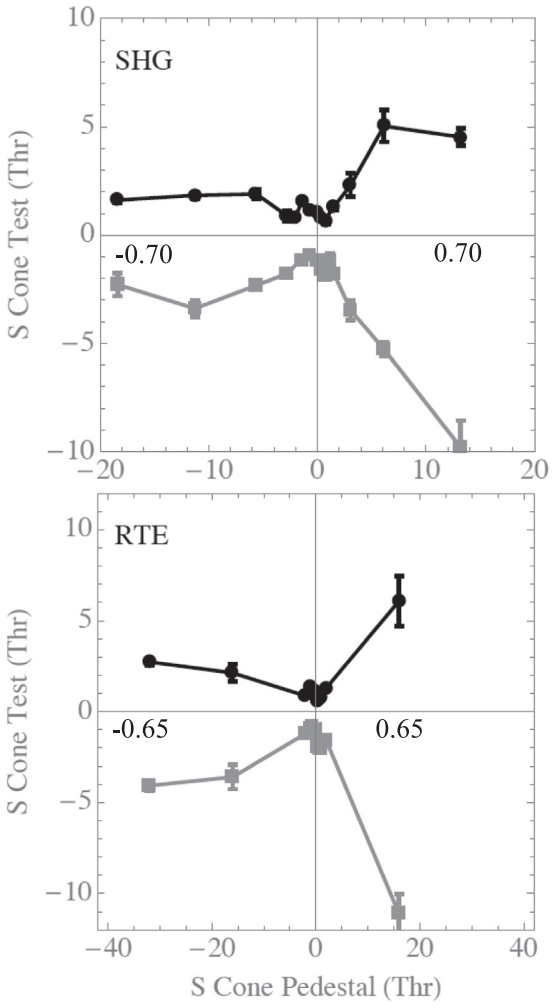


**Fig. 2.** TvC functions for S tests on S pedestals, for two observers. The horizontal axis represents, in no-pedestal threshold units, the pedestal contrast, with S− pedestals to the left and S+ ones to the right in each panel. The vertical axis represents, also in threshold units, the S+ test (upwards) and S− test (downwards). RTE was tested with higher contrast S− pedestals than were those used for SHG (note different horizontal axis scales). The numbers near the horizontal axis give the cone contrast vector lengths of the most extreme pedestals. Error bars, plotted when larger than the symbol, represent plus and minus one standard error (based upon between-run variance).

showing the asymmetry, the pedestal is presented at much higher contrast than the test, suggesting that the asymmetry is only apparent at high contrasts (see Discussion and Wang et al., 2014). The asymmetry is not reduced if the data are replotted in cone contrast units.

Vingrys and Mahon (1998) found a limited version of this same asymmetry. In their experiment, the test and pedestal had the same chromaticity (i.e. tests on pedestals were S+ on S+ or S− on S−, as in Quadrants I and III of Fig. 2). S+ tests were masked by strong S+ pedestals, but S− tests were not masked (but were facilitated) by S− pedestals. From those results it cannot be determined whether the polarity difference is a property of the test polarity, the pedestal polarity, or both. By adding the cases in Quadrants II and IV, in which S+ tests were shown on S− pedestals and S− tests on S+ pedestals, respectively, we show that the effect is due to the pedestal (i.e. high contrast stimulus) polarity.

This increment-decrement pedestal asymmetry is novel: it is not seen in the red/green or luminance TvCs of Cole et al. (1990), and it cannot be seen in studies using bipolar stimuli (Chen et al., 2000; Mullen & Losada, 1994) or studies that average over contrast polarities (Cao et al., 2008). It is, so far as we can determine, unique to detection by mechanisms dominated by S cones.

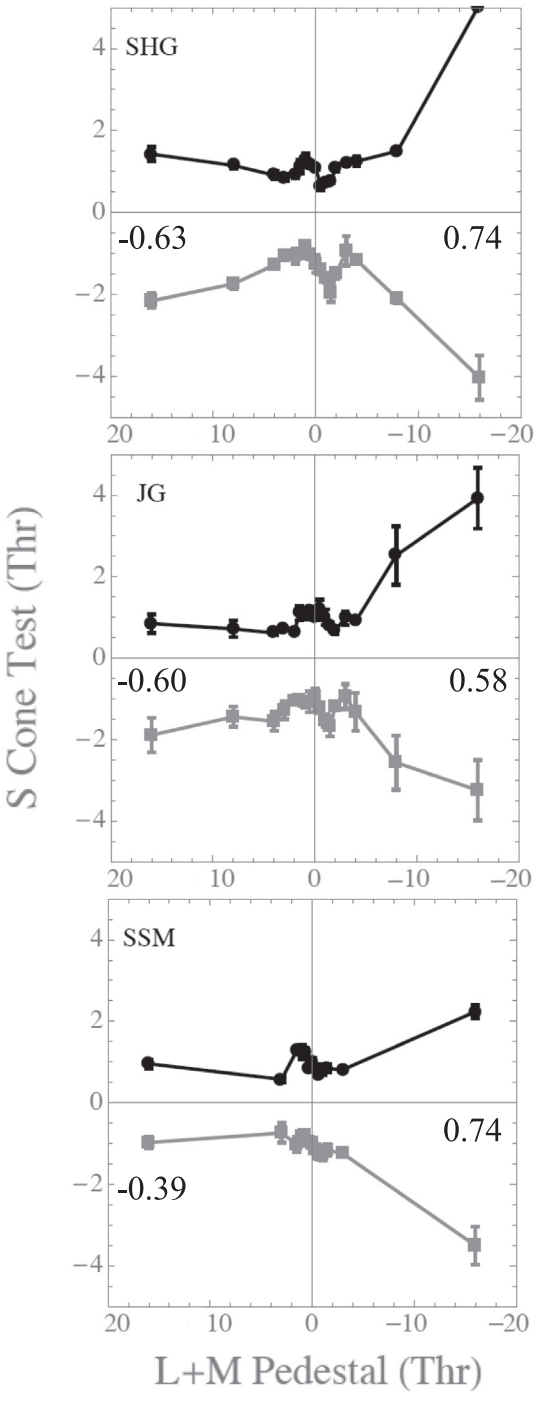


**Fig. 3.** TvC functions for S tests on L+M pedestals, for three observers. All panels show L+M pedestal strength in threshold units (with the yellowish increment, L+M on the left of each panel and purplish decrement, −(L+M) on the right) with S cone tests, also in threshold units (S+ on the top and S− below). The numbers near the horizontal axis give the cone contrast vector lengths of the most extreme pedestals. Error bars, plotted when larger than the symbol, represent plus and minus one standard error (based upon between-run variance).

### 3.3. L+M pedestals

Next, an L+M pedestal (equal L and M cone contrasts) was substituted for the S cone pedestal. If the L+M contrasts are transmitted by the same visual pathways as the S cone stimuli, as predicted by classical

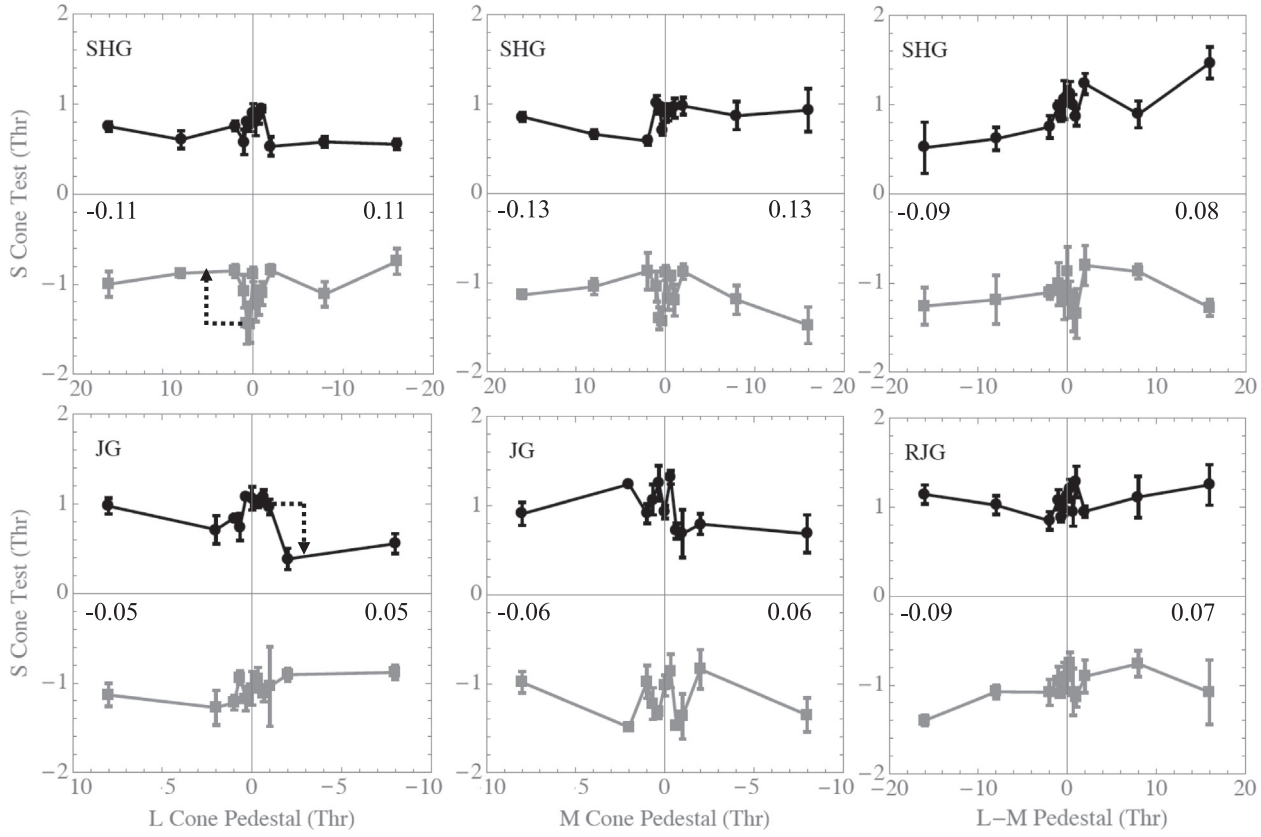


**Fig. 4.** TvC functions for S tests on L, M, and L − M pedestals (left, middle, and right columns, respectively), for three observers (one in the top row and two different ones in the bottom row). Tests and pedestals are expressed in threshold units, as in Figs. 2 and 3. Note the vertical scale only extends to 2× threshold, unlike Figs. 2 and 3. The dashed arrows in the left-most two panels illustrate examples of facilitation, in which the pedestal has reduced the test threshold compared to the no-pedestal and very weak pedestal conditions near the origin (see Section 3.6). SHG and RJG were tested with stronger pedestals than JG (note horizontal axis scales). The numbers near the horizontal axis give the cone contrast vector lengths of the most extreme pedestals. Error bars, plotted when larger than the symbol, represent plus and minus one standard error (based upon between-run variance).

color models that have the 'yellow' signal composed of some mixture of L and M cone signals (e.g., Boynton, 1979), these long-wave pedestals should function like the S cone pedestals in Fig. 2. Fig. 3 shows these results. Note that since incremental L + M stimuli appear yellowish (similar to S −) in color and decremental L + M stimuli appear purplish (similar to S +), in Fig. 3 the horizontal axis is reversed so that the hue polarity of the pedestals agrees with the arrangement in Fig. 2. Fig. 3 shows TvCs for three different observers.

All three observers show the same left-right asymmetry found with S cone pedestals. High contrast, purplish L + M decrement pedestals (right side of each panel) produce more masking than the yellowish L + M increment pedestals (left side of each panel) at high contrast levels, regardless of test polarity. As in Fig. 2, the asymmetry is with respect to the pedestal polarity, not the test polarity. Like the previous results, these results are consistent with greater nonlinearity in the mechanism (s) responsible for 'purplish' stimuli (likely the S ON pathway), compared to those responsible for 'yellowish' ones (likely S OFF). A simple conceptual model of these results will be described in the General Discussion.

Note that there is a difference in the cone contrasts of the most extreme pedestals for SSM (and less so for SHG), because these observers were more sensitive to +(L + M) than −(L + M) stimuli. This sensitivity difference is consistent with prior results (e.g., Giulianini & Eskew, 1998; Shepard, Swanson, McCarthy, & Eskew, 2016), in direction and magnitude (and in showing some individual differences). This sensitivity difference means that replotting the results in cone contrast units, rather than in the threshold multiples used in the design of the study, would slightly reduce the evidence for asymmetry for SSM (but not substantially for SHG, or at all for JG).

Pedestals used in Fig. 3 consisted of equal L and M cone contrasts. Either or both of the L or M signals could be responsible for the pedestal effects. Next, we used the pedestal components in isolation: L cone increment and decrement pedestals as well as M cone ones.

### 3.4. L cone, M cone, and L − M pedestals

Fig. 4 again shows S cone increment tests in the top half of each panel and S cone decrement tests in the bottom half; however, the vertical axis scale has been increased by a factor of 2.5 compared to Fig. 3. The left column shows results with L cone pedestals, the middle column with M cone pedestals, and the right column with L − M ('red/green', approximately equiluminant) pedestals. To parallel Fig. 3, in Fig. 4 the L and M increment pedestals are depicted to the left. In all of these cases there is no consistent effect of the pedestal at any contrast level. Of course, this also means there is no pedestal increment/decrement asymmetry as found with S and L + M pedestals.

The cone contrasts of these L and M pedestals are lower than those of the S or L + M pedestals. This is a consequence of the monitor gamut; we could not produce pedestals of much higher contrast along these color directions. Note, however, that these pedestals are up to 16 times their own detection threshold, because L and M isolating stimuli are detected by highly sensitive mechanisms (Eskew, McLellan, & Giulianini, 1999; Giulianini & Eskew, 1998; Shepard et al., 2016); cone contrast thresholds for these pedestals average 0.0068 for SHG, for example.

The right column shows results with pedestals with equal magnitude L and M cone components like those in Fig. 3 but with opposite polarities (e.g. L cone increment with equal strength M cone

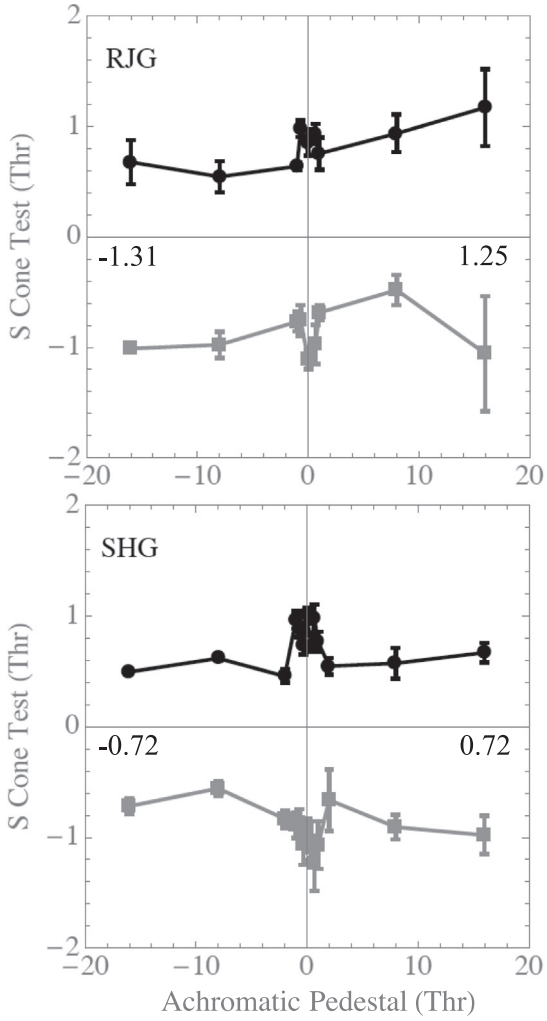


**Fig. 5.** TvC functions for S tests on achromatic pedestals, for two observers. Tests and pedestals are expressed in threshold units, as in Figs. 2 and 3. Vertical scale as in Fig. 4. The numbers near the horizontal axis give the cone contrast vector lengths of the most extreme pedestals. Error bars, plotted when larger than the symbol, represent plus and minus one standard error (based upon between-run variance).

decrement). Like the L and M pedestals, these cone combinations appear red (L > 0, M < 0) and green (L < 0, M > 0) unlike the purplish/yellowish combinations in Figs. 2 and 3; in the plots, 'reddish' is to the right. These pedestals, like those made up of their component L and M contrasts, do not produce masking.

### 3.5. Achromatic pedestals

Our final condition used achromatic pedestals. An achromatic pedestal can be obtained from our L+M pedestal condition by adding equal strength S cone stimulation. The results are plotted in Fig. 5; note again the expanded vertical axis scale compared to Figs. 2 and 3.

Achromatic pedestals produce TvCs similar to those of the L or M cones alone or the L−M condition: no consistent masking. In contrast, L+M pedestals (Fig. 3) cause substantial masking for 'purplish' pedestals. Adding an equal S cone component to the L+M pedestal, producing an achromatic pedestal, eliminated the pedestal effect. Thus, the pedestal signal must be based upon S cones in opposition to L and/or M, and the nonlinearities (e.g., contrast gain control) must operate after the cone signals have been combined. This result parallels the noise masking result of Wang et al. (2014), who found substantial masking by L+M noise but relatively little to achromatic noise.

### 3.6. Facilitation

In Figs. 4 and 5 there is generally facilitation by the weak pedestals: in most quadrants of most of the panels, the thresholds are highest in and near the no-pedestal condition in the center, then drop for the near-threshold pedestals. The two dashed arrows in the left-most panels in Fig. 4 point out examples: facilitation by the L cone pedestals (on S− tests for SHG in the top panel; on S+ tests for JG in the bottom). The length of the vertical arrow represents the reduction in required test contrast in the presence of the pedestal, compared to the no-pedestal threshold plotted at the origin. Although the data are noisy there is evidence of similar facilitation in many cases in Figs. 4 and 5.

This kind of facilitation has been variously interpreted as a reduction in channel uncertainty (Pelli, 1985) or a limit on spatial integration produced by spatially demarcating a region to be detected (Eskew et al., 1991; Gowdy et al., 1999), and it is generally seen for chromaticities detected by distinct chromatic mechanisms (Cole et al., 1990; Mullen & Losada, 1994). The apparent facilitation in Figs.4 and 5, coupled with no masking at high pedestal contrasts, is therefore consistent with the S cone tests being detected by different mechanisms from those processing the L, M, L−M, and achromatic pedestals.

## 4. General discussion

The focus of our research was to more thoroughly study the effects of contrast on the S cone increment and decrement pathways. We studied each combination of S cone pedestals and tests under a variety of different pedestal contrast levels and examined the patterns of masking and facilitation. The main result is the asymmetric masking produced by some high-contrast increment and decrement pedestals, regardless of test polarity, an extension of the limited results of Vingrys and Mahon (1998). The purplish S+ pedestals mask both S+ and S− tests more than yellowish S− pedestals do. Similarly, purplish L+M decrement pedestals mask both S+ and S− tests more than yellowish L+M increment pedestals do. The whole pattern suggests that the L+M pedestals act within the same pathways as the S cone pedestals on the S cone tests, and that the asymmetry reflects a property of a post-receptoral pathway *after* the L and M cone signals have been combined with the S cone signal.

Another important result is that although the L+M pedestals masked S cone tests, the L and M individual components of the L+M pedestal do not. Further, adding an S cone component to the L+M pedestal in the achromatic condition eliminated the masking effect. The pedestal composed of equal L and M contrasts (Fig. 3) acted like the S cone pedestal (Fig. 2), suggesting that both S cone tests are detected via mechanisms that receive an opposing signal composed of both L and M signals, inconsistent with the S+M−L combination found in many of the S OFF cells of Tailby et al. (2008). The failure to observe masking with either the L or M pedestals, while finding them it with their sum, suggests that the opposing signal is a nonlinear combination of L and M, unlike the linear combination proposed in the classical models (Boynton, 1979) and in the more recent model of Wang et al. (2014).[3] However, Wang et al. (2014) obtained substantial masking of both S+ and S− tests using L, M, and L−M noises, and it was possible to model all of the noise masking with linear cone combinations, suggesting that the processes responsible for masking may differ for pedestals and noises.

The asymmetric high-contrast masking might suggest a greater degree of contrast gain control within the S+ than the S− pathway. This is the same conclusion drawn by Vingrys and Mahon (1998) from their

[3] Somewhat complicating this analysis, however, is the fact that L and M stimuli are generally detected by highly sensitive mechanisms (Eskew et al., 1999; Shepard et al., 2016), and thus a pedestal threshold unit in Fig. 4 is of low cone contrast; we cannot rule out the possibility that higher L or M cone contrasts could produce masking, but these higher contrasts are not available on standard displays.

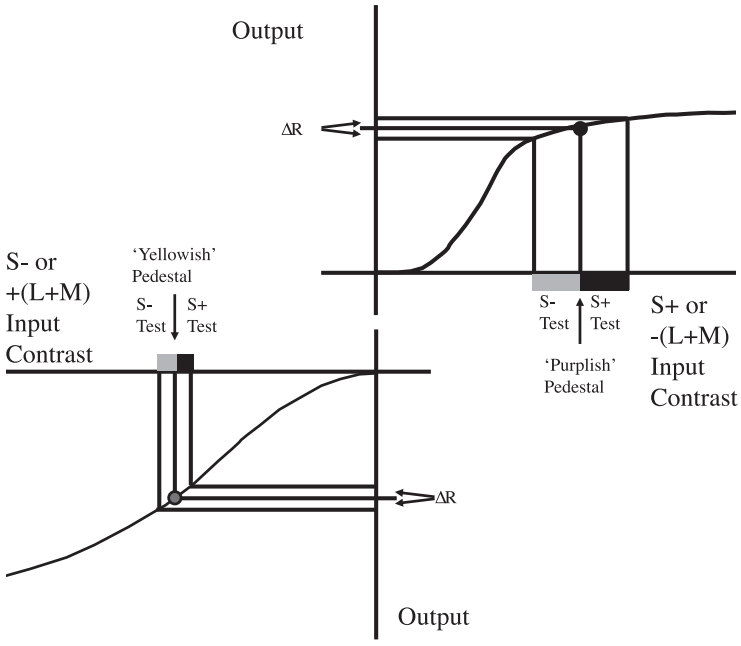


**Fig. 6.** Schematic model of the asymmetric effect of pedestals. The top shows a saturating curve for 'purplish' (S+ or −(L+M)) pedestals. On a high contrast S+ pedestal, a large perturbation in required to reach threshold (ΔR), for either test polarity. The bottom shows a more linear curve for 'yellowish' (S− or +(L+M)) pedestals. On a high contrast S− pedestal, only a small perturbation in required to reach threshold (ΔR), for either test polarity.

limited data. However, the parafoveal LGN cells of Tailby et al. (2008) had a suggestive difference in the opposite direction: S OFF cells showed more habituation to contrast modulation, perhaps due to more gain control. In that same study, however, S OFF cells behaved more linearly with S cone contrast, whereas S ON cells saturated. This contrast linearity difference is completely consistent with our psychophysical result: by saturating at high contrasts, S ON cells would produce psychophysical masking to high-contrast pedestal signals transmitted along the same pathway, regardless of the test chromaticity.

Our major result can be understood in the following way: an S− test could be detected via a decrement in activity in the S+ pathway, and similarly an S+ could be detected via a decrement in activity in the S− pathway; but if there is more saturation or contrast gain reduction in the S+ pathway, there will be a larger effect by S+ pedestals (on both S+ and S− tests) than by S− pedestals (on both S+ and S− tests). The idea is illustrated in Fig. 6. The top half represents processing in the S+ pathway, with the nonlinear 'transducer' representing either a static nonlinearity or the effects of contrast gain control. The gray and black boxes on the horizontal axis represent the amount of perturbation in the channel required to produce a constant, threshold response (ΔR) on top of a S+ pedestal. The two test contrasts are approximately equal. The bottom half shows less saturation or gain control in the S− pathway; again, gray and black boxes on the horizontal axis represent the amount of perturbation in the channel required to produce a constant, threshold response (ΔR), now on top of a S− pedestal. The S+ and S− threshold *tests* are the same within each channel because they are weak and their effect is local, but the difference produced by the S+ and S− pedestals is large. The implications are that the S ON and S OFF pathways, responsible for detection of 'purplish' and 'yellowish' stimuli in general, can be used to detect the oppositely-signed polarity as a decrease in activity, and that the S ON pathways have greater nonlinearity in contrast processing.

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