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Mechanisms contributing to increment threshold and decrement threshold spectral sensitivities

Rebecca Ijekah, John Erik Vanston, Michael A. Crognale*

University of Nevada, Reno, United States

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ABSTRACT

The shape of the human spectral sensitivity function depends on how it is measured. In the increment threshold (IT) technique, sensitivity is typically measured as the inverse of threshold for detection of increments of monochromatic light presented for relatively long durations on achromatic pedestals. Spectral sensitivity functions derived from IT techniques have long been used to reveal contribution from opponent color channels. Although IT functions have been studied extensively, little attention has been given to functions derived from decrement thresholds (DT), partly due to technical challenges of producing appropriate stimuli. Comparison of IT and DT spectral sensitivities may be of interest because there are known asymmetries in the visual system between on- and off-pathways and between increment and decrement responses within these pathways. Consequently, spectral sensitivity functions obtained using DT measures may reveal a different complement of contributing mechanisms than those that produce IT functions. We report here that IT and DT derived spectral sensitivities were essentially identical over much of the visible spectrum. However, decrement sensitivity was slightly greater than increment sensitivity in the shorter wavelengths at modest light levels. This difference was not present at higher light levels, implicating rod pathways as a possible source of the difference. In sum, it appears that under conditions shown to reveal strong contribution from opponent mechanisms, decrement functions are either 1) determined by a similar complement of spectrally opponent mechanisms as those that define increment spectral sensitivities or 2) that the present conditions are insensitive to underlying asymmetries.

1. Introduction

Most modern models of color processing incorporate several early stages (e.g. De Valois & De Valois, 1993), including trichromatic sampling at the cones (e.g. Palmer, 1777; Young, 1802), color opponent interactions (e.g. Goethe, 1810; Hering, 1920; Hurvich & Jameson, 1957), and cortical processing that results in multiple color channels (e.g. Krauskopf, Williams, Mandler, & Brown, 1986; Webster & Mollon, 1991). In the opponent stage, cone signals are differenced and form major pathways posited to provide input for our red-green) and blue-yellow color vision. In non-color opponent pathways, the cone inputs are summed to provide luminance information (e.g. Lee, Martin, & Valberg, 1988). There is a long history of evidence for color opponent processing from observation and psychophysics (e.g. Hurvich & Jameson, 1957; Sperling & Harwerth, 1971) as well as electrophysiology (e.g. De Valois, Smith, Kitai, & Karoly, 1958; De Valois, Abramov, & Jacobs, 1966; Derrington, Krauskopf, & Lennie, 1984; Svaetichin & MacNichol, 1958).

Spectral sensitivity functions can reveal how different underlying channels or “mechanisms” contribute to the overall sensitivity of a system for a given set of stimulus conditions. Different stimulus conditions can favor different mechanisms and produce vastly different functions (e.g. Wagner & Boynton, 1972). The most commonly employed human spectral sensitivity function, the luminosity function, is often determined using a method known as flicker photometry. This technique relies on minimization of apparent flicker at high temporal rates and consequently favors detection from the transient luminance pathways comprising the non-spectrally opponent magnocellular system (e.g. Lee et al., 1988). The standard luminosity function is broad and has a single peak around 555 nm.

In contrast, increment threshold (IT) spectral sensitivities are usually measured using longer duration stimuli presented as narrowband increments on bright and achromatic pedestals. Spectral sensitivities obtained under these conditions favor detection by the spectrally opponent mechanisms (e.g. King-Smith & Carden, 1976). They are rather broad with well separated peaks corresponding to the

* Corresponding author at: Dept. of Psychology/296, University of Nevada, Reno, Reno, NV 89557, United States.
E-mail address: mcrognale@unr.edu (M.A. Crognale).

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underlying photopigment complement and are nicely modeled using a subtractive combination of these photopigments. If the pedestal intensity is lowered or the test durations become shorter, evidence of contribution from luminance channels can be observed. Furthermore, detection can be biased towards different spectral mechanisms using adaptation by spectrally selective backgrounds (e.g. Stiles, 1959). IT functions have been used extensively to help characterize color vision capacities in both human and non-human species (Blakeslee & Jacobs, 1987; Crognale & Jacobs, 1991; Diaconu & Faubert, 2006; Jacobs, Neitz, & Crognale, 1987; Kalloniatis & Harwerth, 1990; Miyahara, Pokorny, & Smith, 1996; Sperling & Harwerth, 1971; Sperling, Sidley, Dockens, & Jolliffe, 1968; Stiles, 1959). Anecdotal observation supports the opponent basis of IT functions as threshold detections are generally reported by observers to be based on a slight change in color of the test stimulus rather than a change in luminance.

Although IT functions have been well characterized, the nature of spectral sensitivities to decrements of test light has not been thoroughly investigated. It is likely that the paucity of data for decrement threshold (DT) spectral sensitivities is in part due to the technical challenges with producing a full complement of spectrally narrow decrements in a controlled and systematic manner that would allow for the acquisition of threshold measurements. However, recent advances in commercially available devices capable of producing specific, arbitrary spectral distributions have been developed that can perform the precise filtering necessary to obtain DT spectral sensitivities.

There are several reasons to investigate the contribution of underlying mechanisms to DT functions. First, there are known asymmetries in the spectrally opponent responses (e.g. Boynton, Ikeda, & Stiles, 1964; Gabree, Shepard, & Eskew, 2018; Klug, Herr, Ngo, Sterling, & Schein, 2003; Shinomori, Spillmann, & Werner, 1999, Shinomori & Werner, 2008; Stockman et al., 2017, Stromeyer, Lee, & Eskew, 1992). Additionally, S-ON signals appear to travel via different pathways than S-OFF signals (e.g. Bosten et al., 2014; Chichilnisky & Wandell, 1996; DeMarco, Smith, & Pokorny, 1994; Klug et al., 2003; McLellan & Eskew, 2000; Smith, Harwerth, Crawford, & Duncan, 1989). Whereas the koniocellular pathway is believed to transport S-ON signals, there is some evidence that S-OFF signals may also be carried by the magnocellular pathways (Chatterjee & Callaway, 2002, 2003; Tailby, Solomon, & Lennie, 2008; Tailby, Szmajda, Buzas, Lee, & Martin, 2008). Additionally, S-ON cells greatly outnumber S-OFF cells (Klug et al., 2003; Lee, Telkes, & Grünert, 2005; Smith et al., 1989). Consequently, IT spectral sensitivities may differ from DT spectral sensitivities because of different characteristics of the ON- and OFF-divisions of spectrally opponent pathways and any other inherent asymmetries in the opponent pathways.

DT spectral sensitivities may be of further interest because in real-world situations, color differences between broad-band (desaturated or white) objects or backgrounds and those that are more colored are often decrements of light rather than increments. This of course, is due to the spectrally selective absorption of light by surface pigments. Thus, the brightest regions in the natural scene tend to be broad-band and/or specular. Exceptions to this in nature include phenomena such as fluorescence and phosphorescence.

In this present study, we compared IT and DT spectral sensitivities using conditions known to elicit strong contribution from the color opponent mechanisms. Specifically, we wished to quantify and compare the relative contributions of the different opponent mechanisms to both IT and DT spectral sensitivity functions. Our findings show that increment and decrement threshold spectral sensitivities likely result from a similar relative contribution from the chromatic opponent mechanisms.

2. Experiment 1: Full IT and DT spectral sensitivity functions

2.1. Methods

Four males and five females between the ages of 21 and 43 years participated in the experiment. Participants had normal or corrected to normal visual acuity and normal color vision as assessed by the Ishihara 38-plate test. Participants provided informed consent and experiments were conducted in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

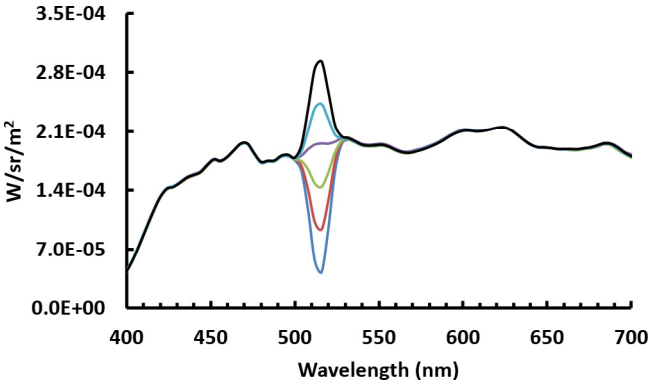

Fig. 1. Example spectra for increments and decrements at 512 nm.

We used a xenon arc source with a tunable filter (OL490 Agile Light Source: Gooch and Housego, Ilminster, UK) with an integrating sphere to display stimuli with precisely defined spectra. The stimulus area was a field comprising the 10 cm circular exit port of the integrating sphere. Spectral output was calibrated and verified using a Photo Research SpectraScan PR-655 spectroradiometer.

Subjects were asked to identify which one of three temporal presentations contained an increment or decrement of monochromatic light on an otherwise broad-band, white pedestal (temporal, three-alternative, forced-choice discrimination). Fig. 1 shows representative spectra for example increments and decrements of 512 nm light. Fig. 2 plots the difference in these spectra from the broadband white for the increments and decrements of Fig. 1. The integrated energies of the difference spectra were used to define the magnitude of the increments and decrements. The mean luminance for the broadband white pedestal was ca. 11 cd/m^2 with a range of 9–13 cd/m^2 and a CIE chromaticity of x = 0.352 and y = 0.357.

Participants were seated 56 cm from the exit port of the integrating sphere. At this distance the stimuli subtended 10 deg. of visual angle. Participants sat in a darkened room for at least 3–5 min and fixated on the white pedestal at the start of each session. For each trial, three successive stimuli were presented for 300 ms each. The presentations and return to pedestal were separated by 200 ms of dark. An audible voice cued each presentation period with a “one”, two”, or “three”. The participant indicating on a keypad which of the three periods differed from the other two in appearance (color and/or brightness). The next trial was presented following each response. The broadband white

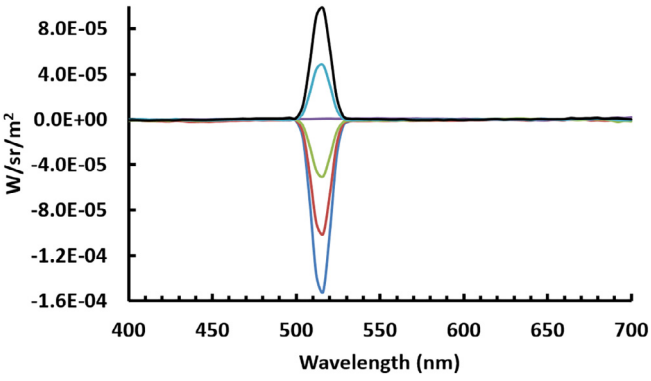

Fig. 2. Difference spectra from the white pedestal for the increments and decrements of Fig. 1.

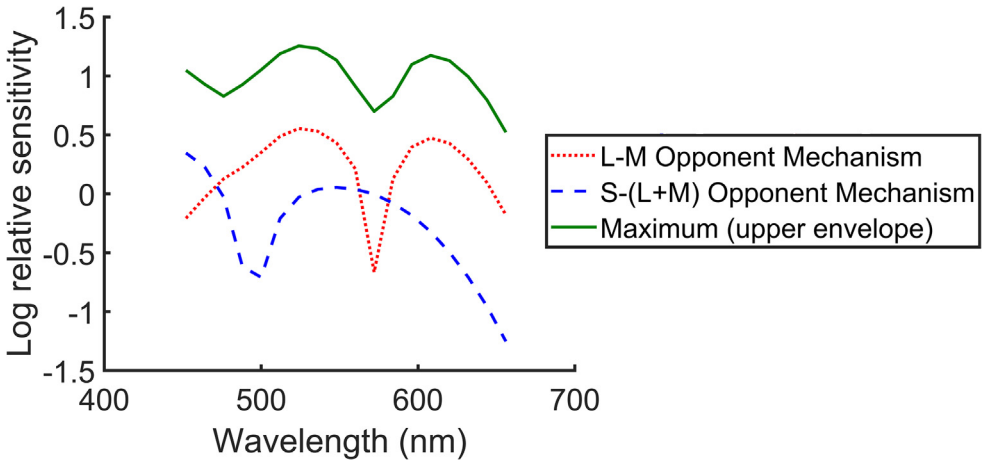

Fig. 3. Opponent model components.

pedestal remained visible between trials. Most participants completed the experiment in 2 sessions.

We used an adaptive staircase paradigm to determine ITs and DTs at wavelengths from 452 to 656 nm in 12 nm steps. We combined a weighted up/down method (Kaernbach, 1991) with optimized step sizes (García-Pérez, 1998). The mean value of the last six reversals was taken as that wavelength's increment or decrement threshold. The inverse of these threshold energies was taken as sensitivity. For each staircase wavelength and condition (IT or DT) were randomly chosen.

We modeled the data based on subtractive and additive combinations of cone fundamentals (Stockman & Sharpe, 2000) (see Fig. 3) in order to assess opponent contributions to the spectral sensitivities. We started with four free parameters: 1) L to M cone ratio – when the fundamentals are differenced and rectified, this ratio defines the shape of the L − M opponent channel; 2) the S to (L + M) cone ratio – here the S cone fundamental is differenced with an additive combination of the L and M fundamentals (using the same ratio as determined in 1) and rectified. This ratio determines the shape of the S − (L + M) opponent channel; 3) opponent channel weight – the relative contributions or weights given to each of the two opponent channels (S − (L + M) and (L − M)); 4) overall sensitivity – essentially a vertical or DC shift of the upper envelope of the combined opponent channels. The final model was thus the shifted upper envelope (maximum sensitivity) of the underlying opponent mechanisms at each wavelength, fit to the data by minimizing the mean squared error (MSE).

We first averaged the increment and decrement data for all participants in Experiment 1 and allowed the four parameters of our model to vary to find reasonable starting values for individual model fitting. We then held the S to L + M cone ratio parameter constant and fit each individual's data for increments and decrements separately to the remaining three parameters. The S to L + M cone ratio parameter was held constant because it is closely related to and largely redundant with the opponent channel weighting parameter.

2.2. Results

In general, the change in the intensity of light needed to detect an increment was comparable to the amount needed to detect a decrement of the same wavelength (see Fig. 4). Although there appears to be a trend in the data indicating perhaps subjects were more sensitive to decrements than increments in the short wavelengths, we found no significant difference between the three parameter fits of the model to the individual IT or DT data. Fig. 4 also shows the average parameter fits of the model to the IT and DT data. There are no obvious differences in contribution from either of the opponent mechanisms, the L to M ratio, or overall sensitivity (see Fig. 5). Two-tailed paired-samples t

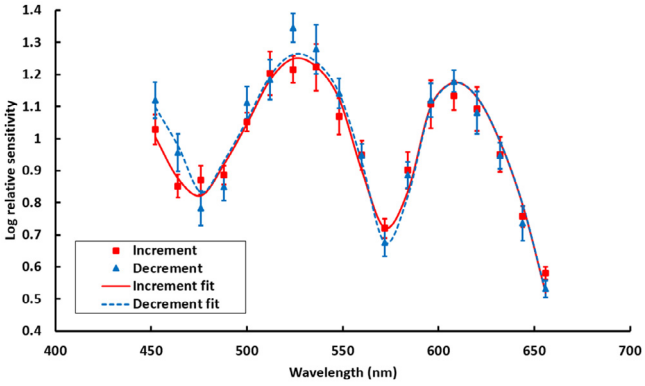

Fig. 4. Increment and decrement threshold spectral sensitivities. Symbols represent data averaged across nine subjects, with error bars showing +/− 1 SEM. Lines through the data are the best fit models with three free parameters.

tests showed no significant differences in model fits between IT and DT for all three of the parameters: L:M ratio ($t(8) = 1.13$, $p = 0.44$); relative opponent weight ($t(8) = 0.39$, $p = 0.71$; overall sensitivity ($t(8) = 1.25$, $p = 0.44$). Because multiple comparisons were made, the p values reported above were corrected using the false discovery rate method (Benjamini & Hochberg, 1995), with the proportion of allowable Type 1 errors (q) set to 0.05.

3. Experiment 2: Increment and decrement threshold spectral sensitivity at short wavelengths

Even though there was no significant difference in the parameters fits to the individual IT and DT data from Experiment 1, there was a trend toward greater DT sensitivity in the short wavelengths (see Fig. 4). This effect became more pronounced when we removed three of the participants who did not complete all the wavelengths for both IT and DT conditions. Consequently, we wished to rule out a Type II error due to sampling bias or inadequate power. In Experiment 2, we retested IT and DT spectral sensitivities at the short wavelengths where trends toward a difference were observed in Experiment 1.

3.1. Methods

The second experiment included 13 participants, one of whom also participated in Experiment 1. There were six males and seven females between the ages of 22 and 49 (mean age = 30 years). The same equipment was used as in the first experiment. However, prior to testing, the xenon arc bulb lamp was replaced in the OL490 Agile Light

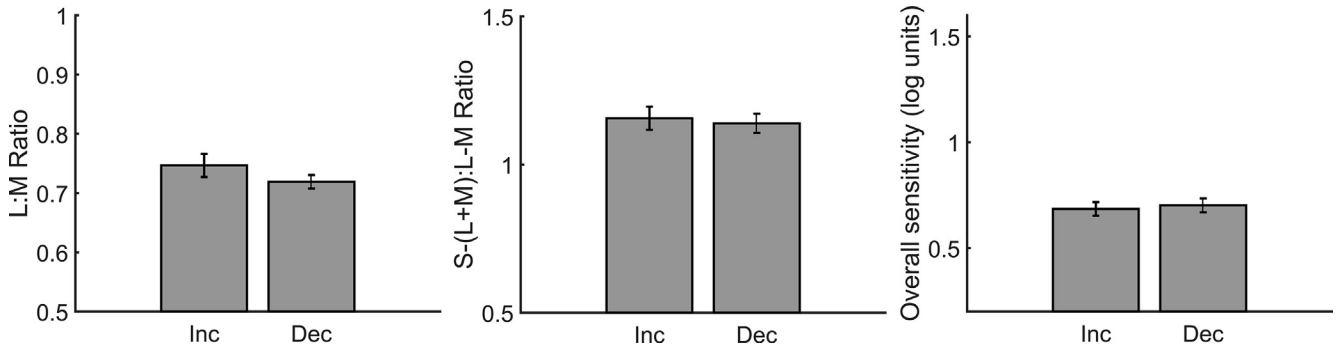

Fig. 5. Best fit model parameters averaged across nine subjects. Left) L to M cone ratio contribution to best fitting (L − M) opponent mechanism. Middle) Relative weight of the two opponent mechanisms, S-(L + M) and (L − M). Right) Overall sensitivity (DC) shift on a log scale. Error bars represent +/− 1 SEM.

Source and the system was recalibrated. The same stimuli were used as in the first experiment, keeping the white pedestal luminance near 11 cd/m^2 (9.5–12.3 cd/m^2). Data were collected at five wavelengths (440, 452, 464, 476, 488) except that four initial participants were not tested at 440 nm.

Data collection was performed in the same way as Experiment 1, but with only the short wavelengths listed above. In addition, rather than using calibration tables to calculate threshold, we used the spectroradiometer to measure the energy at each threshold directly. As in Experiment 1, we took the inverse of threshold energy and performed quantal corrections to arrive at log quantal sensitivity.

We started our model fitting with the final parameter values determined in Experiment 1. Since the data for Experiment 2 reflects primarily short wavelength mechanisms, the overall sensitivity parameter was taken as an indicator of short wavelength contribution. Consequently, we allowed the overall sensitivity (DC shift) parameter to vary, while holding all other parameters constant.

3.2. Results

We found a modest but significant difference between the mean sensitivity for increment and decrement threshold spectral sensitivities ($t(12) = 3.32$, $p < 0.01$, $d = 0.53$). Fig. 6 plots the spectral sensitivities with error bars and also shows the two data sets fit to the model.

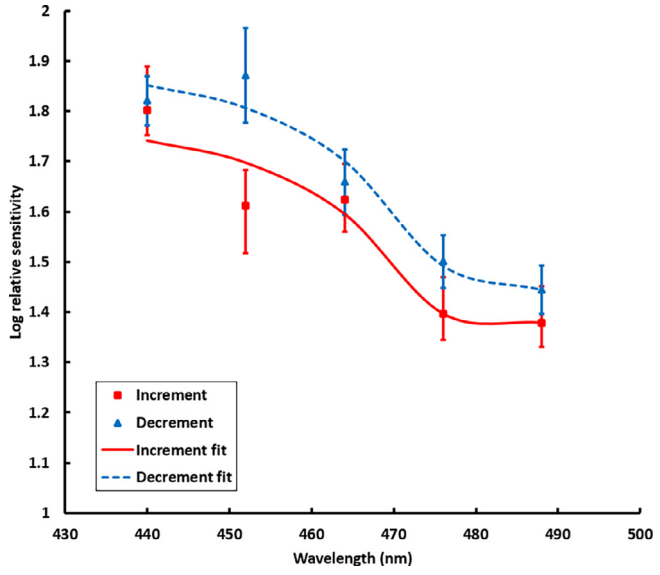

Fig. 6. IT and DT spectral sensitivities for short wavelengths. Symbols represent data averaged across 13 subjects, with error bars showing +/− 1 SEM. Lines through the data are best fit models with only overall sensitivity allowed to vary.

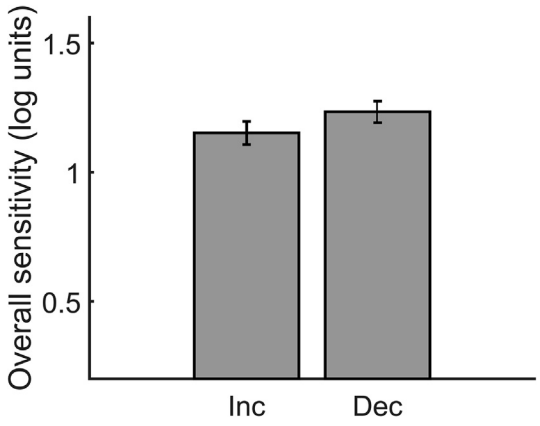

Fig. 7. Best fit model parameters averaged across 13 subjects, with error bars showing +/− 1 SEM. These bars represent the function's overall sensitivity and correspond to the models shown in Fig. 6.

The mean increment sensitivity was 1.15, (SEM = 0.045) and the mean decrement sensitivity was 1.23 (SEM = 0.042), yielding a difference of about 0.08 log units, with a greater decrement threshold sensitivity compared to increment threshold sensitivity (see Fig. 7). If the data at 440 nm with fewer subjects is omitted this difference becomes larger.

4. Experiment 3: Increment and decrement threshold spectral sensitivity from 440 nm to 488 nm wavelengths with higher pedestal luminance

Since the differences from Experiment 2 and the trend seen in Experiment 1 were small and the light levels employed were relatively modest, we tested the possibility that asymmetries in on- and off-rod pathways may be contributing to the effect. We reasoned that if rods were playing a role then the difference in sensitivity should be less pronounced at higher light levels. We repeated Experiment 2 at higher light levels to test this hypothesis.

4.1. Methods

Nine of the same participants from Experiment 2 provided data for Experiment 3. The same methods were used as in Experiment 2. However, we increased the pedestal luminance to ca. 40 cd/m^2 (35.4–45.2 cd/m^2).

4.2. Results

We found no significant difference between the fits of IT and DT spectral sensitivity data to the model at this higher pedestal luminance ($t(8) = 2.18$, $p = 0.06$). The data are shown in Fig. 8 along with the

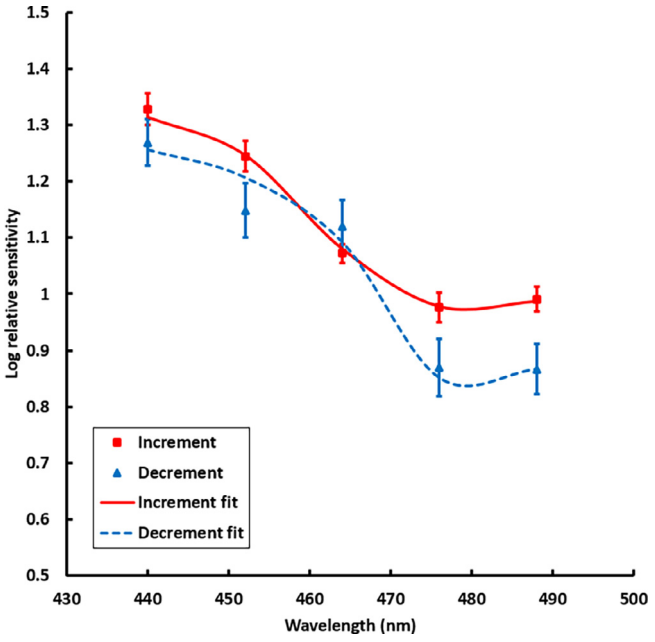

Fig. 8. IT and DT spectral sensitivities for short wavelengths, measured with a mean luminance of 40 cd/m^2. Symbols represent data averaged across nine subjects, with error bars showing +/− 1 SEM. Lines through the data are best fit models with only overall sensitivity allowed to vary.

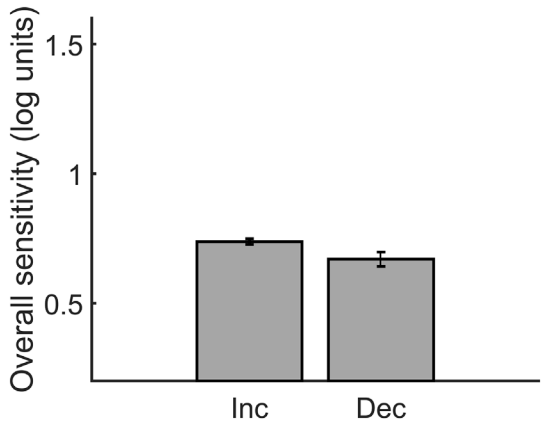

Fig. 9. Best fit model parameters averaged across nine subjects, with error bars showing +/− 1 SEM. These bars represent the function's overall sensitivity and correspond to the models shown in Fig. 8.

model fits to the data. The mean sensitivity parameter for increments was 0.74, (SEM = 0.011) and for decrements was 0.67 (SEM = 0.028). This yielded a difference of about 0.06 log units as seen in Fig. 9. Note that this small and non-significant difference is also in the opposite direction from the small but significant difference noted in Experiment 2. These results are consistent with the suggestion that the small increase in sensitivity for decrements over increments noted in Experiment 2 may be due to rod influence.

5. Discussion

We initially suggested that asymmetries in chromatic mechanisms (e.g. asymmetries in short wavelength ON- and OFF-pathways) may manifest in differences between IT and DT spectral sensitivities. Consequently, we directly compared IT and DT spectral sensitivities. We believe this report is the first to directly compare full IT and DT spectral sensitivity functions. In Experiment 1, we replicate prior characterizations of IT spectral sensitivity and further characterize DT spectral sensitivity. Comparison of these functions by eye and with model fitting to opponent mechanisms reveal little difference between the two methods across most of the spectrum. Although specific testing of model parameters failed to reveal any significant differences in opponent mechanism contribution, there appeared to be a trend in the short wavelengths for relatively greater DT sensitivity. In addition, there have been reports in the literature (e.g. Vingrys & Mahon, 1998) that subjects are more sensitive to S-cone decrements than to S-cone increments.

The trend observed in Experiment 1 for greater DT than IT sensitivity in the short wavelengths was tested with additional subjects in Experiment 2. A modest but significant difference was revealed for these short wavelength stimuli. A suspicion that rods may be contributing to these results led to a repeat of this experiment at higher light levels in Experiment 3. The advantage for decrements over increments disappeared at these higher light levels, suggesting that the small differences observed in Experiment 1 may have been rod driven.

Signals from M and L cones likely share the same pathways given that a relatively recent mutation in the L cone opsin gene gave rise to the M cone opsin (e.g. Nathans, Thomas, & Hogness, 1986). Therefore, it is perhaps not surprising that we find no difference in increment and decrement threshold spectral sensitivities for responses dominated by L − M opponent mechanisms (in the long and middle wavelengths). However, as noted above, asymmetries for responses in the L − M opponent mechanisms have also been reported.

Similarly, even though we found no difference between opponent contribution to IT and DT sensitivities, there are characteristics of the short-wavelength opponent mechanism such as the predominance of ON-cell over OFF-cells (e.g. Malpeli & Schiller, 1978; Martin, 1998; Zrenner & Gouras, 1981) and the distinct ON- and OFF-S-cone pathways (e.g. Crook, Packer, & Dacey, 2014) that could result in different IT and DT spectral sensitivities. As discussed in the introduction, much evidence for asymmetries in increments and decrement sensitivities for S-cone pathways can be found in the literature (reviewed by Buck, 2014, 2004; Smithson, 2014). One common assumption is that nonlinearities such as response compression and rectification in these pathways would make ON-cells relatively more sensitive to increments and vice versa for OFF-cells. This assumption and the preponderance of ON-cells would lead to the prediction that the short wavelength opponent mechanism might be more sensitive to increments than to decrements. Our results do not provide support for this prediction.

An observed difference between IT and DT in Experiment 2, agreed with previous reports in the literature of a relative advantage of decrement vs. increment for S-cone mediated detection and for asymmetries in S-cone contrast gain control (e.g. Gabree et al., 2018). However, upon further examination at higher light levels in Experiment 3, it appears that rods may have contributed to the results of Experiments 1 & 2. Rod-cone interaction would be possible if the intensity of the pedestal was insufficient to result in rod saturation. Based on spectral-radiometric measurements and pupil sizes estimated from Watson and Yellott (2012), the lower pedestal (5.03 scotopic cd/m2) yielded a scotopic luminance of ca. 133 scotopic trolands and the higher pedestal (18.3 scotopic cd/m2) produced ca. 367 scotopic trolands. These light levels produce a steady-state bleaching of approximately 0.56% and 1.52% respectively (Thomas & Lamb, 1999). Psychophysical evidence for asymmetric rod-cone interactions with S-cone pathways at the lower light levels is abundant (reviewed by Buck, 2004, 2014). This interpretation is also consistent with previously reported asymmetries in rod pathways that result in relative greater sensitivity for rod decrements than increments (e.g. Patel & Jones, 1968). It should also be noted that some studies (Knight, Buck, & Pereverzeva, 2001) show greater S-cone suppression by rods for decrements than for increments which is not consistent with the above interpretation of our results.

We employed stimuli known to reveal underlying opponent mechanisms to determine whether IT and DT functions differed under such conditions. It is possible that these increment and decrement stimuli are

not optimal for revealing more subtle underlying differences between the mechanisms contributing to these functions. For example, temporally symmetric increments and decrements may not bias ON- and OFF-pathway responses sufficiently to result in observed differences. Future experiments may employ stimuli such as temporal sawtooth patterns which are more effective at biasing ON- and OFF-pathway responses (e.g. DeMarco et al., 1994; Kremers, Lee, Pokorny, & Smith, 1993).

In sum, it appears that IT and DT spectral sensitivity functions measured with long duration tests on bright achromatic pedestals do not differ significantly in shape. It can be deduced that, using the current paradigm, either 1) the pathways contributing to increment and decrement detection have functionally identical sensitivities, or 2) the conditions that are typically employed to reveal opponent interactions in spectral sensitivity functions are themselves not sensitive to underlying asymmetries in the relevant pathways.

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Disclaimer

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