

Link-Specific Adaptation in the Luminance and Chromatic Channels

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We present evidence that adaptation occurs in the separate links that connect the receptors to the luminance and the chromatic channels. The relative effectiveness of the L and M cone inputs to the luminance and red/green chromatic channels was determined by using, respectively, heterochromatic flicker photometry and a cancellation technique which maintained a pure yellow. The findings provide evidence for a link-specific adaptation model, wherein one receptor system provides two separate links to the luminance and chromatic channels and the outputs of an individual cone to these two postreceptoral channels can be separately attenuated or weighted at each of these links by colored adapting lights. One line of evidence for link-specific adaptation is that colored adapting fields selectively suppress L and M cone inputs to the red/green chromatic channel by a smaller factor than the luminance channel. A second line of evidence is that there is not only a magnitude difference but also a dynamic difference between adaptive processes operating in the luminance and chromatic channels: the luminance channel has a faster gain change and recovery from adaptation than does the chromatic channel. The results, together with other evidence, make it plausible that an important component of light adaptation in cone vision occurs at the cone-bipolar synapse.

Luminance channel Chromatic channel Adaptation Link-specific adaptation Sensitivity

INTRODUCTION

For over a century (Donders, 1881), it has been recognized that signals from the cones are transmitted through color-opponent pathways, which extract the difference between signals from different cone types, and a non-opponent luminance channel that adds them. Here we consider the sites of visual adaptation to light and color in relation to this “zone” model of the visual system (Fig. 1).

Psychophysical and physiological studies (see for instance reviews by MacLeod, 1978; Boynton, 1979; Mollon, 1982; Lennie & D’Zmura, 1988; Walraven, Enroth-Cugell, Hood, MacLeod & Schnapf, 1990) have provided evidence for adaptation processes both in the receptors and at later stages that follow the recoding into color-opponent and non-opponent channels. The possibility that a component of adaptation might proceed independently in the connecting links that transmit signals from the cones to the channels, has not, however, been considered. Our experiments test this proposition, and the results (first described in Ahn & MacLeod, 1989, 1990) support it.

Heterochromatic flicker photometry and a chromatic cancellation technique were used to estimate the selective

suppression of the L and M cone inputs to the luminance and red/green chromatic channels, respectively, for different wavelengths of an adapting background. Heterochromatic flicker photometry is a method that isolates the achromatic from the chromatic channels on the basis of their different temporal sensitivities (Ives, 1912; King-Smith & Carden, 1976; Boynton, 1979). Chromatically different and spatially coincident lights are alternated at a flicker frequency too high for the sluggish chromatic channel to track but low enough for the fast luminance channel to follow.

To monitor the output of the red/green opponent channel, we adopted an equally standard technique, that of chromatic cancellation. We assume that a colored stimulus, which appears neither reddish nor greenish, produces a zero output from the red/green opponent channel (Jameson & Hurvich, 1955; Larimer, Krantz & Cicerone, 1974).

The luminance channel simply adds the signals from L and M cones (Eisner & MacLeod, 1981). Under most conditions, the S cones do not contribute to luminance (Eisner & MacLeod, 1980; Tansley & Boynton, 1978). Thus, we assume that only L and M cones contribute to the luminance channel in the experiments reported here. The red/green opponent chromatic channel receives input from S as well as L and M cones (Muller, 1924) but we give evidence below (Expt 2) that under our conditions and with our stimuli, the main factor influencing perceived redness or greenness is the balance of L and M cone inputs.

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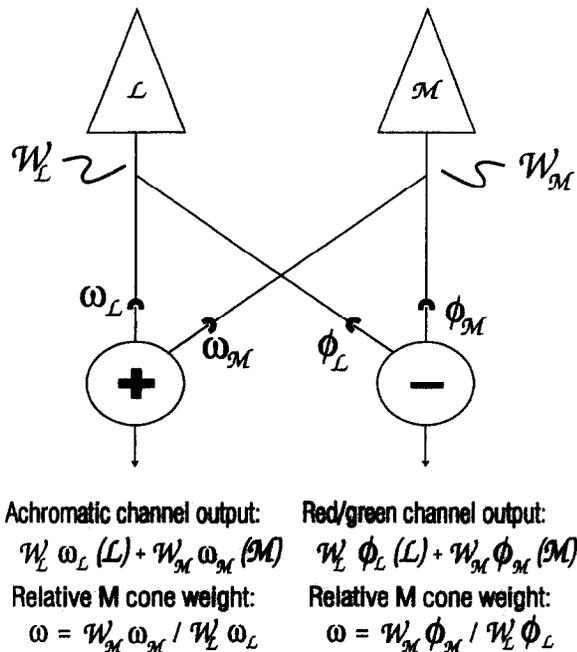


FIGURE 1. The link-specific adaptation model where gain changes occur in the separate connections or the links between receptors and channels. One receptor system provides two separate links to each channel, one link per channel. There are, then, for the L and M cone system, a total of four possible links to the channels. In the link-specific model, cone outputs to the two channels can be separately attenuated at each of these sites. Adaptation occurring at the links between the L cones and the luminance channel is denoted by the term ω_L and adaptation occurring at the link between the M cones to the luminance channel is denoted by the term ω_M . Likewise, adaptation occurring at the link between the L cones to the red/green chromatic channel is denoted by the term ϕ_L and adaptation occurring at the link between the M cones and the red/green channel is denoted by the term ϕ_M . Because each of the four gain factors is unique, the cone outputs arriving at the luminance and red/green opponent channel can vary independently across backgrounds of different wavelengths.

Theoretical framework

The standard conception of the visual system's representation of color is sketched in Fig. 1: only the L and M cones are shown, since these are the focus of interest in this paper. The two idealized schemes of Fig. 1 provide three possible sites of adaptation: within the L and M cones themselves; within the two postreceptoral luminance and chromatic channels that respectively add and subtract the cone outputs; and within the four links that couple the two cones to the two postreceptoral channels. The consequences of adaptation at these three sites are in principle quite different. For example, the spectral sensitivity for test lights flashed as increments on a white background can be described assuming independent detection by the luminance and chromatic channels. If the white adapting field is intense, it selectively reduces the sensitivity of the luminance channel but spares the chromatic channel, something that could not happen with receptor adaptation alone (Jablonowska & King-Smith, 1978).

In this paper we are concerned only with the relative effectiveness of L and M cone input to the postreceptoral channels. Adaptive changes in this are expressed as changes in the relative sensitivity of the channels to lights

of different color. Adjustments of sensitivity applied to the luminance and chromatic signals, after each channel has already appropriately combined its cone inputs, have no effect since the channels are nulled. The remaining possible sites of adaptation are ones that affect the cone inputs to the postreceptoral channels: at the cones, or at the neural links that connect the cones to the channels. Figure 1 represents sensitivity adjustments at the cone level by intensity scaling factors, W_L and W_M , associated with the L and M cones. Sensitivity adjustments in the links are represented by scaling factors ω_L and ω_M for the respective cone inputs to the luminance or achromatic channel, and by factors ϕ_L and ϕ_M for the inputs to the red/green opponent channel.

Each channel's signal is an additive combination of the L and M cone inputs, in which each cone input is equal to the cone excitation, L or M, weighted successively by the cone sensitivity scaling factor (W_L or W_M) and by the link-specific scaling factor (ω_L , ω_M , ϕ_L or ϕ_M). Figure 1 gives expressions for each channel's output as a function of the two cone excitations, L and M. The cone excitations, L and M, are positive for all stimuli: if the weights remain positive, the achromatic channel output is positive at all wavelengths, but its spectral sensitivity to different wavelengths will depend on the "relative M cone weight", $\omega = W_M \omega_M / W_L \omega_L$, changing between a pure M cone sensitivity (if the relative M cone weight is infinite) to a pure L cone sensitivity (if the relative M cone weight is zero). The red/green channel is in general color-opponent, with a spectral cross point where the difference of the weighted cone inputs is zero. This cross point depends on the red/green channel's relative M cone weight, $\phi = W_M \phi_M / W_L \phi_L$.

Current models allow for cone-selective adaptation only at the cones themselves, and not in the links. On that view, the relative M cone weights for the luminance and color-opponent channels must vary together under changes in the state of adaptation. This may be seen by noting the effect of changes in the receptor sensitivities, W_L and W_M , on the relative M cone weights of Fig. 1. Any such changes must alter ω and ϕ by the same factor. Equivalently, the quantity $\log \omega - \log \phi$ must be invariant with adaptation. The following experiments test that prediction, and the results reject it. The inference is that substantial adaptation must occur in the neural links between the cones and the channels.

Experiments 1 and 2 concern steady state adaptation. Later experiments involve time-varying adaptational conditions.

EXPERIMENT 1

Method

Apparatus

The apparatus used for all studies presented in this paper is described in detail elsewhere (Stockman, MacLeod & Vivien, 1993). Briefly, measurements for all of the experiments reported here were made using a

four-channel Maxwellian-view optical system. Alignment of the observer's pupil with the light beam was achieved by having the observer bite onto a dental impression (bite bar) that was fixed to an x - y - z translator. The radiance of light could be adjusted by the subject using a neutral density wedge in each channel. The density of each wedge was calibrated at 15 deg intervals with different Ealing interference filters and neutral density filters by using a EG & G Radiometer/Photometer (Model 450-1) and a PIN 10 DP silicon photodetector from United Detector Technology.

Experimental design and procedure

Steady monocular exposure to four chromatically varying but equiluminant background stimulus fields (2.9 log td) subtending 5 deg of visual angle was used to differentially desensitize cone mechanisms. Four different background wavelengths were used: 639, 601, 574 and 530 nm. Equiluminance of the chromatically varying background fields was based on physical measurement with the EG & G photometer. Subjects adapted to one of these background lights for 2 min at the start of each session. All conditions involved monocular viewing and central fixation.

Superimposed on the background field was a smaller test field subtending 2 deg and consisting of two wavelength components: a 656 nm component and a 543 nm component. In the heterochromatic flicker photometric sensitivity (FPS) task, these components were flickered at 15 Hz in square-wave counterphase, as shown in Fig. 2(a).

The radiance of the 656 nm test component was fixed at four different levels: 0.3, 0.6, 1.2 and 1.8 log-intensity steps above the flicker threshold of each subject. (The retinal illuminance of the 656 nm test component at flicker threshold was in the range of 1.2–1.6 log td across background wavelengths.) At each of the four levels, the subject's task was to set the radiance of the 543 nm test component to a point where flicker was nulled or minimized. Presentation of the test only during flicker bursts of 0.2 sec minimized possible adaptation to the test lights.

For the cancellation task of maintaining a pure yellow, the 656 and 543 nm test components were flashed simultaneously for 0.2 sec, following 2 min adaptation to the background field alone [Fig. 2(b)]. The radiance of the 656 nm test component was fixed at the same four levels used in the FPS task. The subject's task was to adjust the radiance of the 543 nm test component to make the test appear "unique" or pure yellow, i.e. neither greenish nor reddish.

Conditions were blocked by psychophysical criteria (flicker photometry or cancellation), adapting backgrounds (639, 601, 574 or 530 nm), and test-component intensity (0.3, 0.6, 1.2 and 1.8 log-intensity steps above the flicker threshold). The experimenter recorded the radiance of the 543 nm test component at minimum flicker and at pure yellow. The change in the relative effectiveness of L and M cones was derived from the obtained results.

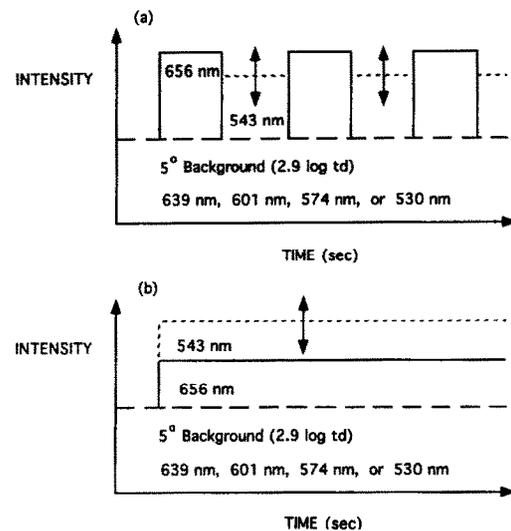


FIGURE 2. (a) The stimulus time-course for the FPS task in Expt 1. (b) The stimulus time-course for the pure yellow task in Expt 1.

A control experiment was conducted with the intensity of the 543 nm test component (rather than the 656 nm test component) fixed at four different levels. At each of these intensity levels, the subject adjusted the radiance of the 656 nm test component to either minimize flicker or to make the flashed test stimulus appear pure yellow.

Subjects

Five subjects were studied: two males of about 25 yr in age (CK and HG), one male of about 40 yr in age (KB) and two females of about 24 yr in age (SA and PM). In the control experiment, only two subjects were studied: SA and CK. Subjects were screened for color defects by the Ishihara Test for Colour Blindness (38 plate edition, 1988). Subjects CK and HG wore their normal prescription contact lenses.

Analysis

Changes in the L and M cone inputs to the luminance and chromatic channels were analyzed for each adapting condition as a function of the radiance of the 543 nm and of the 656 nm test components. The obtained radiance of the 543 and 656 nm test components were used to derive gain factors, ω and ϕ , that denote the relative effectiveness of signals from the L and M receptor systems, inclusive of changes at both the receptor and post-receptor levels. More precisely, the term ω_μ is used here to represent the relative effectiveness of M cone input (as compared with L cone input) for the achromatic channel, while ϕ_μ represents the analogous quantity for the red/green chromatic channel; both quantities will depend upon the background wavelength μ .

Analysis of the flicker photometric sensitivity measurements. Flicker photometric sensitivity for a background light of wavelength μ (FPS_μ) can be expressed as a linear combination of the weighted L and M cone sensitivities for a test light wavelength, as expressed in equation (1) (Eisner & MacLeod, 1981):

$$FPS_\mu(\lambda) = L(\lambda) + \omega_\mu M(\lambda). \quad (1)$$

$L(\lambda)$ and $M(\lambda)$ are the L and M cone spectral sensitivities, respectively. Here ω_μ is the relative gain factor or the coefficient by which the input from the M cones to the luminance channel is weighted (relative to L cone input) in the presence of a background of wavelength μ .

We measured the energies of our two test wavelengths, $E\mu(543)$ and $E\mu(656)$ that were required for a flicker photometric null. By definition, flicker sensitivity is inversely proportional to the energy required for a flicker null:

$$\frac{\text{FPS}_\mu(\lambda_1)}{\text{FPS}_\mu(\lambda_2)} = \frac{E_\mu(\lambda_2)}{E_\mu(\lambda_1)}. \quad (2)$$

Equations (1) and (2) yield the following expression for ω_μ :

$$\omega_\mu = \frac{E\mu(656)L(656) - E\mu(543)L(543)}{E\mu(543)M(543) - E\mu(656)M(656)}. \quad (3)$$

For $L(\lambda)$ and $M(\lambda)$, we adopted the cone sensitivity estimates of Smith and Pokorny (1975); equation (3) then allows the value of ω_μ to be derived from the flicker photometric data.

The relative M cone weight, ω_μ , depends on the state of chromatic adaptation. A green background will desensitize M cones to a greater degree relative to L cones and thereby lead to a decrease in the M cone weight relative to the L cone weight; as a result ω_μ will tend toward 0. Conversely, a red background will desensitize L cones relative to M cones and thereby lead to a decrease in the L cone weight relative to M cone weight; as a result, ω_μ will tend toward infinity. A ω_μ value of 1 results when there is no adapting background, in which case L and M cones are equally effective in determining flicker minima.

Analysis of the pure yellow measurements. In using the hue cancellation task of maintaining the test pure yellow, we assumed that activity in the red/green opponent channel determines subjectively perceived redness or greenness (Jameson & Hurvich, 1955; Larimer *et al.*, 1974; Walraven, 1976; Shevell, 1978) and that a pure yellow setting made by the subject represents the balance between the antagonistic L and M cone inputs to the red/green opponent channels.

At this chromatic balance, activation of the red/green opponent system can be described by a linear combination of the weighted cone outputs (Jameson & Hurvich, 1955; Larimer *et al.*, 1974):

$$L(\lambda) - \varphi_\mu M(\lambda) = 0. \quad (4)$$

As in the equations that described flicker photometric sensitivities, $L(\lambda)$ and $M(\lambda)$ are the Smith and Pokorny L and M cone spectral sensitivities, respectively. Here φ_μ is the derived sensitivity factor, analogous to ω_μ in equations (1) and (3), that represents the relative effectiveness of M cone input (as compared with L cone input) in establishing a red/green equilibrium for color appearance in the presence of a background of wavelength μ . Equation (4) states, in effect, that when the subject sees a pure yellow that is neither reddish nor greenish, it is because the antagonistic L and M cone

inputs to the red/green opponent channel are equal but opposite, so that they cancel (Larimer *et al.*, 1974).

Hence, if λ is the wavelength that looks neither reddish nor greenish,

$$\varphi_\mu = \frac{L(\lambda)}{M(\lambda)}. \quad (5)$$

For the experiments reported here, the pure yellow setting is made by combining red and green primaries, rather than by selecting the appropriate spectral wavelength λ . Equation (4) can be generalized to this case by substituting the L and M cone excitations produced by the compound stimulus for $L(\lambda)$ and $M(\lambda)$, respectively. Each of these excitations will depend on the total quantal catch by a given cone type from each of the two test lights (656 and 543 nm test components) at the chromatic null (pure yellow). The quantal catch by each cone type is the product of the radiant energy (E) of a given test light and the cone spectral sensitivity [$L(\lambda)$ or $M(\lambda)$].

This yields the following expression for the relative M cone weight, φ_μ :

$$\varphi_\mu = \frac{E\mu(656)L(656) + E\mu(543)L(543)}{E\mu(656)M(656) + E\mu(543)M(543)}. \quad (6)$$

The term φ_μ , like ω_μ , depends on the state of chromatic adaptation. A pure yellow test light shifts to a redder appearance as the background becomes greener and leads L cones to dominate over M cones and φ_μ to tend toward 0. Because M cone sensitivity in the yellow spectral region is only about half of the L cone sensitivity [as expressed in the units chosen by Smith and Pokorny (1975) so that FPS is the unweighted sum of L and M cones], the setting of a pure yellow with no background requires a value of about 2 for φ_μ .

Results and Discussion

The ratios of M cone to L cone weight (relative M cone weights) were derived for each of the experimental conditions. Each weight value represents from 12 to 18 radiance settings of the 543 nm test component, measured across 2–3 trials for each subject (6 settings per trial).

Figure 3 shows the obtained data for two subjects, KB and SA. Figure 3(a, c) shows the obtained data for the FPS task; Fig. 3(b, d) shows the obtained data for the pure yellow task.

Data for all five subjects are summarized in Table 1. The ordinate values in Fig. 3 represent the log of the relative M cone weights, ω_μ for the FPS task [Fig. 3(a, c)] and φ_μ for the pure yellow task [Fig. 3(b, d)]. It is important to note here that ω_μ or φ_μ is a relative value. The values will tend to go up when the M cone system dominates over the L cone system, i.e. when the M cone system is less desensitized by a background of wavelength μ than the L cone system.

The abscissa values for all panels in Fig. 3 represent the radiance of the 656 nm test component. The radiance of the 656 nm test component was fixed at 0.3, 0.6, 1.2 and 1.8 log-intensity steps from the flicker threshold

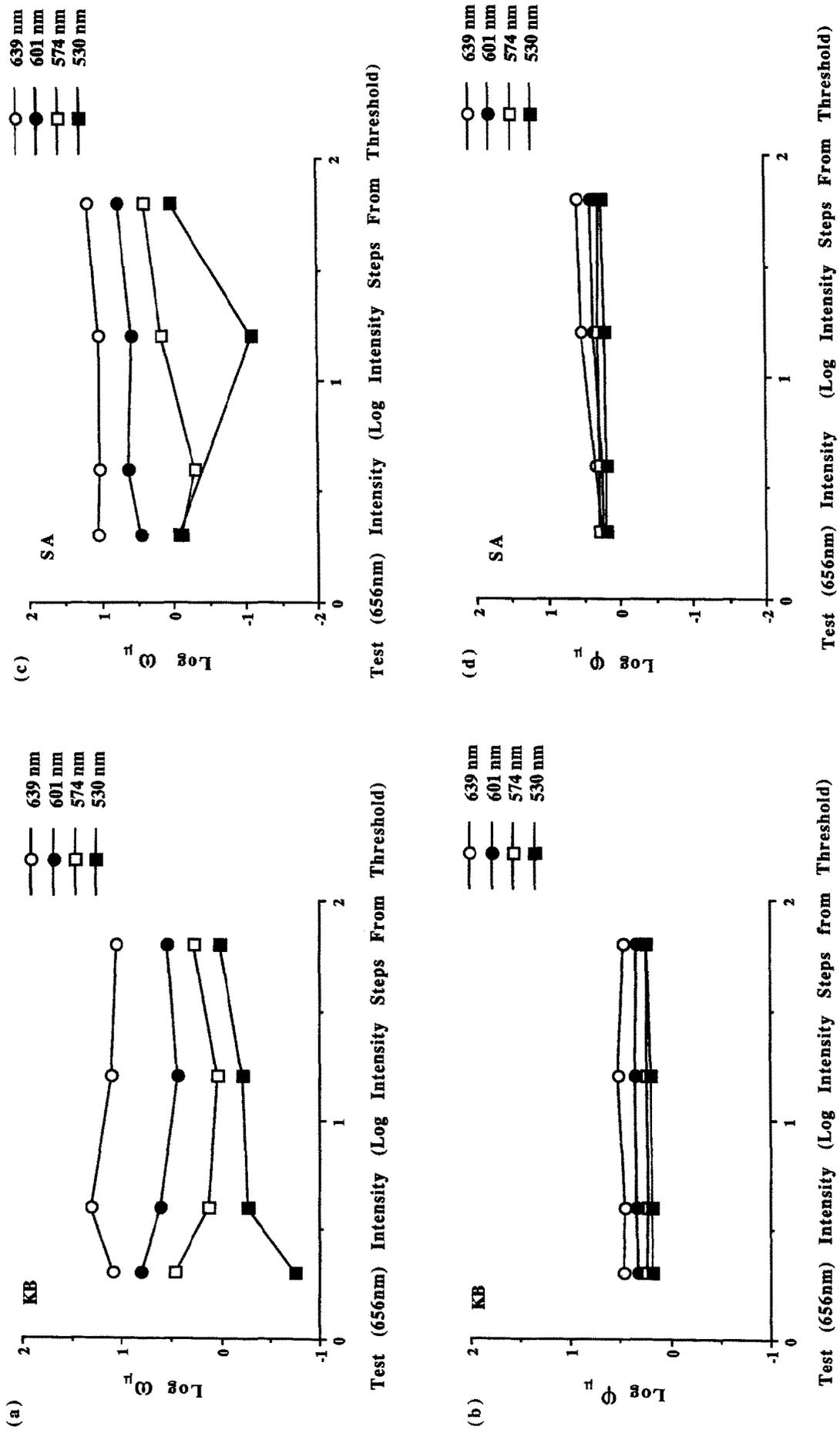


FIGURE 3. The log relative M cone weight values are plotted as a function of the 656 nm test intensity for different background wavelengths. The results from Expt 1 obtained for the FPS task and the pure yellow tasks, respectively, are shown for subjects KB (a, b) and SA (c, d). The retinal illuminance of the 656 nm test component at flicker threshold was in the range of 1.2–1.6 log td across background wavelengths.

TABLE 1. Summary of data for Expt 1

Background wavelength	Subjects				
	SA	KB	CK	HG	PM
<i>(a) FPS task: ω_μ</i>					
639 nm	1.072	1.137	0.963	0.751	0.708
601 nm	0.613	0.600	0.751	0.373	0.590
574 nm	0.041	0.226	0.054	0.372	0.231
530 nm	-0.312	-0.290	-0.160	-0.042	-0.110
Range of $\log \omega_\mu$	1.384	1.427	1.223	1.404	0.818
<i>Mean range of $\log \omega_\mu$ (across subjects) = 1.251</i>					
<i>(b) Pure yellow task: φ_μ</i>					
639 nm	0.570	0.490	0.600	0.754	0.606
601 nm	0.381	0.345	0.435	0.523	0.477
574 nm	0.300	0.239	0.260	0.335	0.337
530 nm	0.231	0.216	0.260	0.213	0.290
Range of $\log \varphi_\mu$	0.370	0.323	0.413	0.456	0.315
<i>Mean range of $\log \varphi_\mu$ (across subjects) = 0.375</i>					

of the 656 nm test component which was determined separately for each background wavelength for each subject. Each curve in Fig. 3 represents relative M cone weights plotted at different intensity levels of the 656 nm test component for a background wavelength.

The effect that background wavelength has on the relative effectiveness of M and L cone inputs is indicated by the vertical separation between the curves. A large separation between the curves would indicate that background wavelength has a big selective influence on the relative M and L cone inputs. Completely overlapping curves would indicate that background wavelength has no selective effect on the relative contributions of the M and L cone inputs. The effect that test intensity levels has on the relative effectiveness of M and L cone systems is indicated by the slope of each curve. A steep slope would indicate that test intensity level has a big selective effect on the effectiveness of the M and L cone systems. A flat curve would indicate no effect of test intensity level on the relative effectiveness of the M and L cone systems.

For the FPS task [Fig. 3(a, c)], $\log \omega_\mu$ values were greatest for the 639 nm background and smallest for the 530 nm background across all four test intensity levels. The range of $\log \omega_\mu$ between these two curves is represented by the separation between these curves. The log M cone weights obtained for different test intensity levels for the FPS task were averaged for each background wavelength and those mean values are presented for each subject in Table 1 (a). The range of mean $\log \omega_\mu$ across background wavelengths for the FPS task was 1.43 for KB [Fig. 3(a)] and 1.38 for SA [Fig. 3(c)]. These range values are fairly typical since the mean range value for all subjects is 1.25 [Table 1(b)].

For the pure yellow task, as shown in Fig. 3(b, d), the relative M cone weights were slightly smaller in the lower test intensity conditions relative to the higher test intensity conditions. The variation in the relative M cone weight as a function of test intensity indicates a possibility of a small additive contribution by the background (e.g. Jameson & Hurvich, 1955, 1972; Jameson,

Hurvich & Varner, 1979; Shevell, 1979, 1982; Shevell & Humanski, 1988; Shevell & Wesner, 1989). A red background, for instance, may affect the appearance of the test by adding redness to it, requiring more green light to maintain a pure yellow test appearance. Therefore, redness added to the test by a red background decreases the relative M cone weight. And, clearly, the additive effect of the background on the test should be less at higher intensity levels of the test stimulus.

For each background wavelength shown in Fig. 3(b, d), $\log \varphi_\mu$ values were averaged across the two highest test intensity levels. These mean $\log \varphi_\mu$ values are presented for each subject in Table 1(b). The relative M cone weights derived for higher test intensities are relatively less influenced by the putative background additive effect and therefore are more appropriately comparable to the relative M cone weights derived for the FPS task (in which the additive effect of the background is irrelevant, being canceled out in the flicker photometric attenuation). The range of these high test intensity values across background wavelength for the pure yellow task was 0.32 for KB [Fig. 3(b)] and 0.37 for SA [Fig. 3(d)]. These values are in close agreement with the mean range value of 0.38 obtained by averaging the range of the log relative M cone weights across subjects [Table 1(b)].

Across all five subjects studied, the main effect of the background wavelength on log relative M cone weight was highly statistically significant [$F(3,12) = 83.21$, $P < 0.0001$] for both the FPS and pure yellow task. Additionally, the difference in the mean range of relative M cone weights across background wavelength between the FPS and pure yellow tasks was highly significant [$F(3,12) = 25.85$, $P < 0.0001$]. The effect of the intensity of 656 nm test component on the relative M cone weights was small but significant [$F(3,12) = 0.22$, $P < 0.05$].

In Fig. 4, log relative M cone weights obtained from subject SA are plotted as a function of background wavelength. Values for the FPS task (i.e. ω_μ) are indicated by open squares. Each open square represents a mean obtained by averaging across all four intensity levels. Values for the pure yellow task (i.e. φ_μ) are indicated by open triangles. Each open triangle represents a value obtained by averaging across the two highest test intensity levels. (The Weber prediction shown by the dashed curve will be referred to later.)

A change in log relative M cone weight with background wavelength is expressed in this figure as the slope of the curve. For FPS and hue cancellation, slope of the relative M cone weights is much steeper for the FPS task than for the pure yellow task, indicating that the weights for the FPS task varied more across background wavelength than they did for the pure yellow task. The results for all other subjects are comparable.

These results allow us to reject the null hypothesis, that adaptation occurs only in the receptors and not in the links. Such a model predicts that the weights will vary together across background wavelengths for the FPS task and the pure yellow task, yielding parallel curves in Fig. 4. Instead these results provide (as explained in the Introduction) evidence for the link-specific

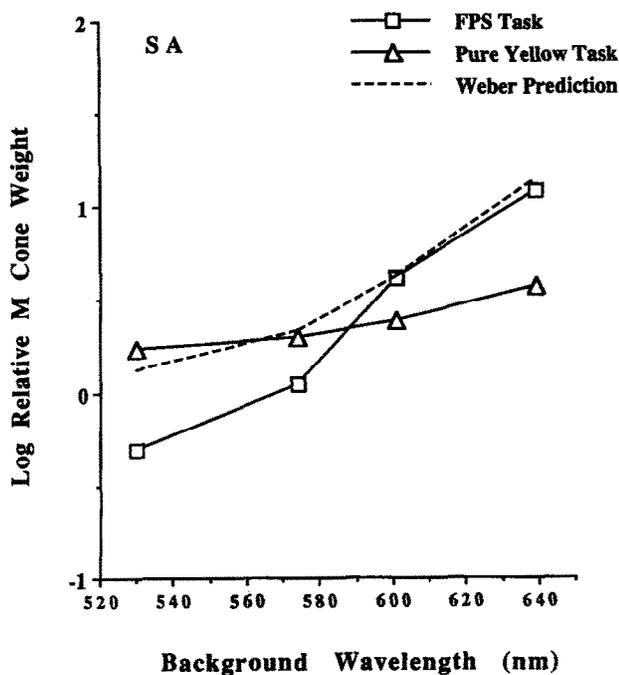


FIGURE 4. The log relative M cone weight values obtained in Expt 1 for the FPS task and pure yellow task are plotted as a function of background wavelength. The Weber prediction is represented by the dashed curve.

adaptation model in which adaptation occurs at the links between the cones and the luminance and chromatic channels, rather than merely at the two possible sites generally recognized, namely the cones themselves and the two postreceptoral channels themselves.

A control experiment tested the possibility that adaptation to the test stimulus itself occurred in Expt 1. When the intensity of the 656 nm test component is fixed, the green test in the cancellation task is of greater intensity than in the minimum flicker stimulus obtained in the FPS task. The results of Expt 1 could be due in part to this difference in test intensity because with a brighter test stimulus in the pure yellow case, the background has less scope to alter the state of chromatic adaptation than with a relatively weak test stimulus. If this interpretation is correct, then the results should be reversed when the intensity of the 543 nm test component, rather than the 656 nm test component, is fixed.

In the control experiment, therefore, the intensity of the 543 nm test was fixed. Thus, the criterion pure yellow stimulus is dimmer relative to the minimum flicker stimulus. If the difference in the intensity between a pure yellow test and a minimum flicker test did not contribute to the results obtained in Expt 1, then no difference in the range of relative M cone weights is expected in the results for Expt 1 and its control. The obtained results for the control experiment, shown in Fig. 5 for subject SA, were similar to those obtained in Expt 1; therefore it is unlikely that the test stimulus contributes to adaptation in the FPS and pure yellow tasks used here.

In Fig. 5, the relative M cone weights are plotted in the same way as for previous figures, except that the abscissa values in Fig. 5 represent the radiance of a

543 nm test component. The radiance of the 543 nm test component was fixed at 0.3, 0.6, 1.2 and 1.8 log steps from the flicker threshold of the 543 nm test component that was determined separately for each background wavelength μ , for each subject. Relative M cone weights for the FPS task and the pure yellow task are shown in Fig. 5(a, b), respectively. Each weight value represents from 12 to 18 radiance settings of the 656 nm test component, measured across 2–3 trials for each subject (6 settings per trial).

The range of log relative M cone weight across background wavelengths obtained from subject SA was 1.94 for the FPS task [Fig. 5(a)] and 0.54 for the pure yellow task [Fig. 5(b)], i.e. the mean separation between the curves for the FPS task is about 3.6 times greater than that obtained for the pure yellow task. As for the original experiment, the main effect of the background wavelength on log relative M cone weight for the FPS and for the pure yellow task was highly significant [$F(3,12) = 70.48$, $P < 0.005$]. Additionally, as for Expt 1, the difference in the mean range of log relative M cone weights across background wavelength between the FPS and pure yellow tasks was significant [$F(3,12) = 17.63$, $P < 0.05$]. These findings indicate that the test stimulus does not contribute significantly to adaptation and provide further confirmation for the link-specific adaptation model.

EXPERIMENT 2

In Expt 1, L and M cone weights were derived for the FPS and pure yellow task with the assumption that S cone signals did not affect the radiance of the 543 and 656 nm test components needed to achieve a flicker minimum and a chromatic null. This assumption was tested in Expt 2 by determining the effect of S cone desensitization on the derived M cone weights for the FPS and pure yellow. If S cones do contribute to the visual signals at flicker minimum (Stockman, MacLeod & DePriest, 1991) and chromatic null (Muller, 1924), then when Expt 1 is replicated with S cone signals suppressed, the relative M cone weights derived for the FPS and pure yellow tasks will be different than those observed in Expt 1. Additionally, if the S cones do contribute to the flicker minima and chromatic null, then this contribution should be greatest for a background wavelength that produces the least adaptation in the S cones, namely the longest wavelengths. Therefore, in Expt 2, the relative M cone weights were compared (for the FPS and pure yellow tasks) in two different long wavelength background conditions. In the first condition, the S cone signals were desensitized and in the second condition, S cones were not desensitized.

Method

Experimental design and procedure

There were two adapting conditions. In the first condition only a 640 nm background was used and in the second condition a 440 nm auxiliary background was

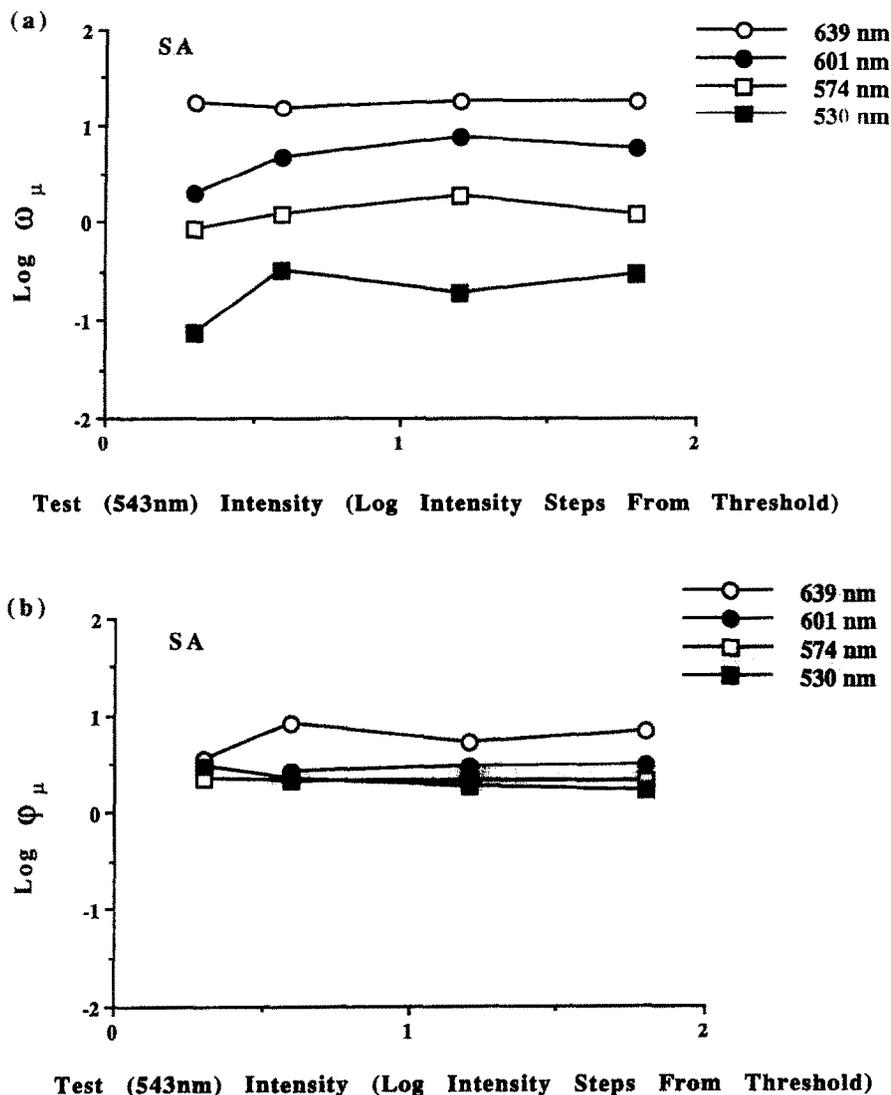


FIGURE 5. The log relative M cone weight values are plotted as a function of the 543 nm test intensity for different background wavelengths. The results obtained for the FPS task and pure yellow tasks, respectively, for subject SA (a, b).

added to the 640 nm background. The 640 nm background, in both conditions, produced a retinal illuminance of 2.93 log td. In the second condition, the retinal illuminance produced by the 440 nm background and the 640 nm background together was 2.96 log td. The radiance of the 440 nm background, in the second condition, was set at a level which produced S cone desensitization in preliminary studies. The first condition will be referred to as the "640 nm-alone" background condition and the second condition will be referred to as the "640 nm-plus-440 nm" background condition.

For each background condition, relative M cone weights were derived for the FPS and pure yellow tasks as a function of the intensity level of the 656 nm component. The intensity of the 656 nm test component was fixed at two different levels: 1.2 and 1.8 log units above the flicker threshold for each subject. The experimental procedures used, for each test intensity level in each background condition, are essentially the same as those used in Expt 1. The subject adjusted the radiance of the 543 nm test component to minimize flicker in the

FPS task or to maintain the test pure yellow in the pure yellow task. The experimenter recorded the radiance of the 543 nm test component at minimum flicker and at pure yellow.

Conditions were blocked by psychophysical criteria (FPS or pure yellow task), background wavelength (640 nm-alone or 640 nm-plus-440 nm), and test intensity (two levels).

A total of three subjects were studied, and results were similar in each case.

Results and Discussion

The relative M cone weights were derived for the FPS and pure yellow tasks for each of the two adapting conditions at two intensity levels of the 656 nm test component by the same procedures used in Expt 1. Each weight value represents from 12 to 18 radiance settings of the 543 nm test component, measured across 2-3 sessions for each subject (6 settings per session).

In Fig. 6, data for the higher intensity level (1.8 log units above threshold) of the 656 nm test component

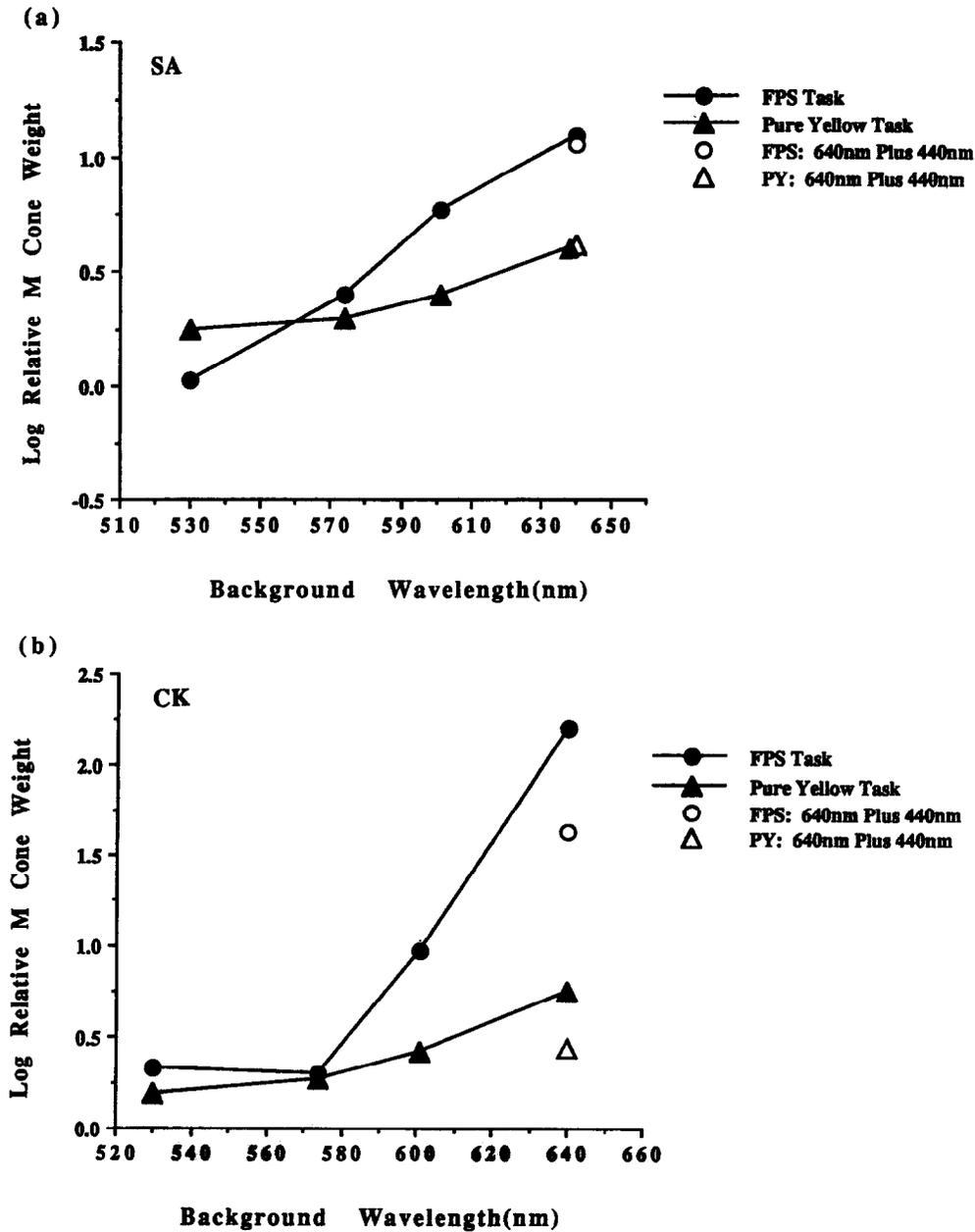


FIGURE 6. The log relative M cone weight values for the FPS and pure yellow tasks are plotted for different background wavelengths. Solid symbols show data from Expt 1; and open symbols show data from Expt 2 (for conditions where the intensity of the 656 nm test component was 1.8 log units above threshold).

obtained for the FPS and pure yellow tasks in Expt 2 are plotted for two subjects. These values are plotted together with each subject's Expt 1 data for the same intensity level of the 656 nm test component. The relative M cone weights obtained for the 640 nm-plus-440 nm background conditions are shown by the open symbols; for comparison, the data from Expt 1 are shown by the solid symbols. (The data for the 640 nm-alone background condition were very similar to the data obtained from Expt 1.)

The results for subject SA [Fig. 6(a)] show that for both FPS and pure yellow tasks, the range of log relative M cone weight from the 530 nm background condition to the 639 nm background condition is similar to the range of log relative M cone weight from the 530 nm background condition to the 640 nm-

plus-440 nm background condition; the difference between the range of log relative M cone weight between the FPS task and pure yellow is comparable to that obtained in Expt 1. In short, the 440 nm background had negligible, if any, effect on log relative M cone weight. For subject CK [Fig. 6(b)], log relative M cone weight were slightly less with the added 440 nm background, but remained much less than for the FPS task, indicating that any contribution of S cones to flicker null and pure yellow settings does not have much effect on the overall difference in the range of log relative M cone weight between the FPS and pure yellow tasks.

In sum, results for Expt 2 provide evidence that S cones contribute only slightly, if at all, to the obtained flicker minima or chromatic nulls.

EXPERIMENT 3

The results of Expts 1 and 2 show that selective suppression of L and M cone input to the chromatic channel is much less than for the luminance channel, and thereby support the link-specific model of adaptation that allows independent gain change at the links between the receptors and the channels. If the link-specific adaptation model is indeed correct, then it is possible that the gain changes in the two channels are different not only in magnitude but also in dynamics. The results of the following experiment, first reported in Ahn and MacLeod (1990) and subsequently supported by Hayhoe and Wenderoth (1991), found channel differences in dynamics consistent with our model. Selective suppression of the L and M cone inputs in the determination of color appearance seems to vary only slowly when the background conditions are changed abruptly, whereas the relative contribution of the L and M cones to flicker sensitivity under similar conditions of stimulation is adjusted rapidly. It has long been clear (e.g. Jameson *et al.*, 1979; Augenstein & Pugh, 1977) that at least some components of chromatic adaptation can take considerable time to develop or recover. What is novel here is the indication that rapid changes of gain, selective for L and M cone input, that are demonstrable in flicker sensitivity, are nevertheless not reflected in the balance of L and M cone inputs determining color appearance.

In Expt 3, we assessed the time-course of gain changes in the luminance and the red/green chromatic channels in two different ways: first, by varying the duration of the background adaptation and measuring the resulting changes in the effectiveness of the L and M cone systems

relative to steady state adaptation; and second, by measuring how quickly the effectiveness of the L and M cone systems recovers after the offset of the adapting background. The effectiveness of the L and M cone systems was evaluated in terms of the L and M cone weights as derived by the procedures used in Expts 1 and 2.

The results of Expt 3 indicate that the suppression of L and M cone effectiveness by chromatic adaptation and its recovery from chromatic adaptation takes only a fraction of a second for the luminance channel, as measured by flicker photometry, but several seconds for the red/green chromatic channel, as measured by the cancellation technique of maintaining the test pure yellow. These results indicate that the independent gain changes contributing to the luminance and the red/green chromatic channels are different in their dynamic properties.

Method

Experimental design and procedure

The stimulus field was identical to that used in Expt 1. In this experiment, the radiance of the 656 nm, red test component was fixed at only three different levels above the flicker threshold for test flicker pulses observed as increments on a steadily presented background. These intensity levels were 0.3, 0.6 and 1.2 log-intensity steps above flicker threshold for all background wavelengths, except for the 530 nm background, for which test intensity levels were set at 1.2, 1.5, and 1.8 log-intensity steps above flicker threshold.

The experimental conditions are shown in Fig. 7. In two of the four temporal conditions, indicated as SP

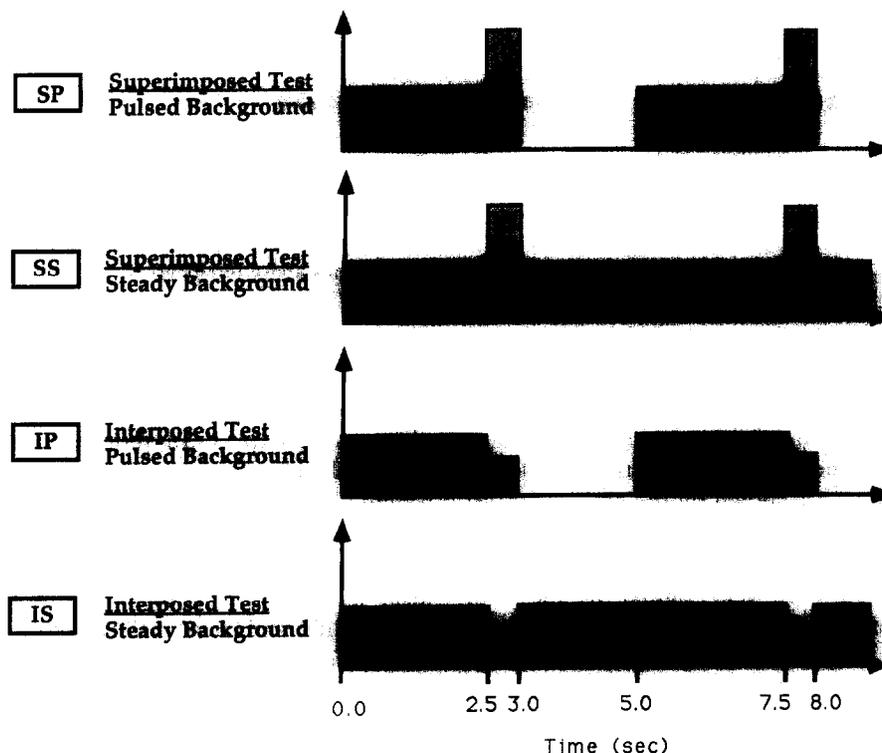


FIGURE 7. Diagram of the temporal conditions for Expt 3. The background was either pulsed or presented steadily. For each background condition, the test was either superimposed on the background or presented alone upon background offset.

and SS in Fig. 7, the test was superimposed on the background and the background was either pulsed or remained steady, i.e. it was continuously presented. We refer to the condition where the test was *superimposed* on a *pulsed* background as the SP condition. We refer to the condition where the test was *superimposed* on a *steady* background as the SS condition. In the SP condition, the background was on for 3 sec and off for 2 sec per cycle and the test came on 2.5 sec after the background for a stimulus duration of 0.5 sec in each cycle. In the SS condition, the test came on for 0.5 sec every 5 sec, which was the same inter-test interval used for the SP condition. (The term "inter-test interval" is used here to mean the time between successive onsets of the test.)

In the remaining two conditions, shown as IP and IS in Fig. 7, the test field was not superimposed on the background but instead was temporally interposed after the background had been switched off, and hence appeared on a dark field spatially concentric with the (now offset) background field. The test onset times for these conditions, on an absolute temporal baseline within a cycle, were identical to the SP and SS conditions but the test was initiated immediately upon the offset of the background field. We refer to the condition where the test was *interposed* in a *pulsed* background as the IP condition, and to the condition where the test was *interposed* in a *steady* background field, which remained on *except* when the test was on, as the IS condition.

Conditions were blocked by psychophysical criteria (FPS or pure yellow task), background wavelength (640, 601, 577 or 530 nm), temporal conditions (SP, SS, IP or IS), and test intensity (three levels). The change in the relative effectiveness of L and M cones was derived from the psychophysically determined radiances of the 543 nm test component (while using experimenter-determined radiances of the 656 nm test components) by the same analytical procedures used in Expts 1 and 2.

Results and Discussion

Flicker photometry

Figure 8(a) shows the obtained data for the FPS task (subject SA). The relative M cone weights are plotted as a function of adapting background wavelength; for clarity, the figure shows only the mid-intensity level (a 1.2 log-intensity step above the flicker threshold for the 640, 601 and 577 nm background conditions and a 1.5 log-intensity step above the flicker threshold for the 530 nm background condition) of the 656 nm test component. The ordinate values in Fig. 8(a) represent the log of the relative M cone weight. Each weight value plotted represents from 18 to 24 radiance settings of the 543 nm test component, measured across 3–4 sessions (6 settings per session). Data for the two conditions where the test was superimposed on the background (SP and SS) are represented by solid lines. Data for the two conditions where the test was introduced after background offset (IP and IS) are represented by dashed lines. Conditions where the background was pulsed are represented by

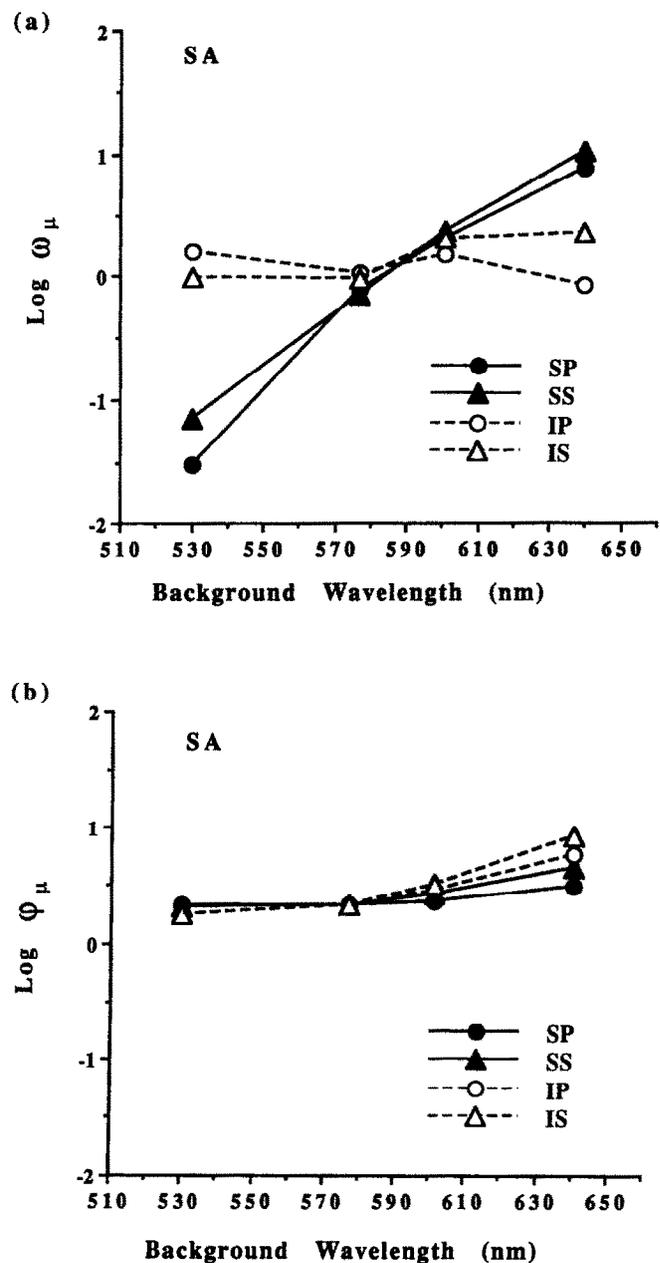


FIGURE 8. The log relative M cone weight values are plotted as a function of background wavelengths for each of the four temporal conditions for subject SA. The results obtained for the FPS task and pure yellow tasks, respectively, are shown in (a) and (b). Solid curves represent data from superimposed test conditions; dashed curves represent data from interposed test conditions. Circles represent data from pulsed background conditions; triangles represent data from steady background conditions.

circles and conditions where the background was steadily presented are represented by triangles.

There are two important comparisons to be made in Fig. 8(a). The first comparison is between the superimposed test conditions and the interposed test conditions, which indicates how complete the recovery from chromatic adaptation is during the 0.5 sec test duration following background offset. This involves, in effect, a comparison of the slopes between the two dashed lines (IP and IS) and the two solid lines (SP and SS). A steep slope means that the relative effectiveness of the L and M cone systems changes as a function of the background

wavelength and therefore indicates chromatic adaptation, i.e. selective suppression of the L and M cone systems across background wavelengths. The slopes of the solid lines representing the superimposed test conditions (SP and SS) are steep, indicating substantial chromatic adaptation. The dashed lines representing the two interposed test conditions (IP and IS), however, are nearly flat, indicating that the relative effectiveness of the L and M cone systems was not much different across background wavelength.

For the interposed test conditions (IP and IS), $\log \omega_\mu$ value is close to 0, implying that the effectiveness of the M and L cones is equal, as the definition of L and M cone effectiveness would imply for a no background condition. For the 640 nm background, when the test is presented alone, i.e. in the IP and IS conditions, the relative weight decreased compared to when the test was superimposed on the background, i.e. in the SP and SS conditions, indicating a functional recovery of L cone sensitivity. Likewise, for the 530 nm background, the weight increased in the IP and IS conditions relative to the SP and SS conditions, indicating a recovery of M cone sensitivity. These results show that when the test is presented alone, there is an immediate functional recovery from chromatic adaptation in the FPS task, within the 0.5 sec duration after the background offset.

The second comparison is between the superimposed pulsed background and the superimposed steady background conditions. This comparison indicates how complete the gain change of the L and M cone systems are after 2.5 sec of exposure to the background relative to steady state adaptation. The results show that relative M cone weights do not change significantly between the pulsed background condition and the steady background condition. This weight equivalence obtains both when the test is superimposed on the background and when the test is presented after background offset. This completion of gain change at 2.5 sec was observed across all four background wavelengths for all subjects. For the FPS task, therefore, the results indicate that the gain change resulting from chromatic adaptation is complete after 2.5 sec exposure to the background and that recovery from this gain change is complete <0.5 sec after the background offset. Note that the most negative logarithmic values of ω_μ in Fig. 8 are not well defined, since a very small M cone weight is not experimentally distinguishable from no weight at all (which would put the logarithm at minus infinity). The 95% confidence interval for the 530 nm background, SP condition, extends up to about $\log(\omega_\mu) = -0.71, -0.57$ and -0.21 for low, mid and high test intensity levels, respectively. But even if these most negative values are rounded up to that limit, the difference between the M cone weights on green and red backgrounds still exceeds 1 log unit or a factor of 10.

Pure yellow settings

The data for the pure yellow task [Fig. 8(b)] show a very different pattern. The relative M cone weights are plotted as a function of the adapting background wave-

length for the mid intensity level of the 656 nm test component, as in Fig. 8(a). Comparison between the superimposed test conditions and the interposed test conditions in Fig. 8(b) indicates, as with the FPS task, how complete the recovery from chromatic adaptation is during the 0.5 sec test duration after background offset. The results show no recovery but if anything an increase in suppressive effect, as if there is a further polarization of L and M cone dominance when the test is presented alone relative to when the test is superimposed on the background.

Comparison between the pulsed background and the steady background conditions shows that in contrast to the results obtained for the FPS task, there is a significant difference between the pulsed background conditions and the steady background conditions both when the test is interposed in the background and when it is superimposed on the background [$F(3,3) = 214.91, P < 0.001$]. Thus the change in gain is not complete after 2.5 sec for the red/green chromatic channel relative to greater gain change in steady state adaptation.

For both FPS and pure yellow tasks, the SS condition where the test was superimposed on a steady background was, in effect, a replication of Expt 1. Figure 8 shows that, as was demonstrated in Expt 1, the range of log relative M cone weight across background wavelength for the SS condition is greater (> 1 log unit, or a factor of 10) for the FPS task than for the pure yellow task (< 0.5 log units, or a factor of 3). This confirms the independent gain changes in the luminance and the red/green opponent channels shown in Expt 1. Results for subjects CK and SH are similar to those obtained from subject SA and support the basic findings described for subject SA.

Figure 9 shows the relative M cone weights for all the experimental conditions for the FPS task for subject SA. Each panel in Fig. 9 represents the results of one of the four temporal conditions (SP, SS, IP and IS). In each panel, the relative M cone weights are plotted for each of the four background wavelengths (640, 601, 577 and 530 nm) as a function of the intensity of the 656 nm test component. What is strongly evident is the convergence of weights toward a relative M cone weight of 0 in going from the superimposed test conditions, SP and SS, to the interposed test conditions, IP and IS. Also, as described previously, there is no significant difference between the pulsed and steady background conditions, i.e. there is no significant difference between the SP and SS conditions and between the IP and IS conditions. The apparent large variation in M cone weight for test fields superimposed on the 530 nm background may be due to experimental error as discussed above.

Figure 10 shows the relative M cone weights for all the experimental conditions for the pure yellow task for subject SA. What is strongly evident for the pure yellow task is that the relative M cone weights do not converge as was the case with the FPS task but fan out progressively in proceeding from the SP condition to the IS condition.

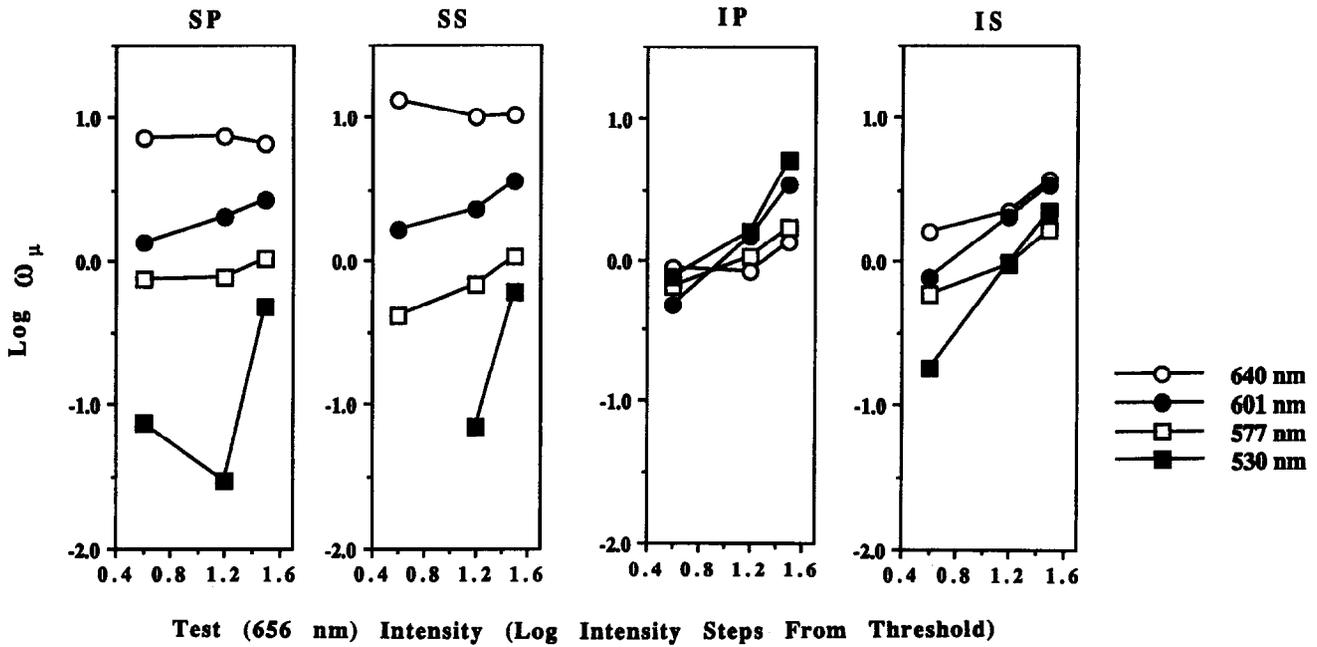


FIGURE 9. Summary of results for the FPS task for subject SA in Expt 3. The log relative M cone weight values are plotted as a function of the intensity of the 656 nm test component for each temporal condition. (The 530 nm background data points are shifted laterally to the left and aligned with data points for the low, mid and high test intensity levels of the other three background conditions.)

The fanning of the weights suggests that the gain change in the L and M cone systems is greater in the steady background conditions relative to the pulsed background condition. The marked dependence of the relative M cone weight on test intensity in the pure yellow task could result from an additive effect of the background, perhaps greater here than in the true steady state conditions of Expt 1. The data do not clearly demonstrate a constant high test intensity asymptote for

the M cone weight, but the results of Shevell (1978) and Shevell and Wesner (1989) suggest that the values for the higher intensities are probably close to asymptotic. And even at these levels, the M cone weight varies by <0.4 log units when the test field is superimposed on the differently colored backgrounds, much less than the variation seen in the FPS task.

We repeated this experiment with a temporal delay of 0.5 sec, rather than 2.5 sec, between the onset of the

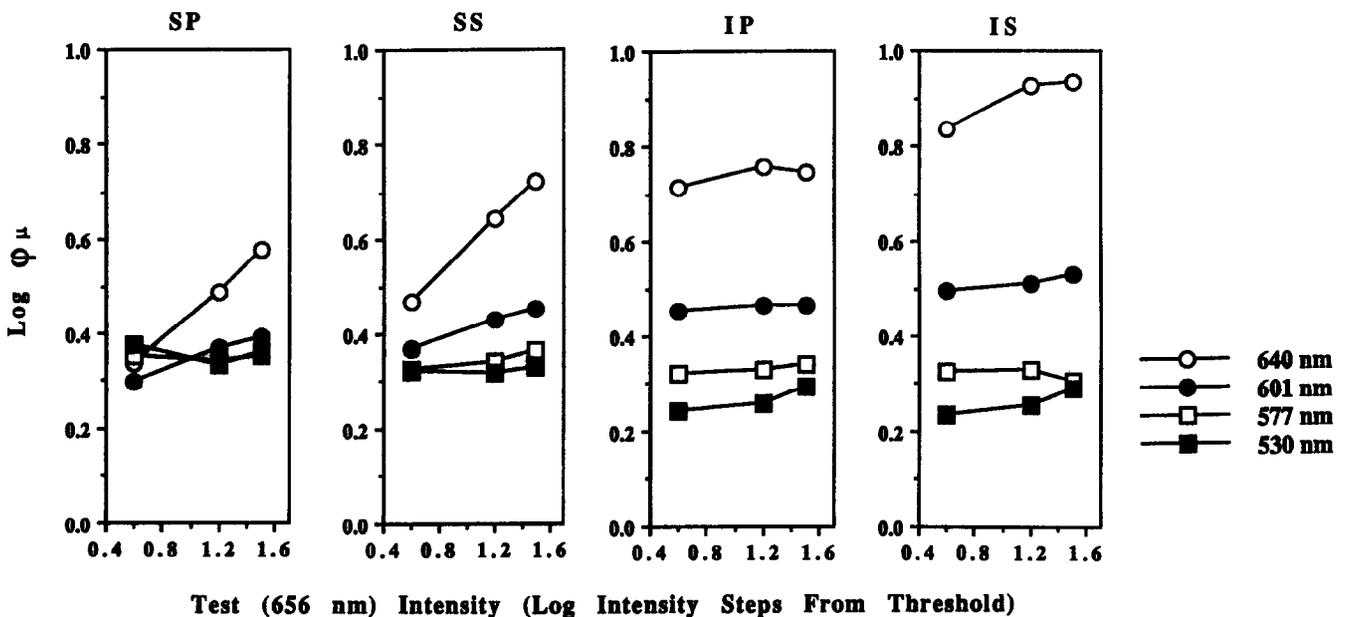


FIGURE 10. Summary of results for the pure yellow task for subject SA in Expt 3. The log relative M cone weight values are plotted as a function of the intensity of the 656 nm test component for each temporal condition. (As with Fig. 9, the 530 nm background data points are shifted laterally to the left and aligned with data points for the low, mid and high test intensity levels of the other three background conditions.)

background and the onset of the test (in the pulsed conditions), using background durations of 0.5 sec (IP) and 1 sec (SP). The results were very similar to those of Figs 8–10, demonstrating, for instance, that for FPS the gain change is complete by 0.5 sec after background offset.

The results obtained for the interposed test conditions (IP and IS) may, however, have been in part due to adaptation to the test field itself. The intensity of the 656 nm test conditions did not vary across the different temporal conditions. The baseline flicker threshold, used as the baseline for the log-intensity step increase in the intensity for the 656 nm test component, was determined using the 656 nm test component superimposed on the background. When this baseline threshold is used for the condition where the test is presented alone on a dark field interposed in the background (i.e. in the IP and IS conditions), the test appears bright and could well affect the state of adaptation.

We, therefore, conducted an additional experiment where the baseline threshold for the interposed test condition was measured separately from the baseline threshold for the superimposed test condition and used a 656 nm test component interposed in the background on a dark field. If the test field did contribute to adaptation, then the results obtained here should be different than those obtained with a test of fixed intensity; on the other hand, if the results are similar to those obtained in the previous experiment, then it can be concluded that adaptation to the test was not a substantial factor.

Experimental conditions were blocked by psychophysical criteria (FPS or pure yellow task), background wavelengths (640 or 530 nm), and temporal conditions (SP, SS, IP or IS). Only two background wavelengths were used: 640 and 530 nm. For each background, the intensity of the 656 nm test component was fixed at a single multiple of flicker threshold, which was defined separately for the superimposed and interposed conditions, so that the test intensity was lower in the latter case. The four temporal conditions were identical with the original experiment. For the SS and IS conditions, the radiance of the 656 nm test component was fixed at a 1.5 log-intensity step from the flicker threshold measured with the 656 nm *superimposed* on the background. And for the IP and IS conditions, the radiance of the 656 nm test component was fixed at a minimal level, 0.6 log units above the flicker threshold measured with the 656 nm test component *interposed* in the background on a dark field. As with Expt 3, the experimenter recorded the radiance of the 543 nm test component at minimum flicker and pure yellow. One subject (SA) was studied.

This experiment was different from that of Figs 8–10 only in that the 656 nm test stimulus in the IP and IS conditions was set at a minimal intensity, 0.6 log units above its detection threshold, which was measured separately for each condition. The results did not differ to any important extent from those of Figs 8–10 obtained with a fixed test intensity, and thus support the

conclusion that the selective suppression of L and M cone input has different dynamics for the chromatic and achromatic systems.

GENERAL DISCUSSION AND CONCLUSION

Data obtained for the FPS task in Expts 1 and 2 are roughly consistent with a chromatic adaptation mechanism which follows Weber's law. In Fig. 4, relative M cone weights obtained for the FPS and pure yellow tasks (solid curves) for subject SA in Expt 1 are plotted as a function of background wavelength. The dashed curve in Fig. 4 represents the Weber prediction for the relative M cone weight, derived from the Smith–Pokorny cone spectral sensitivities for a given background μ (L_μ and M_μ), with k as an arbitrary constant reflected in the vertical position of the theoretical curve:

$$\omega = k \frac{L_\mu}{M_\mu}. \quad (7)$$

The data obtained for the FPS task show a clear deviation from Weber's law in the direction of greater selective suppression of L and M cones by chromatic backgrounds than is consistent with Weber's law: this is the same result reported by Eisner and MacLeod (1981), but less pronounced. The selective suppression (beyond the Weber prediction) can be enhanced by the optimal choice of background intensity (Stockman *et al.*, 1993). Whether Weber's law is satisfied or not, the weight determined within the FPS task can be accounted for by postulating an appropriate degree of independent adaptation in the L and M cones. However, if adaptation is within the cones, effect of chromatic adaptation on color appearance should parallel its effect on flicker spectral sensitivity, yielding vertically displaced curves for the two tasks in Fig. 4; it can not, therefore, account for the much smaller sensitivity change obtained in the pure yellow task. The shortfall from Weber's law in pure yellow settings is reflected in the simple observation that red flashes retain a reddish appearance on a red adapting field, and similarly for green flash on a green field. This observation has also been made by Whittle (1973). His results, like our own, depend little on the flash intensity, and hence reflects sensitivity changes rather than an additive effect of the background. If Weber's law applied independently to the L and M cones, the reciprocal adjustments of sensitivity would cancel out the selective excitation of the L and M cones when the test flash is the same color as the adapting field, and all such flashes would appear alike in color; that this does not happen implies a shortfall from Weber's law. We note, however, that by the use of a test stimulus designed to minimize both spatial and temporal transients, Thornton and Pugh (1983) were able to demonstrate chromatic adaptation effects consistent with (though not exceeding) Weber's law for color appearance.

Stromeyer, Cole and Kronauer (1985) found evidence that a red/green opponent mechanism operative at the detection threshold for chromatic pulses evaluates the difference between the contrasts seen by L and M cones,

as if each cone's effectiveness in the presence of colored backgrounds varied in accordance with Weber's law. There are at least three ways to reconcile these results with ours: Weber's law may apply to the chromatic signals under Stromeyer *et al.*'s conditions but not under ours; the chromatic mechanism responsible for detection could be different from the one determining color appearance [but Akita, Takahashi and Ejima (1985), presented data for white background that uphold the assumption that these are identical]; or the model of color appearance implied in equation (4) might be wrong. If the model implied in equation (4) is accepted, however, our results provide evidence for link-specific adaptation.

The anatomical substrate of the "links" in the formal scheme of Fig. 1 is not very obviously demarcated. There is evidence (e.g. Sperling & Mills, 1991) that in primates, as in lower vertebrates, the distinction between color-opponent and achromatic channels is already at least partially established at the bipolar cells. This would allow for link-specific adaptation as early as the synapses between cones and bipolar cells: the receptor-bipolar synapse does contribute to adaptive sensitivity changes in toad rods (Belgum & Copenhagen, 1988), and it is not unreasonable supposition (Ahn & MacLeod, 1989) that synapses onto different bipolars can introduce different sensitivity losses. The central terminus of the "links" is less well-defined, at least in the case of the color-opponent system, where different classes of cell are excited by the L and M cones so that selective suppression of the two cone inputs is in principle possible even centrally. Whatever cone-selective sensitivity losses may be added postreceptorally, however, our results, interpreted with the theoretical framework outlined in the Introduction, imply that at most limited adaptation occurs prior to the cone-bipolar synapses (since only limited adaptation is reflected in the unique yellow settings). An adaptation process at the cone synapses is one way to reconcile psychophysical evidence that a major component of light adaptation in the cone system occurs locally [without prior spatial integration (MacLeod, Williams & Makous, 1992; Makous, Williams & MacLeod, 1993)], with the primate photocurrent recordings of Schnapf, Nunn, Meister and Baylor (1990) showing that the sensitivity regulating mechanisms in the cone outer segment do not reduce sensitivity substantially at the moderate photopic luminances used here.

Another way in which the scheme of Fig. 1 perhaps dangerously simplifies the flow of information in the retina is that it expresses the losses of sensitivity at each point in the chain of transmission by a single number, whereas in fact the losses may depend on the spatial and temporal characteristics of the test stimulus. The effect of adaptation on different tasks might be different for that reason, and not because different sites of adaptation are involved. Could our results then be explained by invoking adaptation only at the cone level, none of it link-specific? This seems unlikely, because sensitivity losses in cone vision are less for rapid flicker than for

sustained test stimuli (Kelly, 1961) and yet in our experiments it is the flicker task that shows the greater selective suppression of L and M cone input. Possibly a dependence of sensitivity loss on the spatial waveform of the signal (less for high spatial frequency components) might help explain the reduced effects for the unique yellow task, on the assumption that flicker visibility depends on lower spatial frequency components than does color appearance. But according to Chen, MacLeod and Stockman (1987) the effect of adaptation in cone vision does not depend much on the spatial parameters of the test stimulus.

The results obtained in Expt 3 show that the luminance channel has a faster gain change and recovery from adaptation than does the red/green chromatic channel. The recovery of gain from chromatic suppression due to the background in the chromatic channel occurs at a later time after background offset. That chromatic adaptation includes a slow component is not a great surprise in the light of both previous psychophysical findings (Augenstein & Pugh, 1977; Jameson, Hurvich & Varner, 1979) and current physiological ones (DePriest, Lennie & Krauskopf, 1991; Yeh, Lee & Kremers, 1992). More surprising is the near-absence, in the unique yellow task, of the fast, cone-specific sensitivity adjustments that are implicit in the flicker sensitivity. The difference in the time course between the adaptive gain change and recovery in the luminance channel and the red/green chromatic channel is consistent with the independent gain changes predicted by the link-specific model.

Previous studies, both psychophysical (e.g. Wisowaty, 1981; King-Smith & Carden, 1976; Lennie & D'Zmura, 1988) and physiological (e.g. Lee, Martin & Valberg, 1988, 1989; Kulikowski, Dickinson & Murray, 1987) have shown that the non-opponent luminance channel is associated with relatively rapid processing mechanisms (a relatively greater sensitivity to stimuli modulated at high temporal frequencies) and that the opponent chromatic channel is associated with relatively sluggish processing mechanisms. The results of Expt 3 suggest a comparable difference between these channels in the dynamics of their adjustment of sensitivity to M and L cone input.

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