PERGAMON

Vision Research 40 (2000) 3083–3088

Vision Research

www.elsevier.com/locate/visres

Pre-exposure to contrast selectively compresses the achromatic half-axes of color space☆

R. Dirk Beer *, Donald I.A. MacLeod

Department of Psychology, University of California at San Diego, La Jolla, CA 92093-0109, USA

Received 8 August 1999; received in revised form 3 May 2000

Abstract

The gamut of perceived colors can be represented in a space with bright–dark, red–green and blue–yellow axes. Pre-exposure to a field that changes periodically over time in luminance or along one of the color axes reduces vividness of colors along the entire axis [Webster and Mollon (1991) *Nature*, *349*, 235–238]. But is it possible to reduce vividness or perceived contrast selectively for half-axes in color space? We assessed such selective compression of the bright–dark axis using a task where subjects matched tests in a pre-adapted region to ones in an un-adapted region. Tests were bright or dark pinstripes on a gray background, and pre-exposure was to multiple drifting pinstripes. Matches made after pre-exposure indicate a combination of symmetric and asymmetric compression, with more compression when adapting and test stimulus were similar in contrast polarity.

Keywords: Contrast adaptation; Opponency; Coding; Cortical mechanisms; Pattern adaptation

1. Introduction

The range of perceived colors can be represented in a space with three orthogonal axes: bright–dark, red–green and blue–yellow. In the standard model, these axes represent the level of activity of three separate visual mechanisms. Each mechanism responds only to specific attributes of a stimulus. For instance, the bright–dark mechanism responds, roughly, to stimulus intensity.

These mechanisms have been identified and characterized both psychophysically and physiologically (Kaiser & Boynton, 1996). In psychophysical experiments, pre-exposure to temporal or spatial changes in brightness or color that selectively excite one mechanism is most effective at changing detectability or appearance of colors along the associated axis. Pre-exposure has least effect on stimuli detected by a different mechanism, and these stimuli are usually represented as lying on an orthogonal axis (Krauskopf, Williams, & Heeley, 1982; Webster & Mollon, 1991; Giulianini & Eskew, 1998). For example, there is little change in detection thresholds or appearance of bright or dark stimuli after exposure to red–green variation. This indicates more or less independent mechanisms at work. Some exceptions to the basic three-mechanism model have been noted (Krauskopf, Williams, Mandler, & Brown, 1986; Webster & Mollon, 1991; Li & Lennie, 1997).

Electrophysiological measurements in the macaque monkey lateral geniculate nucleus have revealed neurons that selectively respond to changes in the stimulus along three axes conforming loosely to the above description (Lennie, Krauskopf, & Sclar, 1990; Derrington, Krauskopf, & Lennie, 1984). Some cells, for example, respond to the sum of activity of long- and medium-wavelength receptors, which corresponds to the brightness or darkness of colors. But in addition to their selectivity for direction in color space, individual neurons are also selectively responsive to one polarity of spatial contrast (Kuffler, 1953; Schiller, 1995). In retina, lateral geniculate nucleus, and cortex, ON cells increase their firing rate in response to a spot of light

☆ This work has not been published elsewhere, and is not under review with another journal. If it is published in Vision Research, it will not be reprinted elsewhere in any language in the same form without the consent of the publisher. These experiments were performed on human subjects with their full understanding and consent.

* Corresponding author.

0042-6989/00/$ - see front matter
PII: S0042-6989(00)00151-6

brighter than the surround, while OFF cells increase their firing rate in response to a dark spot on a lighter surround. Because they have relatively low spontaneous firing rates, these cells respond little to stimuli that are opposite their preferred contrast polarity. Although retinal and lateral geniculate cells do not seem to be adaptable (Derrington et al., 1984), cortical cells are (Vautin & Berkley, 1977; Sclar, Lennie, & DePriest, 1989).

The presence of adaptable, contrast-polarity selective cells suggests that there may be separately adaptable, polarity selective perceptual mechanisms. Previous psychophysical experiments that tested the effect of adaptation on *appearance* of stimuli involved pre-exposure to both contrast polarities (e.g. bright and dark, or red and green) at once, and would not have revealed polarity-selective mechanisms. Two studies of adaptation have found polarity-specific effects on the perceived form of stimuli (De Valois, 1977; Burton, Nagishneh, & Ruddock, 1977), and studies of detection thresholds after adaptation suggest polarity-selective detection mechanisms (Hanly & MacKay, 1979; Krauskopf, 1980; Krauskopf et al., 1982).

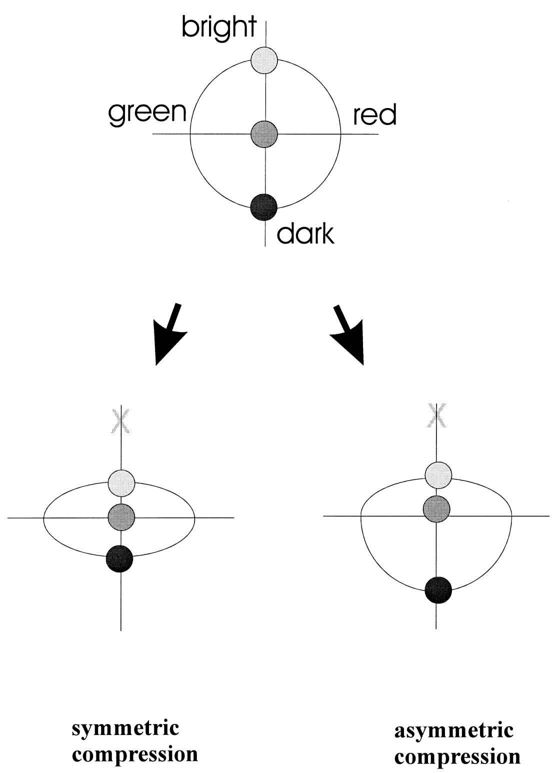

Fig. 1. Two possible effects of adaptation to a pattern of one contrast polarity. Adaptation to a bright white pattern on a mid-gray background (indicated by the X) could cause s*ymmetric* compression of the achromatic axis (both bright and dark patterns would appear reduced in contrast), or *asymmetric* compression (only patterns of the same polarity as the adaptor, in this case bright patterns, would appear reduced in contrast).

In these experiments, we tested to see if pre-exposure to spatially contrasting patterns of one luminance polarity would cause a selective reduction in perceived contrast for patterns of the same luminance polarity. Our stimuli can be represented on the bright–dark axis of a color contrast space (Fig. 1), where the background color is at the origin, and distance from the origin indicates the contrast. A reduction in perceived contrast can be thought of as a compression of this color space. Polarity specific (half-axis selective) reduction in contrast is an asymmetric compression. Reduction in contrast for the whole axis is a symmetric compression.

2. Asymmetric matching experiment

2.1. Methods

Results of previous experiments by the authors (Beer & MacLeod, 1998) suggested asymmetric compression of the bright–dark axis based on the comparison of brightness differences. To measure the effect of adaptation on perception of brightness more directly, we used an asymmetric matching procedure. Subjects were pre-exposed to a pattern of pinstripes in one part of their visual field, and to a uniform gray background in another part. The adapting region had either bright contrast, dark contrast, or it was a uniform gray, depending on the adapting condition. To ensure that there was no difference in light adaptation between the two regions, both were set to have the same time- and space-average luminance. To prevent local light adaptation, pinstripes in the adapting region were drifted slowly (~ 2 Hz) as subjects fixated the center of the display. After adaptation, subjects were shown two stripes: one in the unadapted region (the standard), and one in the adapted region (the match). They were asked to adjust the match stripe so that it looked like the standard stripe. We found that one-dimensional matches, in which the subject could vary only the luminance (not chromatic) contrast between test stripe and background, were subjectively acceptable. Fig. 2 illustrates the stimuli.

The matching method provides a fairly direct measure of the reduction in perceived contrast of stimuli at various points in the color space. For this experiment, we chose 12 test luminance levels along the bright–dark axis to determine if the effect of adaptation to one achromatic contrast polarity is symmetric or asymmetric.

If adaptation to one polarity selectively affects appearance of tests of the same contrast polarity (asymmetric compression), bright test stripes would look dimmer after adaptation to bright stripes, but dark test stripes would be unaffected (or less affected). This

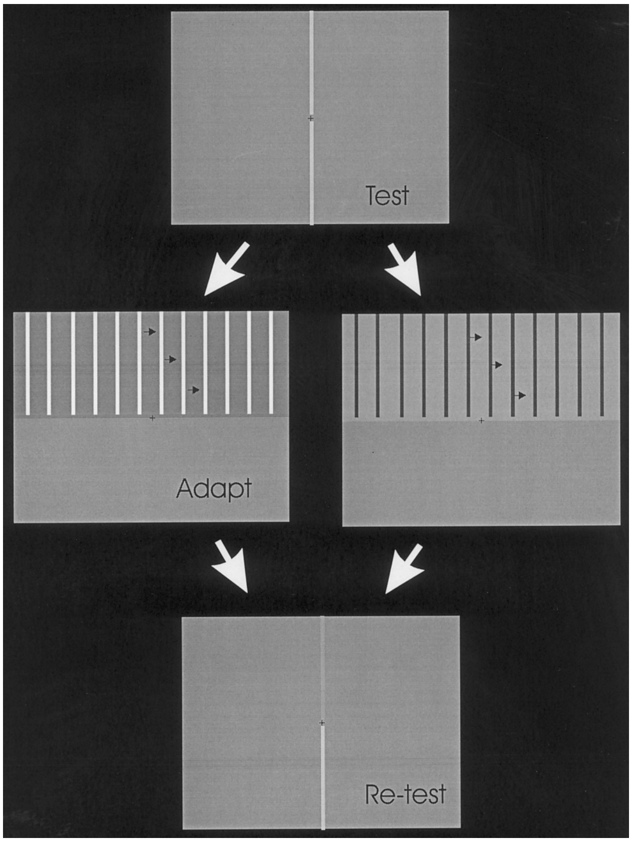

Fig. 2. Matching stimuli. Subjects adjusted the top stripe of the test stimulus to match perceived contrast of the top and bottom stripes. This was done after adapting to bright or dark stripes, or without adaptation. The background of the upper region of the adapting stimulus was fixed to yield equal average luminance top and bottom. The pinstripes of the adapting stimulus drifted slowly to prevent afterimages. Adaptation resulted in a decrease in perceived contrast of the top stripe, and a corresponding increase in the contrast set by subjects.

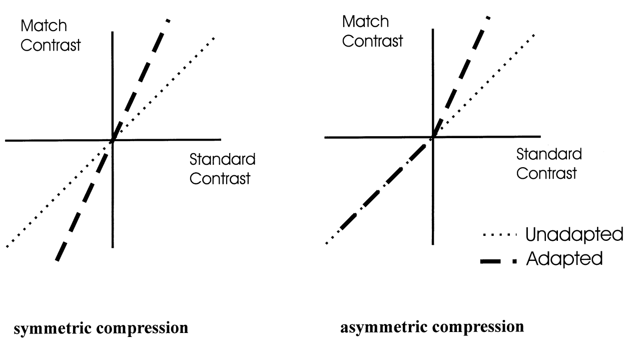

Fig. 3. Matching predictions. Pre-exposure to a unipolar stimulus could result in *symmetric* compression, where match settings of both polarities would be affected. Alternatively, it could result in *asymmetric* compression, where only match settings of the same polarity as the adaptor would be affected. The slope of a line drawn through match settings indicates the gain of hypothetical polarity-specific contrast mechanisms.

would be indicated by high match contrast settings for increment standards, but more nearly veridical match settings for decrement standards (Fig. 3). Conversely, dark test stripes would look less dark after adaptation to dark stripes, but appearance of bright tests would be less affected.

If color space is compressed symmetrically, one would predict that both increment and decrement stripes would look less vivid (bright stripes would look dimmer, and dark stripes would look less dark). Subjects would then set higher match contrast settings for both bright and dark standards after adaptation (Fig. 3). The same would be true for adaptation to dark stripes: both bright and dark standards would be matched by a higher match contrast.

Sessions of the experiment usually consisted of two blocks of up to 50 trials each, where each block was one adapting condition. Subjects made practice settings at the beginning of each block, which allowed about 2–4 min for adaptation to develop. Blocks took about 25 min to complete and a full session lasted about 50 min.

Each trial consisted of a repeated cycle of 3000 ms of adaptation, a 200 ms blank interval, a 150 ms test interval, and another 200 ms blank interval. Subjects adjusted the match stripe seen during the test interval, and pressed a mouse button to make a setting. They were then presented with the next trial. If the subjects did not respond within 30 s, the trial was recorded as invalid.

Twelve contrast levels of the standard were presented, and a total of 15–20 match settings were made for each data point. The stimulus levels were randomly interleaved within each of the three adapting conditions. There were a total of about 500 settings per subject. Three subjects participated in the full experiment.

Stimuli were presented on a Sony GDM-2000TC color display driven by a Cambridge Research Visual Stimulus Generator at 69 frames/s. The maximum luminance of the stimuli was 83 cd/m^2, and the display was calibrated so that the luminance of the display is linearly related to the 12-bit RGB values specified in the controlling program. We developed a precise calibration procedure that ensured that deviations of the display output from linearity were less than the difference caused by one step in RGB value (less than 1 part out of 4096). The pinstripes displayed had a width of 10 arc sec of visual angle and were separated by 1.6°. The luminance of the area between the adapting pinstripes was set so that the average luminance of the adapting region was 42 cd/m^2, the same as the luminance of the uniform region. Also, adapting pinstripes drifted slowly ($\sim$2 Hz) to prevent local light adaptation.

3. Results

Four subjects were initially tested. An ANOVA indicated that interaction between contrast polarity of the adaptor and polarity of the standard was a significant factor in explaining the match settings ($F = 14.3$, 27.3, 12.0; $P < 0.0001$ for subjects RDB, NH and JMH, respectively). The interaction was such that when the standard and the adaptor were the same polarity, subjects set higher contrast matches than when the standard and adaptor were of opposite polarity. A fourth subject did not show the effect during initial testing ($F = 0.97$, $P = 0.33$), and because of that did not finish the lengthy experiment.

The first plot for each subject shows the Michelson contrast of the match stripe versus the contrast of the standard stripe (Fig. 4). An adjustment of the match stripe contrast data was necessary because we found that the match contrast set in the control condition was systematically lower than veridical although we did not investigate this deviation from veridical matches in detail, it seems from our experiments that the perceived contrast of a physical stimulus can vary slightly depending on location in the visual field). Thus, 'match contrast' in these plots is the match contrast after adaptation minus the (signed) difference of control match settings from veridical. The 95% confidence intervals plotted are for the difference between adapted and control settings. Asymmetric compression is indicated in these plots by open circles (adapt contrast same sign as test contrast) lying farther from the horizontal than closed symbols (adapt contrast opposite sign from test contrast) for both positive and negative contrast tests. To show the change in settings due to adaptation more clearly, the difference between matching contrasts chosen with adaptation and without adaptation (control settings) is also plotted (Fig. 5). The 95% confidence intervals shown are for this difference. They indicate that there are significant, consistent differences in match settings between adapting conditions.

4. Analysis

If one considers the effect of adaptation to be simply a reduction of the apparent contrast by some factor, then the slope of a line fit to the data is equal to that factor (Fig. 4). We used the slope as an indication of contrast reduction. A slope of one indicates no change in apparent contrast; a slope greater than one (higher contrast settings in the preadapted region) indicates a reduction in apparent contrast of the matching stimulus in the adapted region (see Table 1).

The slopes are significantly greater than one for both bright and dark standards for all subjects, with an exception for subject RDB, who showed no reduction in apparent contrast for one of four adapt-test polarity combinations. This indicates that for most subjects, there is some degree of symmetric compression caused both by dark adaptors and bright adaptors.

Most relevant to our hypothesis, there is a difference in slopes for increment versus decrement tests after adaptation for all three subjects. This indicates an asymmetric compression of the bright–dark axis in color space. As a measure of the degree of asymmetry, we used the ratio of same-polarity compression to opposite-polarity compression. A ratio greater than one indicates greater contrast reduction for tests of the

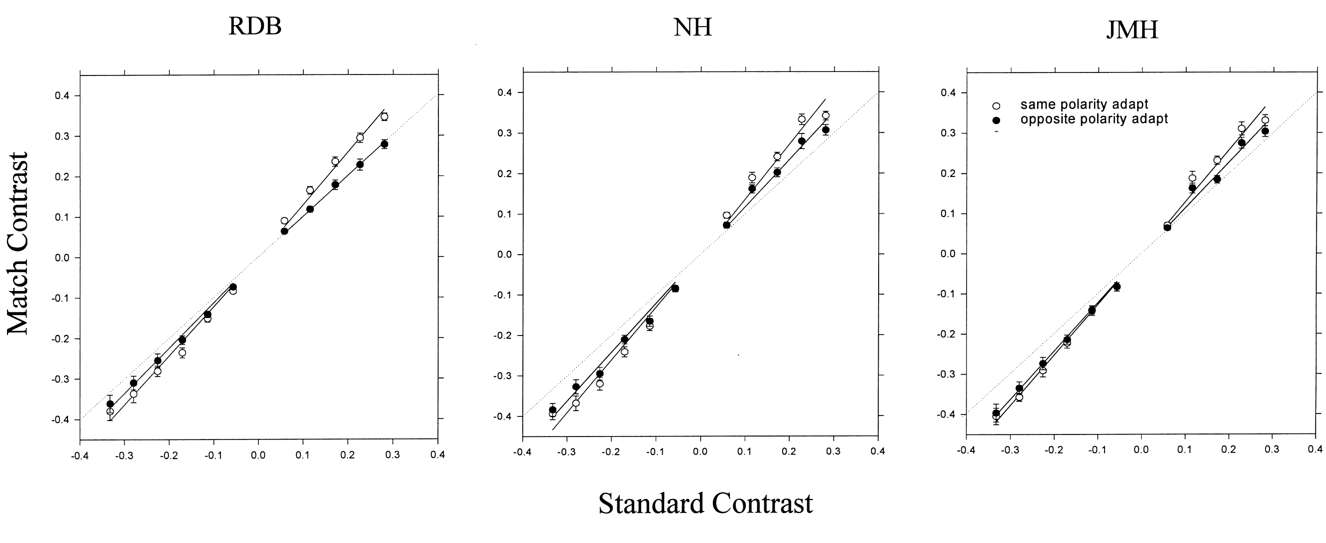

Fig. 4. Match contrast (adjusted for control matches) vs. standard contrast. Units are signed Michelson contrast $(I_{stripe} - I_{background})/(I_{stripe} + I_{background})$. Line fits to the match setting indicate gain of hypothetical polarity-specific contrast mechanisms. Slopes greater than one indicate a reduction in gain after adaptation, and a compression of the corresponding half-axes. Compression is always greatest when test and adaptor are the same polarity.

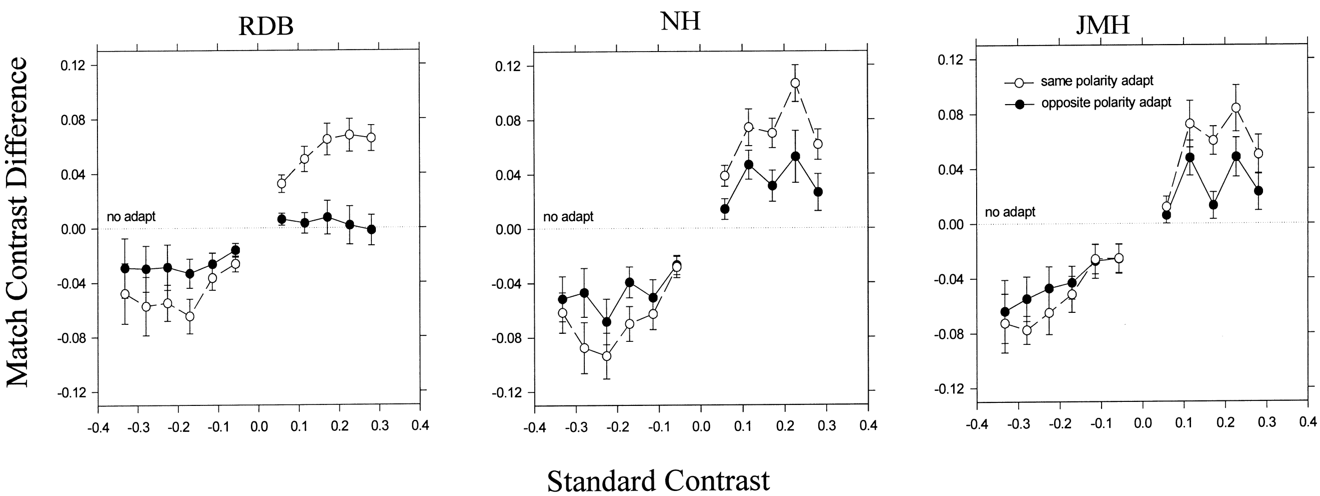

Fig. 5. Change in match settings after adaptation. Results of Fig. 4 are replotted to show the difference in Michelson contrast units between match settings with and without adaptation. Error bars are 95% confidence intervals.

same polarity as the adaptor. These asymmetry ratios are listed in Table 1.

5. Discussion

Several recent experiments have explored the validity and characteristics of the standard three-mechanism model of color vision in more detail. One line of research has been to understand, in the framework of the model, how the appearance of lightness and color is modified by adaptation to the prevailing distribution of intensities and wavelengths in the environment. In classic color constancy, the visual system adapts to the mean color of the visual scene (Kaiser & Boynton, 1996). Another type of adaptation has also been demonstrated: adaptation to the variance of color either within a scene (Brown & MacLeod, 1997) or over time (Webster & Mollon, 1991). Our visual system seems able to adapt to an environment in which there is high variance in, for example, brightness by adjusting the activity of the bright–dark mechanism to encode an adaptively appropriate range. It is the polarity-specificity of this adaptation to variation or contrast, that we investigated.

The possibility of polarity-specific effects of pre-adaptation on perceived brightness had not been investigated until now: previous studies of color appearance have employed pre-adapting stimuli that were modulated symmetrically, precluding polarity-selective effects. But the presence of neural ON and OFF mechanisms does suggest that if we are pre-exposed to a field containing objects that are bright relative to the background (positive luminance contrast), we would adapt by becoming less responsive to positive luminance contrast — without a commensurate change in the appearance of luminance decrements. This is in fact approximately correct — we found a sizeable polarity-selective effect of adaptation.

Our subjects made match settings after adaptation that imply a combination of an overall compression and an asymmetric compression. It is interesting, and perhaps surprising, that the effect of adaptation is only weakly selective to contrast polarity. There are several

Table 1
Contrast reduction ratios give an indication of the degree of asymmetry[a]

Subject	RDB		NH		JMH	
Test	Bright	Dark	Bright	Dark	Bright	Dark
Slope						
Bright adapt	1.30	1.12	1.26	1.20	1.30	1.21
Dark adapt	1.01	1.21	1.14	1.30	1.14	1.26
Asymmetry ratio						
Bright adapt	1.16		1.05		1.08	
Dark adapt	1.20		1.14		1.10	

[a] The ratios are of slope when adapting to the same polarity versus slope when adapting to the opposite polarity. Ratios indicate 5–20% greater compression when test and adaptor are the same polarity versus the opposite polarity.

possible reasons. One is that the stimuli used may not excite one contrast-sensitive pathway exclusively. An ON pathway may respond best to bright pinstripes, but an OFF pathway could also be stimulated when a receptive field crosses a bright–dark edge. Another possibility is that moderate spontaneous activity in ON and OFF pathways allows each pathway to respond to the non-preferred contrast by a reduction in firing rate. This response to the non-preferred contrast polarity may also be adaptable, resulting in the combination of polarity-specific and non-specific adaptation we found. A third possibility is that the adaptation is specific to a spatial pattern, and is adapting cortical pattern-specific cells, which may be combining to some degree input from independent ON and OFF pathways.

References

Beer, R. D., & MacLeod, D. I. A. (1998). Pre-exposure to contrast asymmetrically compresses the achromatic axis of colour space. Poster presented at the 1998 Conference of the Association for Research in Vision and Ophthalmology, Fort Lauderale.

Brown, R. O., & MacLeod, D. I. A. (1997). Color appearance depends on the variance of surround colors. *Current Biology*, *7*, 844–849.

Burton, G. J., Nagishneh, S., & Ruddock, K. H. (1977). Processing by the human visual system of the light and dark contrast components of the retinal image. *Biological Cybernetics*, *27*, 189–197.

De Valois, K. K. (1977). Independence of black and white: phase-specific adaptation. *Vision Research*, *17*, 209–215.

Derrington, A. M., Krauskopf, J., & Lennie, P. (1984). Chromatic mechanisms in lateral geniculate nucleus of macaque. *Journal of Physiology*, *357*, 241–265.

Giulianini, F., & Eskew, R. T. Jr. (1998). Chromatic masking in the (delta L/L, delta M/M) plane of cone-contrast space reveals only two detection mechanisms. *Vision Research*, *38*, 3913–3926.

Hanly, M., & MacKay, D. M. (1979). Polarity-sensitive perceptual adaptation to temporal sawtooth modulation of luminance. *Experimental Brain Research*, *35*, 37–46.

Kaiser, P. K., & Boynton, R. M. (1996). *Human color vision* (2nd ed.). Washington, DC: Optical Society of America.

Krauskopf, J. (1980). Discrimination and detection of changes in luminance. *Vision Research*, *20*, 671–677.

Krauskopf, J., Williams, D. R., & Heeley, D. W. (1982). Cardinal directions of color space. *Vision Research*, *22*, 1123–1131.

Krauskopf, J., Williams, D. R., Mandler, M. B., & Brown, A. M. (1986). Higher order color mechanisms. *Vision Research*, *26*, 23–32.

Kuffler, S. W. (1953) Discharge patterns and functional organization of mammalian retina. *Journal of Neurophysiology*, 37–68.

Lennie, P., Krauskopf, J., & Sclar, G. (1990). Chromatic mechanisms in striate cortex of macaque. *Journal of Neuroscience*, *10*, 649–669.

Li, A., & Lennie, P. (1997). Mechanisms underlying segmentation of colored textures. *Vision Research*, *37*, 83–97.

Sclar, G., Lennie, P., & DePriest, D. D. (1989). Contrast adaptation in striate cortex of macaque. *Vision Research*, *29*, 747–755.

Schiller, P. H. (1995). The ON and OFF channels of the mammalian visual system. *Progress in Retinal and Eye Research*, *15*.

Vautin, R. G., & Berkley, M. A. (1977). Responses of single cells in cat visual cortex to prolonged stimulus movement: Neural correlates of visual aftereffects. *Journal of Neurophysiology*, *40*, 1051–1065.

Webster, M. A., & Mollon, J. D. (1991). Chnages in colour appearance following post-receptoral adaptation. *Nature*, *349*, 235–238.