

EFFECTS OF CHROMATIC ADAPTATION ON COLOR DISCRIMINATION AND COLOR APPEARANCE¹

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Abstract—Color discrimination and color appearance were examined at a number of chromaticities along an equal luminance line running from red to green as a function of adaptation to several lights along the same line. Like K. J. W. Craik's results for brightness discrimination [*J. Physiol.* 92, 406–421], color discrimination proved best for chromaticities nearest the adapting light with a worsening of discrimination (relative to neutral adaptation) for more distant chromaticities. This result is explicable in terms of a sliding of the "working range" of red–green opponent cells along an axis of chromaticity. Consistent with this interpretation are the systematic changes in color appearance brought about by preexposure to chromatic light.

An ancillary part of the investigation revealed that a flickering adapting light produces lesser adaptive shifts than steady light of the same time average luminance. This latter result rules out the possibility that photopigment bleaching, under these conditions, plays more than a minimal role in controlling the sensitivity of the cones or more proximal neurons.

INTRODUCTION

A primary function of light and dark adaptation is to optimize the sensitivity of the eye to spatial and temporal luminance differences in the neighborhood of the prevailing luminance level. Perhaps the first to fully appreciate this function of visual adaptation was K. J. W. Craik (1938) who, in an important paper, established that the differential brightness sensitivity of the eye is greatest where the test luminances are centered about the adapting luminance. This shifting of the contrast sensitivity of the eye with adaptation level is one mechanism that contributes to good brightness discrimination throughout the full range of luminances over which the eye operates. Using the analogy of a multirange ammeter having various shunts, Craik (1938) interpreted this shifting contrast sensitivity in terms of a limited response vs intensity function which shifts along the log intensity axis such that its region of maximal slope corresponds to the adapting level. Despite the convincing psychophysical evidence of Craik and others (cited in Byzov and Kuznezova, 1971), this conception of visual adaptation has only recently attained prominence with its confirmation by direct physiological experiment. Thus, in a variety of species, the response vs log intensity curves of various visual neurons, both central (Jacobs, 1965) and retinal (Byzov and Kuznezova, 1971; Normann and Werblin, 1974; Werblin, 1974), have been observed to shift along the log I axis in concert with the adapting luminance.

The present investigation was undertaken to determine whether similar shifts occur in color discrimination with moderate levels of chromatic adaptation, levels which produce dramatic changes in color appearance without bleaching large fractions of the

cone photopigments. Specifically, we examined color discrimination along a constant luminance red–green line in chromaticity space as a function of chromatic adaptation to several lights along this same line. If the analogy with brightness discrimination should hold, then color discrimination should be optimal at the adapting chromaticity for each adaptation condition. Although no other investigation of which we are aware has made a systematic effort to look for shifts in color discrimination like those Craik found for brightness, several psychophysical and physiological studies point in that direction.

In the psychophysical literature there are at least three relevant studies. Pointer (1974) investigated color discrimination over an extensive range of chromaticity as a function of adaptation to red, green and blue lights as well as to white lights of various color temperatures. While showing little effect of color temperature on discrimination, the results he presents for one observer show measurable effects of chromatic adaptation. In particular, color discrimination in the presence of an adapting surround improves in the vicinity of each of the adapting colors relative to the neutral adaptation condition. In a related experiment, Hurvich and Jameson (1961) measured wavelength discrimination in the presence of red and blue–green chromatic surrounds to which the observer had adapted. They found that wavelength discrimination was better in the red part of the spectrum in the presence of the red adapting surround and better in the blue–green region with the blue–green surround. Finally, an experiment by Brown (1952) showed that the variability of small-field color matches was minimized with spatial surrounds of matching chromaticity.

The physiological evidence is also indicative of the predicted shifts in color discrimination. Of relevance are many of the studies by DeValois and his colleagues. In addition to confirming that color vision

¹ The results of the first experiment were reported at the 1976 annual meeting of ARVO, held in Sarasota, Florida.

of the macaque is virtually identical to that of humans (DeValois and Jacobs, 1968; DeValois *et al.*, 1974), they have presented convincing evidence that behavioral measures of macaque color vision can be accounted for by the response activity of single cells in the LGN; in particular, saturation discrimination (DeValois and Jacobs, 1968; DeValois and Marrocco, 1973; DeValois *et al.*, 1974) and wavelength discrimination (DeValois *et al.*, 1967; DeValois *et al.*, 1974) have been closely tied to the activity of spectrally-opponent red-green and yellow-blue cells of LGN. In addition, DeValois *et al.* (1963), have shown that the responses of spectrally opponent cells are drastically altered by selective chromatic adaptation, one consequence being that the wavelength which elicits a response equal to the spontaneous firing rate is shifted toward the adapting light. The most pertinent study involved an extensive analysis of wavelength discrimination in spectrally-opponent cells (DeValois *et al.*, 1967). They adapted red-green and yellow-blue cells of LGN to various spectral lights and observed their responses to alternations between the adapting light and other spectral lights. Following adaptation, the cells responded essentially with the spontaneous rate to continued exposure of the adapting light; for changes to wavelengths in one direction the cell was excited and for changes to wavelengths in the other direction the cell was inhibited, with the change in response dependent upon the extent of the wavelength shift. For a considerable range of adapting lights, the region of the response curve having maximal slope was centered on the adapting light. The effect of this shifting of the response curve with chromatic adaptation, the authors conclude (p. 432), is to improve color discrimination over a broader region of color space than would otherwise be the case. This conclusion is tantamount to the prediction being made here.

The experiment below examined the effects of 5 different states of chromatic adaptation on color discrimination at 9 locations along a line of constant luminance running from a saturated red through a slightly yellowish white to a moderately saturated green. In addition, the dependence of color appearance on the state of chromatic adaptation was investigated by having subjects make saturation estimates of the same nine lights under each of the five adaptation conditions.

METHOD I

Apparatus

The optical system was fashioned after that used by Pointer (1974) and is represented in Fig. 1. There are three channels, one for each of the adapting, test, and comparison fields. Each channel provided for variation in chromaticity along a red-green line of constant luminance using a two-filter Burnham-type colorimeter. The back-illuminated diffusing surfaces defining the three fields were viewed by the left eye through an artificial pupil.

Source S_1 was a tungsten coil filament (General Electric 1195) run at a constant 12 V, 2.9 A using a regulated d.c. power supply (Sorensen DCR 40-20A). S_2 was a 45 W tungsten-iodine source (Bausch and Lomb 33-86-39-01) run on 115 V a.c. The diverging light defining each channel first encountered heat absorbing filters H and neutral density filters N (Wratten #96) used to adjust the relative luminances of the three fields. Emerging slightly converged

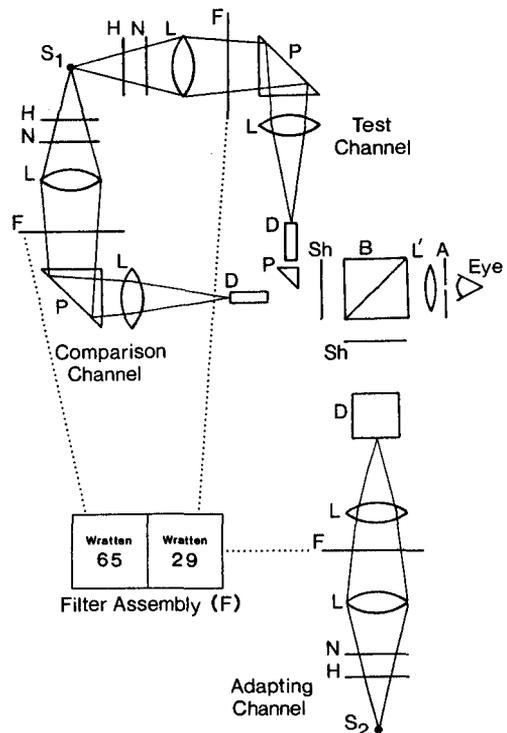


Fig. 1. Optical system used in the first experiment and in part of the second. See text.

from lenses L , the beams then passed through filter assemblies F consisting of photometrically balanced Wratten #65 and #29 gelatin filters mounted on glass. These were attached to X-Y positioners (Edmund Scientific) which permitted precise horizontal positioning of the filter assembly in each beam. Upon being brought to a focus by condensing lenses, each beam illuminated the end of a clear plexiglass rod which had been sanded to a fine grain. The effect of the plexiglass rod was to diffuse and integrate the light such that the surface at the other end, also finely sanded, presented a field homogeneous in color and brightness. The test and comparison fields were optically juxtaposed by prism P and then superimposed upon the adapting field by beam combiner B . Uniblitz shutters Sh (Vincent Associates) were used to present the adapting fields and the two smaller fields in alternation. Auxiliary lens L' permitted the observer to view the three fields, all at the same optical distance, without accommodative effort. The artificial pupil (dia. = 2 mm) controlled for variations in the natural pupil. Accurate placement of the left eye was accomplished using a precision 3-axis stage positioner to which the observer's bite plate was firmly attached.

The circular test and comparison fields were 1.3° in diameter with a horizontal spacing between them of 0.6° . The 5.2° adapting field was centered on these two fields. Automatic timing was provided by a Uniblitz 300 C shutter-timer and 100-2 drive unit (Vincent Associates) in conjunction with two Hunter timers.

Calibrations

All luminance and color temperature calibrations were made by a Spectra Spotmeter. Luminance measurements of the three fields were made *in situ* with auxiliary lens L' and artificial pupil removed; color temperature measurements were done with the filter assemblies F also removed.

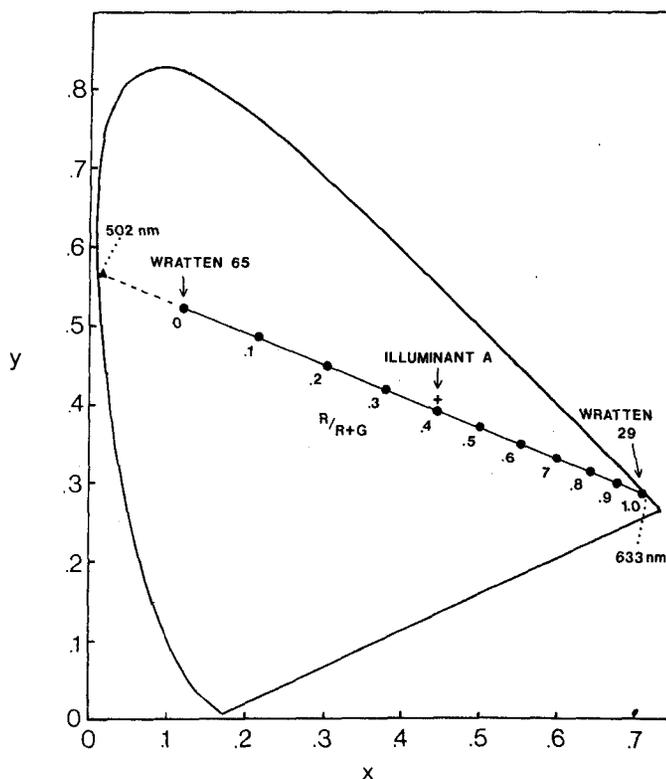


Fig. 2. The stimuli used in both experiments. All stimuli produced with the filter colorimeters are plotted as solid circles. The monochromatic adapting light used in the second experiment is represented by the solid triangle.

The color temperature of the test and comparison channels was approximately 2600 K; that for the adapting channel was about 2900 K. These values are both close to that of illuminant *A* (2856 K).

The red (Wratten #29) and green (Wratten #65) filters constituting each filter assembly were balanced for luminous transmittance by adding a 0.2 neutral density filter to the Wratten #29 in both the test and comparison channels and a 0.1 neutral density filter to the Wratten #29 in the adapting channel. These values were judged to most nearly provide for photopic equivalence of the two filters given the nominal transmittance values (re: illuminant *A*)², the photometer readings, and subjective brightness matches by the two authors.

Luminances were equated between the three channels by means of neutral density filters *N* interposed in each channel. With the Wratten #65 fully occupying each channel, the photometer readings were all close to 17 fL with the degree of imbalance not exceeding 10%. With the artificial pupil in place, retinal illuminance in this experiment was constant for all stimuli at close to 180 td.

The final calibrations involved determining the variation in chromaticity from red to green as a function of the vernier scale reading of each filter assembly. These determinations were conducted by carefully blocking out the red filter and then recording the luminance of the Wratten #65 contribution at each scale value. A check was made showing that the Wratten #29 luminance did vary in compensatory fashion and that, for a sampling of scale values, the sum of the two contributions equaled the photometer reading when both filters were exposed.

By expressing the luminance value (denoted *G*) recorded for the Wratten #65 filter at each position as a fraction of the constant red plus green luminance (*R* + *G*), the ratio $G/(R + G)$ or its complement $R/(R + G)$ was obtained. Color discrimination was measured with the comparison field set to each of these $R/(R + G)$ values: 0.1, 0.2, 0.3, ... 0.9. The five adapting lights corresponded to $R/(R + G)$ values of 0, 0.2, 0.4, 0.7 and 1.0. All 11 lights are plotted in the CIE chromaticity diagram shown in Fig. 2. The endpoints of the solid line define the nominal positions of Wratten filters #29 and #65 (re: illuminant *A*).² Wratten #29 under this illuminant appears as a saturated red with the slightest tinge of yellow; Wratten #65 appears a somewhat less saturated green with perhaps a tinge of blue. The light corresponding to the $R/(R + G)$ value of 0.4 is reasonably neutral, being close to illuminant *A*. All other stimuli are desaturated reds or greens. After the calibration procedure was complete, a check showed that filter settings of equal $R/(R + G)$ value led to good color matches between the channels.

Subjects

Four subjects, the two authors JL and TB, and two naive observers, EE and GR, participated in the color discrimination part of the experiment. In the segment dealing with color appearance all but EE participated. All subjects were judged normal trichromats on the basis of the AO Pseudo-isochromatic plates. In addition, EE, JL and GR have since been checked with the Farnsworth-Munsell 100-Hue test. JL was the only subject with extensive prior experience in making psychophysical judgments. TB acted as experimenter for the other three subjects while JL did so for her.

² Source: *Kodak Filters for Scientific and Technical Uses* (Standard Book 0-87985-029-9) published by Eastman Kodak Co., 1970.

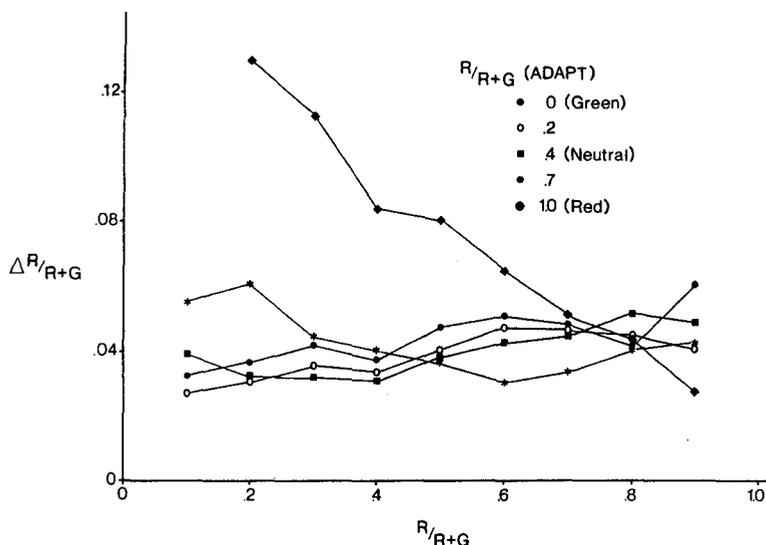


Fig. 3. The results of the discrimination task of the first experiment. The average just-noticeable difference, expressed as a change in $R/(R+G)$, is plotted as a function of the comparison field chromaticity under each adaptation state, as designated by the adapting field chromaticity.

Procedure

Because of the large number of conditions and the tedious nature of the task, the method of adjustment was chosen for determining the just-noticeable chromatic differences. The same method was employed by Pointer (1974) and similar methods have compared favorably with a four-alternative forced-choice procedure in a wavelength discrimination task (DeValois *et al.*, 1974). The basic procedure in the discrimination task went as follows. The subject first adapted for 5 min to the light for that condition; during this and subsequent adaptation periods, the subject continually moved his gaze over the adapting field to prevent local edge adaptation. While the subject adapted, the experimenter set the test and comparison fields to the desired chromaticity. The discrimination task began with the slow alternation between the adapting field and the two smaller fields, the latter appearing for 2 sec once every 10 sec. During successive exposures of the test and comparison fields, the subject adjusted the test field until it appeared just noticeably different in one direction from the comparison field; the subject made this adjustment by turning the knob on the filter assembly in the test channel. The experimenter recorded the scale value, and the subject then repeated the procedure in the opposite direction. In one of the conditions under red adaptation, subjects were unable to find an acceptable setting in one direction because the scale endpoint had been reached. In this case a blank was recorded.

Each session lasted about one hour during which discrimination was measured once at each comparison field chromaticity under the one adaptation state. Adapting conditions were presented in random sequence as were the comparison field chromaticities in each session. Each subject participated in 20 sessions, 4 of each of the 5 adaptation conditions. The first 5 sessions, however, served only for practice.

The second part of the experiment involved estimating the saturation of each comparison field under each state of chromatic adaptation. The procedure was much the same except that only the comparison field was presented in alternation with the adapting field. Subjects used a scale with "0" indicating an achromatic appearance and "20" the most saturated color ever observed; the subject also indicated whether the field was red or green for non-zero estimates. As in the first segment, a single adapting light

was employed throughout each session. Three saturation estimates for each comparison field were obtained in each of two sessions at each adapting chromaticity. In spite of the subjectivity of the task and the arbitrariness of the scale, the judgments within and between the 3 subjects were remarkably consistent, so much so that straight averaging of all 18 estimates in each condition did little injustice to the individual estimates.

RESULTS

The pair of scale values associated with each determination of the JND's on the two sides of the match point were converted to $R/(R+G)$ values using the luminance calibrations. The difference between these values was then taken and halved, the result representing the JND in terms of $R/(R+G)$ for that particular determination, condition and subject. All such JND values were then averaged within and across subjects, a step justifiable on the grounds that subject differences were slight. The results for the discrimination task are given in Fig. 3 where the just-noticeable change in $R/(R+G)$ is plotted as a function of adaptation condition and comparison field chromaticity.

The saturation estimation experiment results are arithmetic means of the individual estimates; these averages are plotted in Fig. 4 as a function of adaptation condition and comparison field chromaticity. Besides their striking regularity, they exhibit a clear effect of chromatic adaptation, that of the curves shifting along some dimension. Because the curves generally slope upward to the right, it is uncertain whether the shift is along the vertical axis, the horizontal axis or both. These changes in perceived color bear some resemblance to the changes in brightness Craik (1940) observed in an investigation of the effect of light adaptation on brightness.

DISCUSSION

Much as expected, optimal color discrimination under each state of adaptation occurred at a chroma-

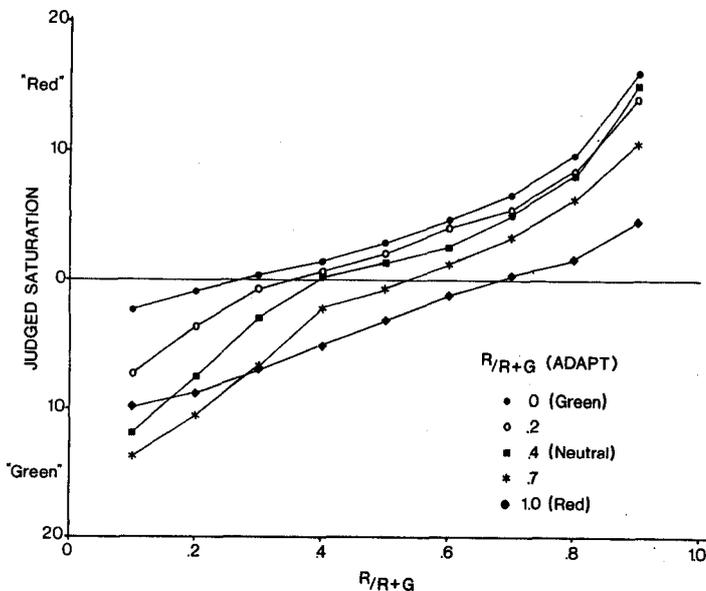


Fig. 4. The results of the saturation estimation task of the first experiment. Judged saturation, averaged across subjects, is plotted as a function of the comparison field chromaticity under each adaptation state, as designated by the adapting field chromaticity.

ticity close to that of the adapting light; in every case, the minimum JND coincided either with the adapting field chromaticity or with the next closest chromaticity tested. This corroborates the earlier observations of others (Brown, 1952; Hurvich and Jameson, 1961; Pointer, 1974) that color discrimination is most acute in the vicinity of the adapting light chromaticity. Furthermore, in relation to discrimination under neutral adaptation ($R/(R+G) = 0.4$), chromatic adaptation has the effect of worsening discrimination in the region which is complementary in hue to that of the adapting light, a finding also evident in the data of Brown (1952) and Pointer (1974); this result is most apparent for the two red adapting conditions (0.7 and 1.0) but is also observable for the higher purity green adaptation (0). Further discussion of the discrimination results is deferred until after the second experiment.

The judgments of saturation confirm for the most part what is generally believed about chromatic adaptation—namely, that adaptation to light of one color reduces the saturation of lights of the same hue, causes normally achromatic light to take on the complementary hue, and increases the saturation of lights of the complementary hue (DeValois and Jones, 1961; Jacobs, 1967; Parsons, 1924). There is, however, one significant departure from this generalization—adaptation to the higher purity red light (1.0) actually reduces the saturation of green lights relative to their appearance under neutral adaptation, an effect observed with all 4 subjects. We are at a loss to account for this result, for it appears quite unlike the absence of supersaturation in green lights following intense red adaptation (2.2×10^4 td) found by DeValois and Walraven (1967), an effect they attributed to the afterdischarge of red-sensitive cones (a red positive afterimage). With the 180 td adaptation level used in this experiment, positive afterimages were never

observed during eyeblinks or in the presence of the test fields.

Aside from the above exception, the saturation results are consistent with an interpretation in terms of shifts in the balance between the opposing processes of red-green cells, shifts like those actually observed (DeValois *et al.*, 1963). The shift in balance could be the result of changes in the sensitivities of the receptors feeding into the opponent cell and/or the direct result of its own recent history of responding, a shift which corresponds to the incremental induction postulated by Hurvich and Jameson (1961; Jameson and Hurvich, 1973).

The second experiment reported below is in many respects a replication of the first. It differs primarily in that the major interest was to compare the adapting effects of two different sequences of light stimulation, the one steady, and the other rectangular flicker (5 Hz) of the same time-average luminance. There are now a number of studies showing that under appropriate conditions the afterimages or after-effects of preadaptation are not predictable solely on the basis of the time-average stimulation (Anstis *et al.*, 1978; Broekhuijsen *et al.*, 1979; Loomis, 1972, 1978; Uhlarik and Brigell, 1977; Virsu and Laurinen, 1977). In particular, Loomis (1978) found that flickering and steady red adapting fields, equated for time-average luminance, gave rise to vastly different bluish-green afterimages, as seen against a neutral post-adapting field. It was expected that a similar difference in adapting effects could be demonstrated with the two dependent variables under investigation here. In addition, a steady adaptation condition using monochromatic green light is compared in its effects with the highest purity green adaptation condition ($R/(R+G) = 0$; excitation purity = 0.74)² of the previous experiment. This was done to determine whether the adapting effects of green light could be

enhanced at all by resorting to a light of greater excitation purity.

METHOD II

Apparatus

This experiment was conducted in 2 parts, the two requiring slightly different optical systems. For the first, which is a comparison of the adapting effects of flickering and steady light, the optical system from the previous experiment was used but with two minor changes. In the adapting channel a sectored disc, driven by a Bodine variable speed motor, was positioned in front of the filter assembly *F*, and the neutral density filters *N* in each channel were reduced in value, giving slightly higher luminances than before. For the second part of the experiment, an examination of the adapting effects of monochromatic green light, all components of the adapting channel except the shutter and plexiglass rod were replaced by a Bausch and Lomb grating monochromator (33-86-25-02) with tungsten source (33-86-39-01). With the shutter open, light from the monochromator illuminated the plexiglass rod directly.

Calibrations

Luminance and color temperature calibrations were made as before. With the filter assemblies removed, the balancing neutral density filters in position, and the sectored disc absent from the adapting channel, the luminance of each field was about 28 fL, including the case of monochromatic illumination; consequently, retinal illuminance was constant throughout at 300 td. The color temperatures of the tungsten sources remained the same.

For the flicker adaptation conditions, the sectored disc was placed in the adapting channel, and a neutral density filter of equal average transmittance removed in order to maintain the time average luminance at 28 fL, the value used for steady adaptation. The filter consisted of a 0.3 Wratten #96 filter enclosed in three slide cover glasses. A spectral calibration of this filter every 20 nm showed a constant transmittance of 40% ($\pm 0.9\%$) from 700 to 500 nm with a gradual decrease to 37% from 480 to 420 nm. The disc was made of heavy cardboard; two symmetric open sectors (72°) were cut to give an average transmittance of 40% over each cycle.

In situ determinations were made of the transmittance values of both the filter and the disc using the Spotmeter; average transmittance values of the disc were obtained by rotating it at a speed high enough to prevent any following by the photometer. Determinations were made with the color filter assembly set to each of three positions, including the two extremes. All transmittance values obtained were between 40.0 and 40.9%. Taken together, the above measurements indicate that the disc and filter were closely matched in average transmittance, thus guaranteeing that the steady and flickering adapting lights were of equal average luminance.

A flicker rate of 5.0 Hz was used throughout. Because of the position of the disc in the adapting beam, the waveform of the flicker was not strictly rectangular in shape; this is of no great consequence, for all that matters here is that the flicker and steady fields were of equal time average luminance.

The 502 nm adapting light used in the second part of this experiment is the wavelength at which the line connecting the chromaticities of the Wratten #65 and #29 filters intersects the spectral locus (Fig. 2). With the configuration of the monochromator we used, the excitation purity was computed to be 0.97. This "monochromatic" adapting light is represented by the triangle in Fig. 2. Because the available luminous output was just sufficient to provide a steady adapting field of 28 fL, no flicker condition was run in this part of the experiment.

Subjects

The three subjects who participated in all phases of the experiment were naive as to its purpose and had had no prior experience in psychophysical tasks of this sort. As judged by the Farnsworth-Munsell 100 Hue test, all had normal color vision. The first author acted as experimenter.

Procedure

Aside from a few slight changes, the procedure was the same as before. After an initial two sessions of practice, each subject ran in 12 sessions of the first part of the experiment, comparing steady and flicker adaptation; these 12 consisted of two each of the six adaptation conditions ($R/(R+G) = 0, 0.4$ and 1.0 ; steady vs flicker). Under each adaptation state, only five comparison field chromaticities were examined ($R/(R+G) = 0.1, 0.3, 0.5, 0.7$ and 0.9). The saturation estimation and discrimination tasks were combined within each session; after discrimination had been measured at each of the above chromaticities, the test field was blocked out and saturation estimates were then obtained. Two determinations were made at each chromaticity, making a total of four determinations for each condition and subject over the entire experiment. After the first part of the experiment was completed, the adapting channel was modified and each subject then participated in two sessions with the monochromatic adapting light.

RESULTS

Unlike the 4 subjects of the preceding experiment, the 3 subjects here varied considerably in terms of the criteria they adopted for the discrimination task. One subject uniformly set much finer differences than any of the previous 4 subjects, while another uniformly required much coarser differences. In order to give the data of the 3 subjects roughly equal weight, the data of 2 subjects were rescaled. After deriving the $R/(R+G)$ differences, the average JND for each subject over the entire experiment was calculated. Then for each of the two extreme subjects, the average JND was divided by that of the third; these ratios were used to rescale the $R/(R+G)$ differences of the two extreme subjects. After rescaling, averages across subjects were computed for each condition. For those few determinations on which the subjects went off scale without observing a just-noticeable difference, the JND was assumed equal to its counterpart in the opposite direction. This treatment of the data probably results in a slight underestimation of the average JND in these few cases ($R/(R+G) = 0$ under red adaptation), but it does permit a comparison of flicker and steady adaptation for these conditions as well. The discrimination results are shown in Fig. 5; all systematic trends in the results were also clearly evident in the data of each subject, despite the uniform differences in criterion.

There are several findings of interest in the discrimination results. First, there is an ever stronger confirmation of the prediction made at the outset than was provided by the data of the first experiment—not only is discrimination optimal nearest the adapting light chromaticity, but the worsening of discrimination in the region of complementary hue is readily apparent for both red and green adaptation. Second, the monochromatic green adapting light has no greater effect on color discrimination than does the Wratten #65 green ($R/(R+G) = 0$). Third, the

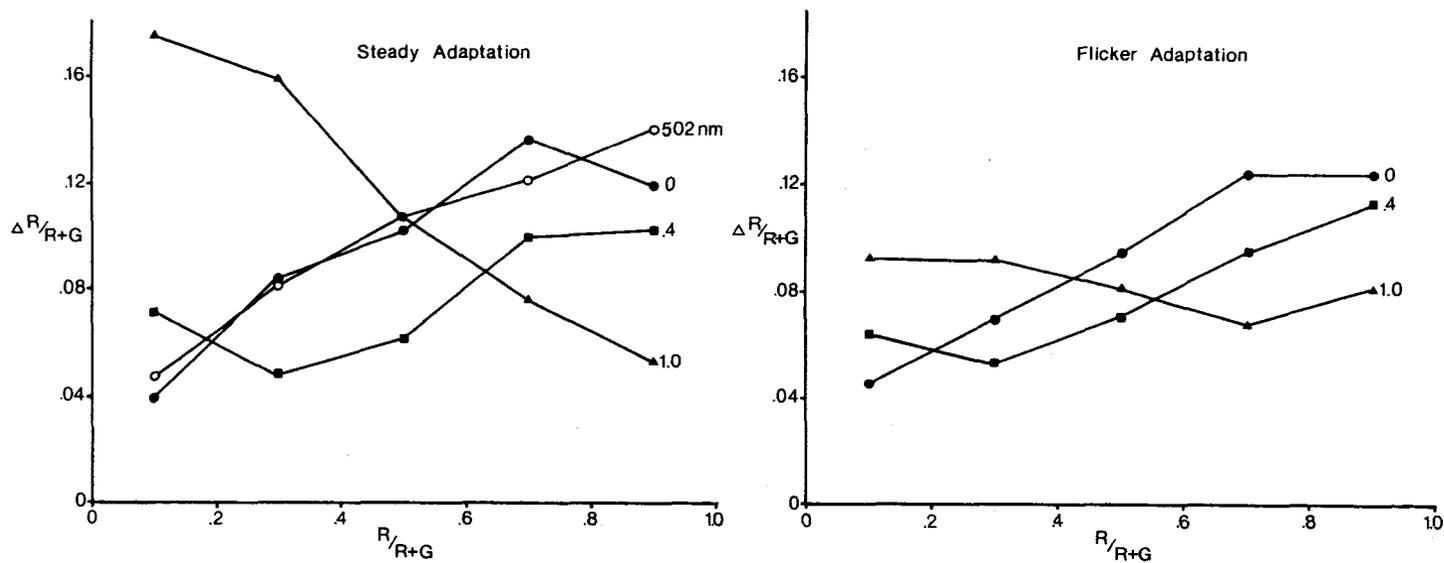


Fig. 5. The results of the discrimination task of the second experiment. The average just-noticeable difference, expressed as a change in $R/(R+G)$ is plotted as a function of the comparison field chromaticity under each of the adaptation states. The parameter refers either to the monochromatic adapting light (502 nm) or to the adapting lights of various $R/(R+G)$ values (0, 0.4, 1.0).

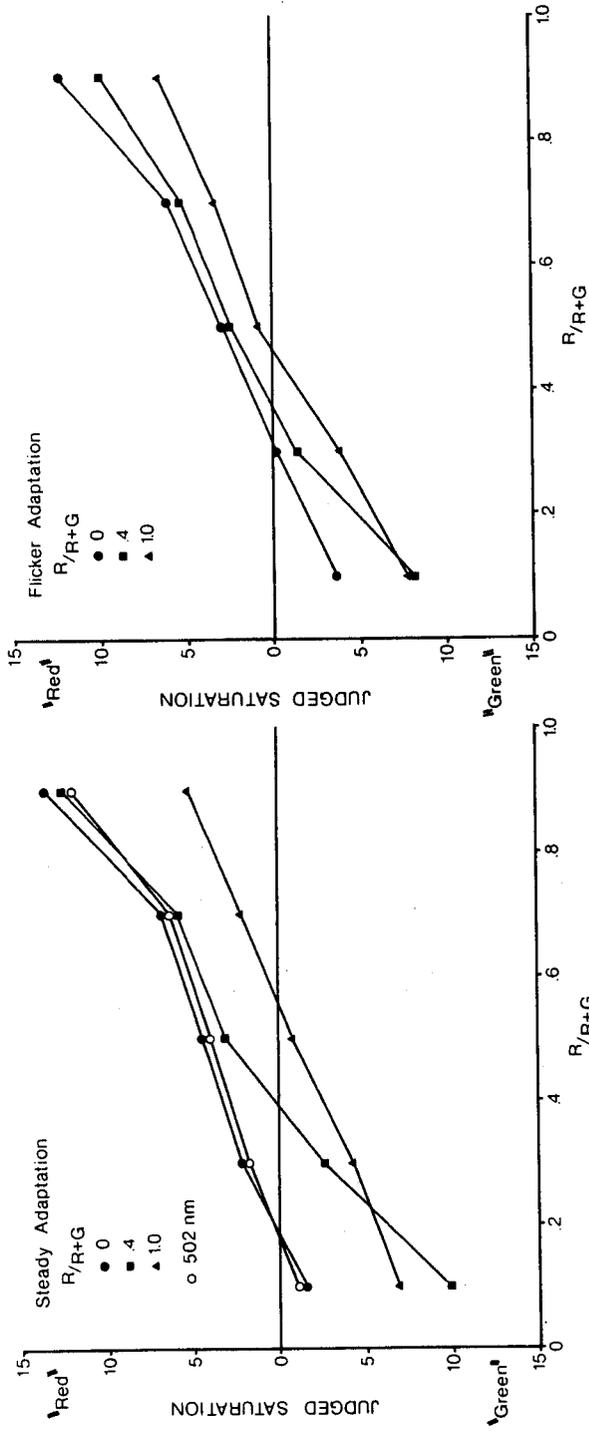


Fig. 6. The results of the saturation estimation task of the second experiment. Judged saturation, averaged across subjects, is plotted as a function of the comparison field chromaticity under each adaptation state. The parameter refers either to the monochromatic adapting light (502 nm) or to the adapting lights of various- $R/(R+G)$ values (0, 0.4, 1.0).

changes in color discrimination brought about by adaptation to flickering light are smaller than those caused by steady adaptation, even though the two lights are equal in average retinal illuminance. This effect of flicker is sizeable and reliable within the data of all three subjects for red adaptation, which in the steady condition alters color discrimination substantially relative to neutral adaptation. With adaptation to green light, which in the steady condition produces a much less pronounced change in color discrimination, the effect is correspondingly less; though small, it was nevertheless a consistent result in the data of two of the three subjects.

The results of the saturation estimation task are given in Fig. 6; as in the first experiment, the values of judged saturation are means of the individual estimates. The results for steady adaptation essentially reproduce the findings of the previous experiment. In addition, they confirm the above finding that monochromatic green has no greater adapting effect than the Wratten #65 green. Finally, comparison of the flicker and steady conditions indicates a slightly lesser adapting effect of flicker, a result which is clear and reliable for two out of the three subjects in both the red and green adaptation conditions; this is particularly apparent in the extent to which the achromatic point shifts along the abscissa as a function of adaptation state.

DISCUSSION

The results of this and the preceding experiment, together with the findings of earlier studies (Brown, 1952; Hurvich and Jameson, 1961; Pointer, 1974) leave little doubt that one effect of chromatic adaptation, at least for lights along a red-green line, is to optimize color discrimination in the vicinity of the adapting light; the consequence of this is to broaden the range of fine color discrimination. This finding is analogous to that which Craik (1938) obtained for brightness discrimination.

Although the analogy with brightness has its limits, given that chromaticity is a more restricted dimension than luminance, the interpretation of shifting differential sensitivity in terms of the sliding response curves of visual neurons seems as plausible for color as it is for brightness. In fact, the behavior of spectrally-opponent cells of LGN in macaque points to just such a mechanism; as established by DeValois *et al.*

³ If we were to assume the relative sensitivities of the *R*, *G* and *B* fundamentals adopted by Vos and Walraven (1971), the implication would be that the two green stimuli used in the second experiment actually stimulate and eventually desensitize the *R* receptors more than they do the *G* receptors. Although these relative sensitivities were determined to provide a good account of dichromatic luminosity, a different weighting would be preferable in explaining receptor desensitization resulting from adaptation; equating the *R* and *G* sensitivities at 580 nm affords a better illustrative example of receptor specific adaptation.

⁴ These values were determined in the usual way by computing the tristimulus values of the *R*, *G* and *B* fundamentals, modified as per above,³ in response to the three stimuli. For the Wratten 29 and Wratten 65 stimuli, their spectral distributions were obtained by multiplying the nominal filter transmittances by the spectral energy distribution of source A (Wyszecki and Stiles, 1967).

(1967), the response curves of these cells shift along the wavelength dimension such that the cells are maximally responsive to small changes in wavelength nearest the adapting light. Since variation in wavelength is equivalent to variation in red-green or yellow-blue chromaticity for a given opponent-cell, the activity of these cells accounts rather well for the discrimination data presented here.

As discussed earlier, the changes in saturation are equally in agreement with the notion of a readjustment in the balance of chromatically opponent cells. It might seem, then, that the discrimination data could be predicted from the slopes of the saturation curves. However, any attempt to ascribe meaning to different slopes outside of the same local region on the scale is fraught with difficulty, for judged saturation can probably be assumed at best a monotonic function of perceived saturation or the corresponding physiological code. Moreover, it is quite possible that even if color discrimination and color appearance are both related to opponent-cell activity, they are related by quite different functions.

This demonstrated parallel between the psychophysical data and the activity of chromatically opponent cells by no means constitutes the final word on color discrimination under these circumstances, for the question arises of whether the discrimination data might also be predictable from the receptor activity directly, in which case the opponent cell activity merely reflects something more basic. Should this be the case, then the effects of adaptation observed here must correspond entirely to alterations in the cone responses. A result which accords with this view is the lesser adapting effect of green light on discrimination. If the primary effect of chromatic adaptation is to displace the working range of each cone type along the log *I* axis by an amount related to the recent cumulative quantum-catch, a scheme favored by Walraven (1976) in an analysis of color appearance, then one would expect changes in color discrimination to be related to the selectivity of cone stimulation during adaptation. For any reasonable set of cone spectral sensitivities, the Wratten #29 (red) light is considerably more selective in exciting the long wavelength cones (relative to the middle wavelength cones) than are the Wratten #65 (green) or 502 nm lights in exciting the middle wavelength cones. For purposes of illustration, we take the fundamentals of Vos and Walraven (1971), adjust the *G* fundamental upward in absolute sensitivity to match that of the *R* fundamental at 580 nm,³ and compute the chromaticity coordinates (*r*, *g*) of the Wratten #29, Wratten #65 and 502 nm stimuli; these coordinates are (0.82, 0.18), (0.34, 0.65) and (0.32, 0.68), respectively.⁴ To pursue this point in any greater detail would appear unwarranted, for the analysis depends critically upon the relative sensitivities of the three fundamentals as well as upon the answers to a number of questions, including whether receptor desensitization is proportional to recent quantum catch (cf. Walraven, 1976).

A more fruitful line of investigation would seem to be to examine directly the assumption that all the important effects of chromatic adaptation are manifest in changes at the receptor level, changes at more proximal levels merely being concomitant variations.

Although there is certainly evidence from a variety of sources that the receptors are desensitized even with exposure to the low photopic levels here (Cicerone *et al.*, 1975; Hood *et al.*, 1978; Normann and Werblin, 1974; Walraven, 1976), there is also evidence of nontrivial sensitivity changes at more proximal levels which are independent of the changes at the receptor level. Loomis (1972), in an investigation of the chromatic afterimage of a repeating sequence of stimulation which was complementary in hue to its major chromatic constituent, found evidence of post-receptor adaptation of sufficient strength to outweigh the desensitizing effects of whatever receptor adaptation were present. More recently, a number of studies (Augenstein and Pugh, 1977; Mollon and Polden, 1975, 1976; Pugh and Larimer, 1978) have shown that adaptation to long wavelength light can reduce the sensitivity of the blue-cone pathway, apparently by a resetting of the balance of the yellow-blue opponent system (Pugh and Larimer, 1978). At the very least, these and other studies of similar import (Anstis *et al.*, 1978; Stabell and Stabell, 1975; Uhlarik and Brigell, 1977) make it unlikely that any psychophysically observed effect of chromatic adaptation is ascribable to receptor desensitization alone.

The present finding of a disparity between the adapting effects of steady and flickering light, equated for time average luminance, has some bearing on this issue. Because the peak amplitude of the flicker was only 750 td (2.5 times that of the steady light) guaranteeing against saturation of the bleaching rate and because the period of each cycle of flicker (200 msec) was well within the critical duration (10 sec) estimated for the bleaching of erythrolabe and chlorolabe (Rushton and Henry, 1968), there is virtually no doubt that the two adapting lights had equivalent bleaching effects. This implies that bleaching alone, especially at these low bleaching levels (3%),⁵ cannot solely determine the sensitivity of the receptors or of more proximal neurons. The implication in turn is either of two possibilities: (1) receptor desensitization underlies these adapting effects but receptor desensitization depends partly upon some cumulative signal activity which, perhaps because of a compressive non-linearity in the receptor response (Virsu and Laurinen, 1977) is different for the two adapting sequences and (2) the observed effects of adaptation on discrimination and color appearance are the result of a post-receptor adaptation process, such as a resetting of the balance of the opponent cell contingent upon its own recent history of activity, which depends quite differently upon the two adapting exposures. Which of these alternatives is correct is unfortunately left unanswered by the present work; however, research to provide the answer is currently underway.

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⁵ This value was calculated using the kinetics equations established for erythrolabe and chlorolabe by Rushton and Henry (1968); the calculation assumed a half bleach intensity of 10^4 red td (quantum catch of R cones in trolands), a maximum R cone stimulation of 240 red td occurring with the 300 td Wratten 29 stimulus, and attainment of bleaching equilibrium.

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