Seeing Gray through the ON and OFF Pathways

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Color appearance judgements revealed fundamental differences in visual processing of incremental and decremental lights. First, the balance of cone activation required for a light to appear achromatic was different for increments and decrements (Judd 1940; Helson and Michels 1948). Second, adaptation - the visual system's adjustment to background light - affected achromatic decrements more than increments. Third, the regulation of adaptation for incremental and decremental stimuli depended differently on background signals from the three cone types. We interpret these asymmetries as differences in mechanisms of adaptation in the ON and OFF pathways, and suggest that they evolved to accommodate the range and physical sources of color signals in the two pathways.

Introduction

A prominent feature of the visual system is the segregation of retinal signals into two neural pathways in which neurons are excited mainly by increments (ON-pathway) or decrements (OFF-pathway) from the background light intensity. In addition to the early observations of Helson and Michels, and Judd (Judd 1940; Helson and Michels 1948), in recent years more psychophysical evidence has accumulated for differential processing of increments and decrements (Walraven 1977; Krauskopf 1980; White, Irvin et al. 1980; Whittle 1986; Bowen, Pokorny et al. 1989; du Buf 1992; Mausfeld and Niederee 1993). These have been complemented by physiological measurements suggesting that the ON and OFF pathways mediate detection of incremental and decremental lights (Schiller, Sandell et al. 1986).

To understand how the visual pathways process increments and decrements to compute color appearance, we made parametric measurements of appearance across a range of adapting conditions. These data revealed systematic differences between increments and decrements in (a)

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how appearance is computed, and (b) how appearance varies with adaptation. We interpret these asymmetries as differences in the mechanisms of adaptation in the ON and OFF pathways.

Methods

Overview

To analyze the role of incremental and decremental cone photoreceptor signals in color appearance, we estimated (see below) the cone absorptions required to cancel the hue of a stimulus. Targets were presented on a large uniform background whose color was set by the experimenter. After adapting to the background light for 2 minutes, subjects adjusted the spectral composition of the target to make it appear achromatic. Subjects made achromatic settings easily and consistently for a range of targets lighter and darker than the background, presented in random order, yielding achromatic shades ranging from black to gray to white. These settings establish the combination of L(ong), M(iddle), and S(hort) wavelength-sensitive cone absorptions needed to achieve achromatic appearance. Hence we measure color appearance by cancelling it.

Stimuli

Stimuli were presented on a color computer monitor (Hitachi HM-4320D) driven by a NNGS video card from an IBM PC. Targets were 1.5° squares viewed foveally at the center of a 45° (vertical) x 60° (horizontal) background. The visual field beyond the monitor was filled with a reflective viewing hood (75% reflectance for all wavelengths between 370 and 730 nanometers).

The monitor was calibrated for phosphor independence and nonlinearity using standard methods (Brainard 1989; Wandell 1995). To estimate the cone quantum absorptions, phosphor spectral power distributions (microwatts/cm^2-nm-sr, PhotoResearch PR-703A) were multiplied by the human cone spectral sensitivity estimates of Smith and Pokorny (Smith and Pokorny 1975). Each cone spectral sensitivity was normalized to a peak of one.

Subjects set matches on a total of 387 backgrounds. These backgrounds spanned most of the range of luminances and chromaticities that could be achieved on the monitor. The background luminances (CIE 1931) ranged from about 20 to 80 cd/m^2. The background chromaticities covered a circular region of the CIE 1931 (x,y) chromaticity diagram centered at (0.3,0.3) with diameter 0.2.As with most monitors, this range of chromaticity coordinates does not approach the spectrum locus.

Subjects

Subjects adjusted the target to appear achromatic by varying the intensity of each of the three monitor phosphors at the target location using a button box. Three paid undergraduates served as subjects (female subjects SY and LW, male subject RR). All subjects had normal color vision according to the Ishihara plates (Ishihara 1977).

Results

Achromatic Appearance

Figure 1a shows the estimated cone absorptions produced by a collection of achromatic targets[2]. The coordinates of each point show the effect of one achromatic target on the L and S cones, expressed as differences (ΔL, ΔS) from the absorptions due to the background light, whose intensity was fixed. (For simplicity, the effect on the M cones is not shown). We refer to the stimuli in the all-positive quadrant as increments because they excite all three cone types more than the background light. Decremental stimuli excite the cones less than the background light and are plotted in the all negative quadrant. Increments include light grays and white, decrements include dark grays and black.

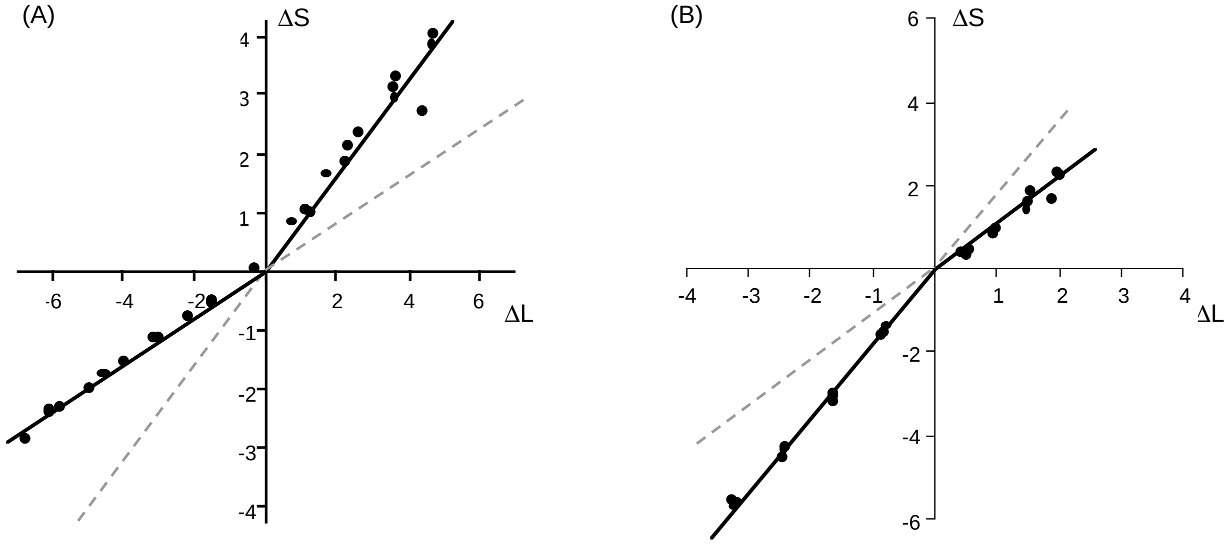

Figure 1: Increment and decrement achromatic settings in two subjects. (A) Each point represents the L and S cone quantum absorptions generated by a target adjusted by the observer to appear achromatic, expressed as differences

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[2] Target color appearance in these conditions is probably due to signals initiated in the cones because (a) there are few rods in the central 1.5° of the retina, and (b) targets were presented on high mesopic or low photopic backgrounds (Wyszecki, 1982, p. 406). We will discuss the possibility of rod contributions to adaptation in the Discussion.

(ΔL,ΔS) from the background. ΔM values, which are approximately proportional to ΔL values in these data, are omitted for simplicity. Increment and decrement cone absorption ratios $\Delta S/\Delta L$ were estimated separately and are indicated by solid lines. Dashed lines extend the solid lines into the opposite quadrant to demonstrate that increment and decrement cone absorption ratios differ. Subject: SY, Background chromaticity (0.29,0.41; CIE, 1931). (B) Similar to A, but for subject RR. Background chromaticity: (0.22,0.19).

Achromatic appearance is computed differently for incremental and decremental cone signals. The solid line through the increments shows where these data would fall if the visual system classified as achromatic those lights that generate a particular ratio of cone absorptions ($\Delta S/\Delta L = 0.83 \pm 0.06$). This type of model fits increments well (Werner and Walraven 1982). However, this ratio fails to make decrements appear achromatic. This is shown by the dashed continuation of the increment line into the opposite quadrant, which systematically misses the decrement settings. Instead, decrements appear achromatic when they generate a smaller ratio of cone absorptions ($\Delta S/\Delta L = 0.39 \pm 0.01$), indicated by the solid line in the negative quadrant. Figure 1b shows similar data for another subject, measured on a different background. In this case, the increment $\Delta S/\Delta L$ ratio required for achromatic appearance was smaller than the decrement ratio. Which ratio was larger varied with the background and the subject. In 6,335 achromatic settings made by three subjects, increment and decrement $\Delta S/\Delta L$ ratios differed ($p<0.01$) for 127 out of 387 backgrounds tested. These systematic differences suggest that two different pathways (e.g., the ON and OFF pathways) process incremental and decremental cone signals.

Light Adaptation

Light adaptation, the visual system's adjustment to background light, affected increment and decrement achromatic appearance asymmetrically. This was shown by examining how subjects' achromatic judgements varied with the background light. Figure 2a shows cone absorptions for achromatic targets seen on two backgrounds which differed only in their S-cone stimulation. Filled symbols represent targets seen on one background, open symbols represent targets seen on the other. The latter have a higher slope: a larger $\Delta S/\Delta L$ ratio is needed to achieve achromatic appearance on the second background, which stimulated the S-cones more. However, increment ratios change differently than decrement ratios. For example, the background change of figure 2a changed the $\Delta S/\Delta L$ increment cone absorption ratio by a factor of 2.65 ± 0.29, but changed the decrement ratio by a factor of 6.01 ± 0.18. This is reflected in the larger slope difference between the two decrement lines than the two increment lines.

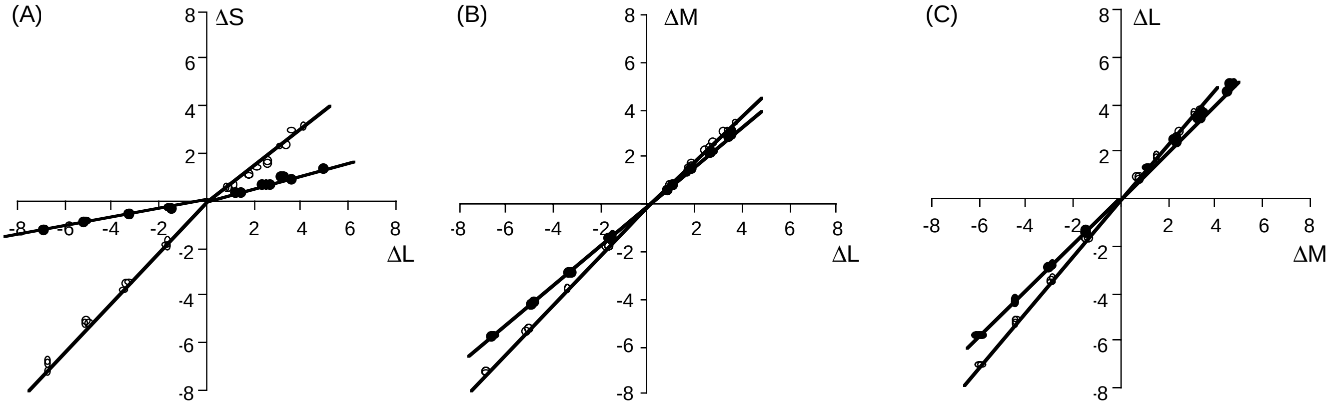

Figure 2. Effect of background changes on achromatic settings. (A) Achromatic settings gathered on two backgrounds that differed only in their effect on the S cones. Stimuli are represented as differences (ΔL,ΔS) from their respective backgrounds. Open symbols represent stimuli seen on the first background (8.76 units of S cone absorption); filled symbols represent stimuli seen on the second background (1.38 units of S cone absorption). The background change caused the estimated increment ratio ΔS/ΔL to change by a factor of 2.65±0.29, and the decrement ratio by a factor of 6.01±0.18. Ratios were computed using multiple regression; "±" indicates a 95% confidence interval computed by separately resampling increment and decrement data 250 times (Efron 1982). Other conditions as in Figure 1. (B) ΔL and ΔM absorptions for two data sets gathered on backgrounds that differ only in their effect on the M cones. Open symbols show data from a background with 8.81 units of M cone absorption, filled symbols from a background with 7.08 units of M cone absorption. The background change caused the increment ΔM/ΔL ratio to change by a factor of 1.12±0.02, decrement ratios by a factor of 1.22±0.01. (C) ΔM and ΔL absorptions for two data sets gathered on backgrounds that differ only in their effect on the L cones. Open symbols show data from a background with 8.92 units of L cone absorption, filled symbols from a background with 7.19 units of L cone absorption. The background change caused the increment ΔL/ΔM ratio to change by a factor of 1.12±0.02, decrement ratios by a factor of 1.23±0.01. Subject: RR.

As the background light changed, the appearance of increments and decrements each varied systematically but according to different rules. Figure 3a shows how the ΔS/ΔL ratio for incremental and decremental achromatic targets varied on backgrounds that differed only in their S-cone stimulation. Filled circles show the ratios for decremental achromatic settings, open symbols show the ratios for incremental settings. These have been normalized by the ratio on the first background to simplify the visual comparison. Although ΔS/ΔL ratios for the increments and decrements both increased with S cone background light, the latter increased linearly and substantially more.

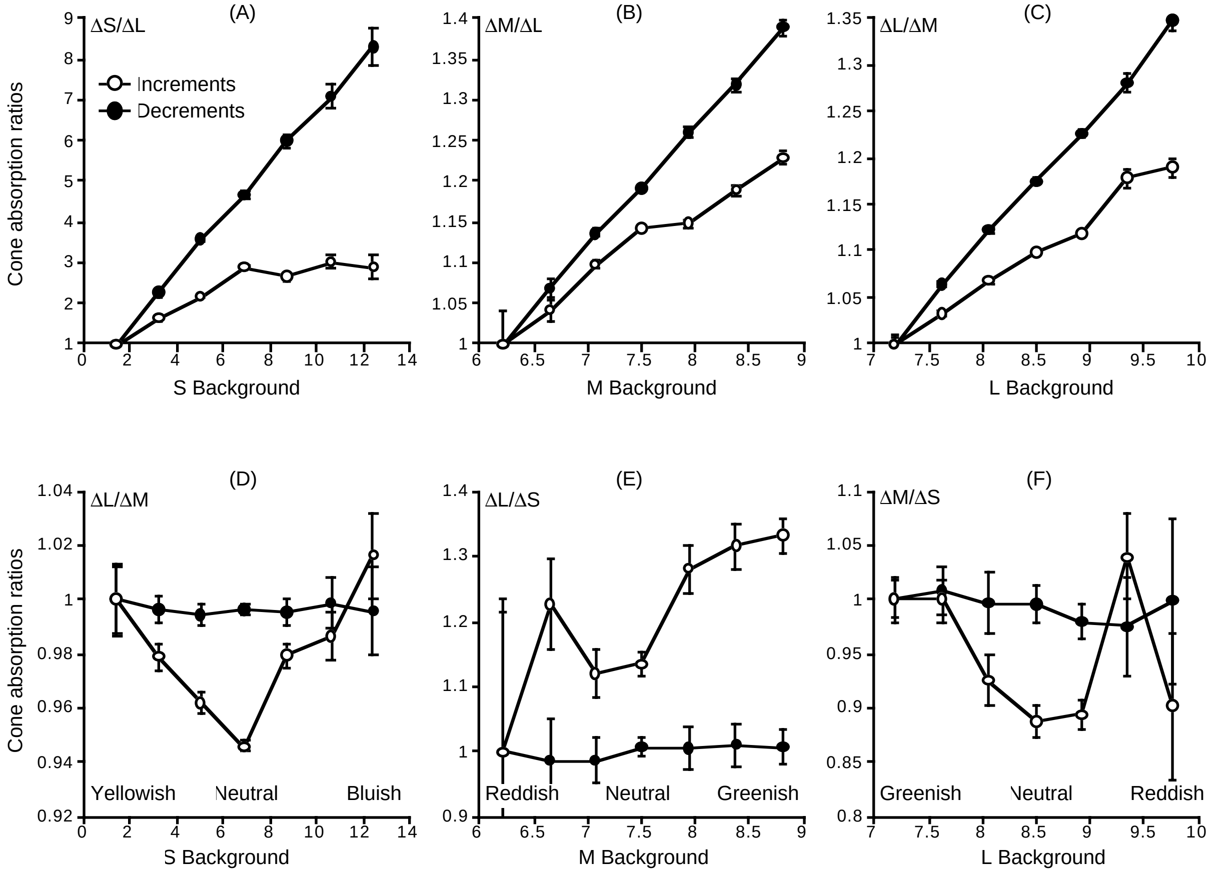

Figure 3. Effect of many background changes on achromatic increment and decrement absorption ratios. (A) Increment and decrement ΔS/ΔL cone absorption ratios of achromatic settings gathered on seven backgrounds which differed only in their effect on the S cones. The horizontal axis indicates S cone absorptions due to each background. Each curve has been normalized by the value on the first background to simplify visual comparison. (B) ΔM/ΔL ratios as a function of background changes selective for the M cones. (C) ΔL/ΔM ratios as a function of background changes selective for the L cones. (D) Increment and decrement ΔL/ΔM for the same data as A. Labels on horizontal axes indicate appearance of background light in a dark room. (E) Increment and decrement ΔL/ΔS for the same data as B. (F) Increment and decrement ΔM/ΔS for the same data as C. Subject: RR.

Changes in M and L cone background absorptions also revealed substantial differences between increment and decrement adaptation. These results are shown in figure 2b-c and 3b-c. Changes in background light always affected decrements more than increments. Large systematic differences in adaptation for increments and decrements, like those shown in Figure 3, were also observed in two other subjects.

How do background absorptions in one cone type affect sensitivity to increment and decrement signals in the other cone types? The effect of background light on decrement appearance was consistent with independent adaptation of signals from each cone type. The filled squares in Figure 3d show that varying the S cone background absorptions did not affect the L and M absorptions required to make decrements appear achromatic. Similarly, varying either the M or L cone background absorptions did not affect the cone absorptions of achromatic decrement measurements in the other two cone classes (filled circles in Figure 3e-f). The fact that adaptation affects achromatic decrement appearance independently in each cone class suggests that segregation into incremental and decremental pathways takes place prior to neural color opponency.

Again, adaptation measured by increments followed different rules. Varying the background absorptions in one cone type affected the cone absorptions in the other two cone classes required to make increments appear achromatic (open circles in Figure 3d-f) (Werner and Walraven 1982). The effect of adaptation reversed as the background hue passed to its complement through neutral gray. This was observed in all three subjects. These data suggest that neural opponent mechanisms affect sensitivity to incremental cone signals (Pugh 1976; Mollon and Polden 1977; Sternheim, Stromeyer et al. 1979; Wandell and Pugh 1980).

Discussion

Our results may be summarized as follows. First, the cone absorption ratios of achromatic increment and decrement lights differed. Second, these ratios were affected differently by adaptation. What do these findings suggest about the organization of the visual pathways?

Primate cone photocurrent varies linearly in response to dim flashes (Schnapf, Nunn et al. 1990). It is therefore likely that cones respond symmetrically to increments and decrements of moderate contrast around the photopic backgrounds used in our experiments. If this is true, sensitivity changes in cone photocurrent (Schnapf, Nunn et al. 1990) cannot explain the asymmetries in increment and decrement appearance changes with background light (Figures 2 and 3).

To manage transduction efficiently, it is sensible that the cones themselves should adapt. Moreover, there is considerable psychophysical and physiological evidence that cone sensitivity depends on the background illumination (Stiles 1959; Boynton and Whitten 1970; Schnapf, Nunn et al. 1990) and that this, in turn, affects subjects' judgments of color appearance (von Kries 1905; Walters 1942; Wright 1947; Burnham, Evans et al. 1952; Hurvich and Jameson 1958; Wassef 1958; Walraven 1976; Shevell 1978; Werner and Walraven 1982; Brainard and Wandell 1992; Chichilnisky and Wandell 1995). There is also a substantial body of psychophysical evidence documenting post-receptoral adaptation under certain viewing conditions (Pugh 1976; Mollon and

Polden 1977; Pugh and Mollon 1979; Pugh and Larimer 1980; Wandell and Pugh 1980; Wandell and Pugh 1980; Stromeyer and Sternheim 1981; Ahn and MacLeod 1993). The results we report here are consistent with a mixture of receptor and post-receptor adaptation. When judging the appearance of decremental lights, subjects' behavior is consistent with separate adaptation within each cone class. When judging the appearance of incremental lights, subjects' behavior is consistent with adaptation being controlled by signals from more than one receptor class. A natural explanation is that the anatomically distinct ON and OFF pathways regulate sensitivity according to different rules. For example, in ON-bipolar cells surround signals from one cone type may affect the sensitivity to signals from another cone type; while in OFF-bipolar cells this interaction may be absent.

As mentioned previously, target appearance is probably based on signals initiated in the foveal cones. However, peripheral photoreceptor signals, including rod signals, may contribute to asymmetric processing of increments and decrements by affecting sensitivity of signals initiated in foveal cones. Consider, for example, the asymmetric effect of S cone selective background changes on increment and decrement appearance, shown in Figures 3a and 3d. These background changes may have also affected rod signals, which could have asymmetric effects on sensitivity of ON and OFF signals initiated by foveal cones. Whether or not the rods play a role, the background changes in Figure 3d were invisible to the L and M cones, whose ratio is plotted on the vertical axis. Thus the data demonstrate interactions between receptor types in increment but not decrement adaptation.

Our findings suggest a neural basis for a classical perceptual observation known as the Helson-Judd effect (Judd 1940; Helson and Michels 1948). These authors observed that targets that are substantially less intense than the background appear achromatic at chromaticities similar to that of the background; targets that are substantially more intense than the background appear achromatic at a background-independent chromaticity[3]. Our observations show that there are sharp differences in cone absorption ratios (Figure 1) and adaptation (Figures 2-3) for achromatic increments and decrements of moderate contrast. This suggests that the neural basis of the Helson-Judd effect is asymmetric processing and adaptation in the ON and OFF pathways.

The data in Figure 3 suggest that more complete adaptation occurs in the OFF pathway, and that light adaptation in the OFF pathway is regulated separately within each cone type whereas adaptation in the ON pathway depends in part on opponent-color signals. Why should there be different rules for adaptation in the ON and OFF pathways? Stimuli that excite these pathways require different visual processing because (a) the range of increment intensities exceeds the range of decrement intensities (increments may be arbitrarily intense while decrements are bounded by

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[3] The Helson-Judd effect is sometimes described in terms of illuminants and surfaces; see for example Hunt (1995), p. 716.

zero), and (b) light sources and specular reflections typically create increments, while diffuse reflections typically create decrements. The ON and OFF pathways may adapt differently because these two pathways usually encode stimuli of different physical origins.

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