

Chromatic adaptation, perceived location, and color tuning properties

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Abstract

We have studied the influence of chromatic adaptation upon the perceived visual position of a test stimulus using a Vernier alignment task. Maximum and minimum offsets in spatial position are generated when the adapting and test stimuli lie on the same and orthogonal axes in MBDKL color space, respectively. When the test stimuli lie on intermediate color axes, the measured positional shifts decrease as a function of the angular separation in color space (ϕ) from the adapting stimulus. At low stimulus contrasts, these shifts follow a sinusoidal function of ϕ and exhibit broad chromatic tuning and can be accounted for by a model in which the centroid is extracted from the linear combination of after-image, formed by the adapting stimulus, and the test stimulus. Such linear, broadband behavior is consistent with the response properties of chromatic neurons in the precortical visual pathway. At high contrast, and when adaptation gets closer to the S/(L+M) axis, the tuning functions become narrower and require sinusoids raised to increasingly higher exponents in order to describe the data. This narrowing of chromatic tuning is consistent with the tuning properties of chromatic neurons in the striate cortex, and implies the operation of a nonlinear mechanism in the combination of cone outputs.

Keywords: Psychophysics, Color, Adaptation

Introduction

The precortical processing of chromatic information in the primate visual pathway is commonly described as taking place within independent “red–green” (L/M) and “blue–yellow” (S/(L+M)) cone-opponent channels. There is an additional “luminance” (L+M) channel, but a key feature of all these opponent mechanisms is that they are generated by linear combinations of receptor outputs (Derrington et al., 1984; DeValois et al., 2000*b*). The opponent model has satisfactorily accounted for numerous psychophysical and electrophysiological observations (DeValois et al., 1966; Derrington et al., 1984; Mullen & Losada, 1994). However, there is a growing body of evidence to suggest that the neural processing of color undergoes a reorganization between the lateral geniculate nucleus (LGN) and visual cortex. Behavioral observations, such as the phenomenal appearance of colors (DeValois et al., 1997) coupled with adaptation, masking, and other aftereffects (Krauskopf et al., 1986; Webster & Mollon, 1991, 1994; D’Zmura & Knoblauch, 1998; Clifford et al., 2003), challenge the primacy of cardinal mechanisms and invoke the existence of more chromatic mechanisms than exist for precortical color processing. Electrophysiological experiments point to a similar conclusion. In V1, there are different populations of neurones responsive to a wider

range of chromatic and luminance stimuli than would be supported by the relatively few cone-opponent mechanisms (DeValois et al., 2000*b*; Lennie et al., 1990; Johnson et al., 2001). Furthermore, approximately one-half to two-thirds of chromatic neurons in V1, and significant numbers in extrastriate areas, exhibit narrower chromatic tuning than their counterparts in the LGN (Thorell et al., 1984; Vautin & Dow, 1985; Komatsu et al., 1992; Kiper et al., 1997; Gegenfurtner et al., 1997; DeValois et al., 2000*a,b*). This is suggestive of the operation of a nonlinearity in their response behavior within the cortex, and is in distinct contrast to the LGN, where responses can be predicted from linear combinations of cone inputs (Derrington et al., 1984; DeValois et al., 2000*b*).

Whilst the existence of multiple “higher-order” chromatic mechanisms is gaining a wider acceptance, there is neither a clear indication as to exactly how many mechanisms there are, nor consensus regarding their spectral bandwidths. Estimates as to the number suggest the presence of at least four (Li & Lennie, 1997), but probably more (Zaidi & Halevy, 1993; Goda & Fujii, 2001), chromatic mechanisms spanning color space. In terms of spectral bandwidth, D’Zmura and Knoblauch (1998) have shown these mechanisms to be spectrally broadband (\approx 60-deg half-height-half-bandwidth), similar to physiological measures from chromatic neurons in the LGN and some V1 cells. The implication of this finding is that “higher-order” chromatic mechanisms are based on linear combinations of receptor outputs (see also, Giulianini & Eskew, 1998). A conflicting view is offered by Goda and Fujii (2001), who found narrower bandwidths (\approx 40-deg half-height-

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half-bandwidth) for the chromatic mechanisms, a key point in that it indicates the operation of nonlinear receptor combinations in their generation.

In previous studies, we have shown that large positional offsets can be generated in test stimuli following prior adaptation to chromatic patterns (McGraw et al., 2001; McKeefry et al., 2002). In addition, we have demonstrated elsewhere (McGraw et al., 2004) that the size of this offset is dependent upon the separation in color space between the adapting and test stimuli. Importantly, maximum and minimum shifts in position are generated when the adapting and test stimuli lie along the same and orthogonal color axes, respectively. This occurs regardless of whether adaptation takes place along a cardinal or noncardinal axis. Such selective adaptation effects are consistent with the operation of multiple chromatic mechanisms in the isoluminant plane, as opposed to just two supported by cone opponency (Webster & Mollon, 1991, 1994). The focus of this study was to examine the spectral tuning characteristics of chromatic mechanisms revealed by this positional adaptation paradigm. This was with a view to exploring possible reasons for the discrepancies between the estimates of spectral bandwidths reported by earlier psychophysical studies.

Materials and methods

A three-element Vernier alignment task was used in which three color-normal observers (DMcK, PVM, and CV) judged the horizontal position of the central Gaussian element in relation to two identical elements that were vertically displaced by 2 deg above and below the fixation point. Readers can verify the phenomenon in Fig. 1.

Each of the Gaussian elements was circularly symmetrical and had a standard deviation of 0.4 deg (see Fig. 1a). Positional judgements were made following 5 s of adaptation to two vertically displaced antisymmetric elements whilst fixation was maintained on a central point. The antisymmetric stimulus represents the first derivative in the x direction of the Gaussian test elements. Following adaptation, the test stimulus was presented for 180 ms and under certain conditions a misalignment of the central element was perceived. The magnitude of this perceived offset was then established using a method of constant stimuli. The data were fitted by a logistic function of the form:

$$y = 100/[1 + e^{(x-\mu)/\theta}], \quad (1)$$

where μ represents the offset corresponding to the 50% level on the psychometric function and θ is an estimate of alignment threshold.

The adaptation and test stimuli consisted of isoluminant chromatic modulation. The chromaticities of the adaptation and test stimuli could be independently controlled so as to produce modulation along a series of axes, of varying azimuth (ϕ), in MBDKL color space (MacLeod & Boynton, 1979; Derrington et al., 1984). These axes are illustrated in Fig. 1b and include six chromatic axes that incorporate the L/M (0–180 deg) and S/(L+M) (90–270 deg) cardinal axes, as well as intermediate, noncardinal orientations. This color space is based upon a transformation of LMS cone contrasts computed using the Judd modified values (x', y', Y') values. X', Y', Z' tristimulus values were then used in conjunction with the Smith and Pokorny (1975) cone fundamentals (see Wyszecki & Stiles, 1982) to obtain the magnitude of cone excitation for each component color from which modulation for each cone was calculated. The neutral point was defined as illuminant C

($x = 0.310, y = 0.316$) located on a plane formed by the L/M and S/(L+M) cardinal axes on which all stimuli are isoluminant, as defined by the V_λ photopic luminosity function (Wyszecki & Stiles, 1982). Despite the fact that this definition of isoluminance is based upon an average observer and may vary from one individual to another, we have been able to verify in previous experiments that this generates minimal luminance-contrast intrusion. Primarily, this is because there is little or no crossover of the positional offset effect between the color and luminance adapting and test stimuli (see McGraw et al., 2004, Fig. 2). Another potential source of luminance-contrast contamination might have arisen due to the nonuniform distribution of macular pigment within the central macular region. Such effects would be most apparent for S/(L+M) stimuli, however, in control experiments where the adaptation and test stimuli were positioned at similar retinal eccentricities (2 deg), the same pattern of results was obtained to those found for central placement of the stimuli.

All stimuli were generated using the macro capabilities of NIH Image (v1.61) and presented on an Apple Cinema LCD display screen that subtended 40 deg \times 27 deg at the viewing distance of 64 cm. The contrasts of the adapting and test stimuli were all expressed in terms of multiples above detection threshold and the mean luminance of the background and all stimuli was 41 $\text{cd}\cdot\text{m}^{-2}$ ($\pm 1 \text{ cd}\cdot\text{m}^{-2}$). All stimuli were calibrated with a Photo Research PR650 spectral photometer.

To examine the linearity of the positional effect as a function of color angle, the data were fitted by sinusoidal functions that were raised to the best-fitting exponent, n . These functions were of the form

$$\text{amp}/2 * \sin(\theta - \theta_{\text{off}})^n, \quad (2)$$

where amp represents amplitude, θ , color angle, θ_{off} , phase offset from sine phase, and n is the exponent of exponentiated sine fit (i.e. if $n = 1$ this constitutes a sine wave). This approach is adapted from nonlinear models that have been deployed to explain neuronal response characteristics in the LGN and V1 (Albrecht & Geisler, 1991; DeValois et al., 2000b).

Results

In an earlier study from this laboratory, Whitaker et al. (1997) proposed a simple model to account for the effects of prior adaptation on the perceived location of subsequently viewed stimuli. In this model, perceived offsets could be explained by the shift in the position of the centroid (the weighted mean of the entire luminance distribution) generated by a linear combination of the negative after-image produced by the adapting stimulus, and the test stimulus (see Fig. 2a). We wished to examine whether a similar mechanism could account for the positional shifts observed with isoluminant stimuli. To this end, we measured the offsets generated by a range of different adaptation and test stimulus contrast ratios for chromatic stimuli located along the same (L/M) axis in color space. The results for two observers are plotted in Fig. 2b (filled symbols). Also shown are the predicted positional offsets (solid line) based upon the computed centroid positions for a number of adaptation and test contrast ratios. The close agreement between the actual data and predictions based upon centroid extraction would seem to suggest that this model is equally applicable to positional shifts induced by chromatic, isoluminant stimuli.

Whilst the above model provided a good prediction of the positional offsets generated when the test and adapting stimuli lie

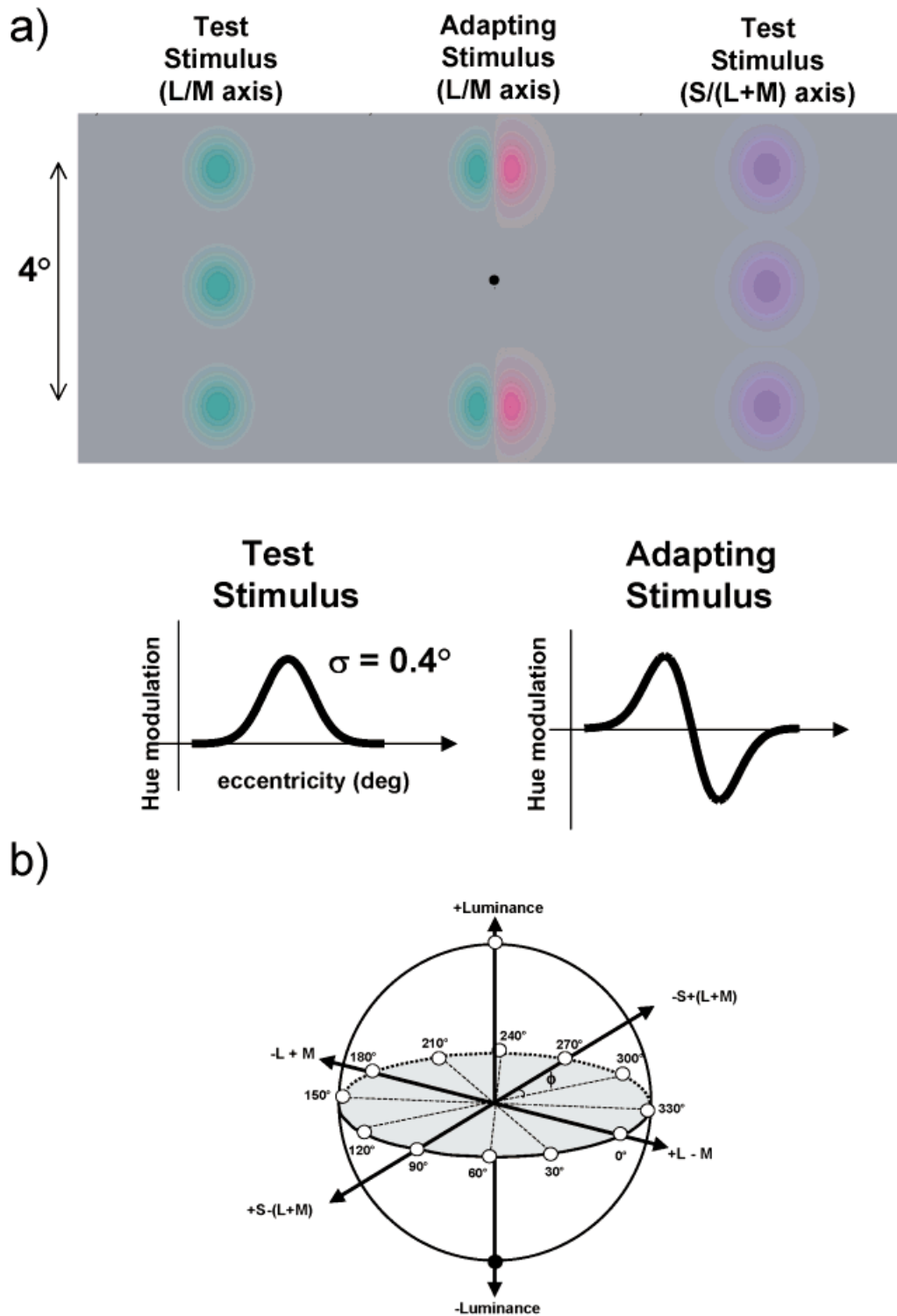


Fig. 1. (a) The spatial configuration and modulation profiles of the adapting and test stimuli used in these experiments. The adapting stimulus comprises two antisymmetric elements (see text for description) located 2 deg above and below a central fixation point. The test stimulus is formed by three Gaussian elements with a central element additional to those above and below the fixation point. The reader should be able to verify the phenomenon under investigation by fixating the small spot at the center of the two L/M axis (red/green) antisymmetric outer blobs in the center of Fig. 1a for a period of 10–15 s. If gaze is quickly shifted to the center of the stimulus on the left, which contains chromatic modulation along the same axis, a perceived offset of the central element should be observed, despite the physical alignment of the stimulus elements. If the adapting process is repeated and gaze transferred quickly to the stimulus on the right, where modulation is along the orthogonal S/(L+M) (blue–yellow) axis, the observer should observe little or no offset. (b) The different chromaticities used to generate the adapting and test stimuli are specified in terms of their location in MBDKL color space. Chromaticity was modulated along 12 different chromatic axes, incorporating the L/M (0 deg & 180 deg) and S/(L+M) (90 deg & 270 deg) cardinal axes.

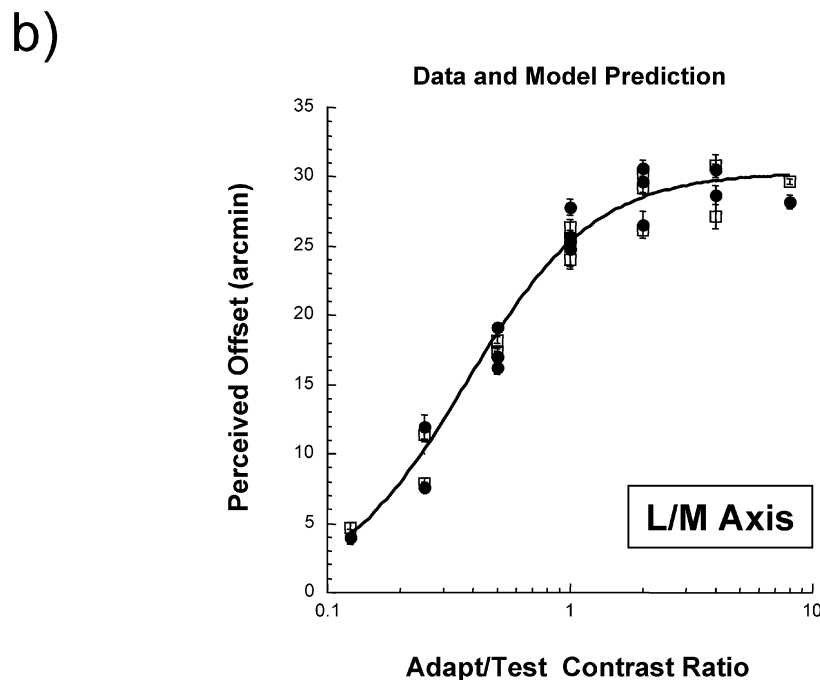
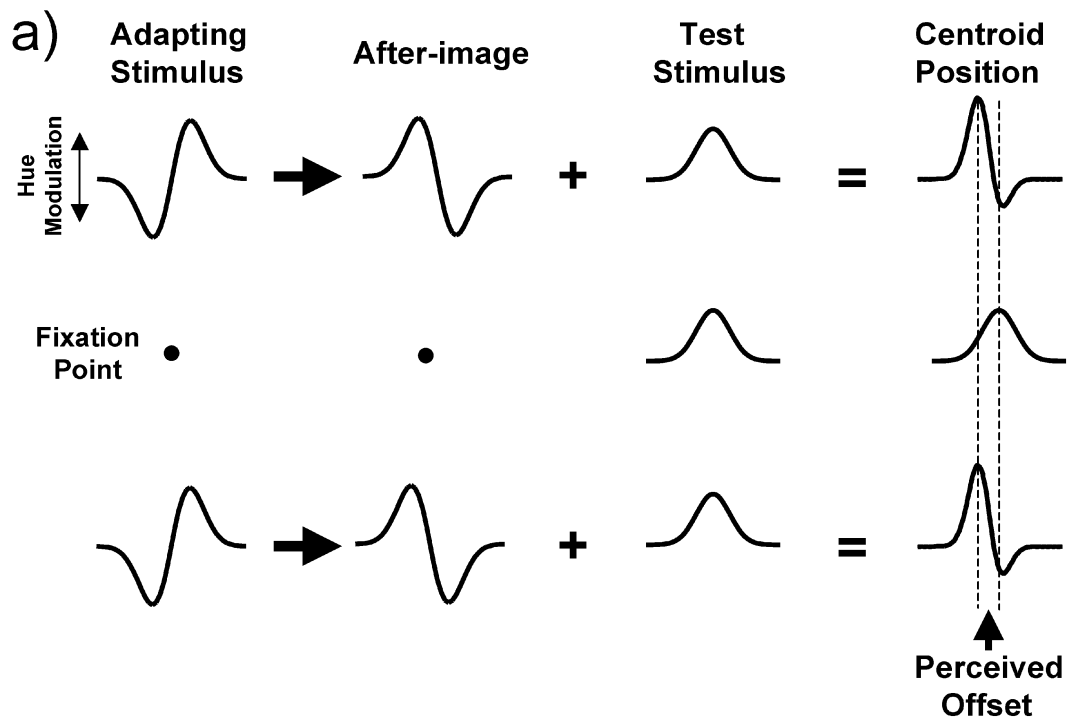


Fig. 2. (a) A schematic representation showing how adaptation to an antisymmetric chromatic stimulus above and below the fixation point can lead to perceived misalignments of a three-element Gaussian test stimulus. The centroid position is extracted from the linear combination of the negative after-image of the adapting stimulus, and the test stimulus. In this example there is a rightwards relative shift of the central test element due to the leftwards displacement of the upper and lower elements. (b) The perceived offsets produced by isoluminant L/M stimuli have been plotted for a range of adapt/test contrast ratios for observers PVM and CV (empty and filled symbols). Also shown are the offsets that are predicted by the centroid extraction model at the same adapt/test contrast ratios (solid line).

along the same chromatic axis in color space, Fig. 3a shows how the shifts varied as a function of the angular separation in color space between the adapting and test axes. Data are shown for just two adapting axes (0–180 deg (L/M) and 90–270 deg (S/(L+M)),

but certain basic characteristics of these data were common to all chromatic axes of adaptation investigated. In particular, the maximum and minimum perceived shifts in position were always generated when the adapting and test stimuli were located on the

same and orthogonal color axes, respectively. This occurred regardless of whether adaptation took place along a cardinal or noncardinal axis (see McGraw et al., 2004). However, a comparison of the functions generated by L/M and S/(L+M) adaptation in Fig. 3a shows that in other respects different axes of adaptation can produce very different chromatic tuning functions. The graphs show how the induced positional offset varies as a function of test chromaticity for two contrast levels; one where the adapting and test stimuli are 1.9 times above threshold, the other where the stimuli are 15 times above detection threshold. For each contrast level, and for both L/M and S/(L+M) adaptation, the data have been fitted by sinusoids (solid lines) raised to the best-fitting exponent. This approach has been adopted in neurophysiological studies as a means of quantifying the response linearity of cortical neurons (Albrecht & Geisler, 1991; DeValois et al., 2000b). In brief, the rationale is that if an exponent close to unity is required to fit the data set, then the magnitude of the positional shift as a function of color angle (ϕ) of the test is sinusoidal, and follows the sinusoidal variation in cone contrast of the stimuli used. Effectively, the shifts can therefore be explained in terms of mechanisms that depend upon linear combinations of cone receptor outputs. However, if exponents of greater than unity are required, then this indicates a nonsinusoidal variation in the magnitude of the shifts generated as a function of ϕ . Such variations cannot be explained in terms of linear combinations of cone responses and therefore must rely upon nonlinear combinations.

In Fig. 3b, the mean magnitude of the best-fitting exponent has been plotted for the three observers. At high suprathreshold contrast levels, there is a clear increase in the value of the exponent as the axis of adaptation shifts from the L/M axis, where an exponent close to unity is required to fit the data, to the S/(L+M) axis where the best-fitting exponent exhibits a four-fold increase. A direct consequence of this increase is the generation of narrower tuning functions for S/(L+M) compared to L/M adaptation. Adaptation to the latter reveals functions with a bandwidth (half-height-half-bandwidth) of 64 deg, falling to 34 deg for the former axis (see Fig. 3c). At contrast levels closer to detection threshold ($< 2x$), the increase in the exponent required to fit the S/(L+M) adaptation data is smaller, rising to a value of 1.4 (Fig. 3b). Consonant with this more linear behavior, the tuning functions produced under these conditions are broader (51 deg) and closer in bandwidth to the L/M tuning functions, which remain just above 60 deg (Fig. 3c). The contrast dependency of this nonlinearity is more clearly shown in Fig. 4 where the variation of the best-fitting exponent for the positional offset data following adaptation to L/M and S/(L+M) stimuli of varying different contrast levels is plotted. The data for the three observers exhibit similar trends, in that the exponent for the L/M data undergoes little or no change from its value close to unity as stimulus contrast changes from high suprathreshold levels to levels lying much closer to detection threshold. This is in stark comparison to the S/(L+M) function, which shows a large increase in best-fitting exponent for stimuli of high contrast from the lower values obtained following adaptation to low-contrast stimuli.

Discussion

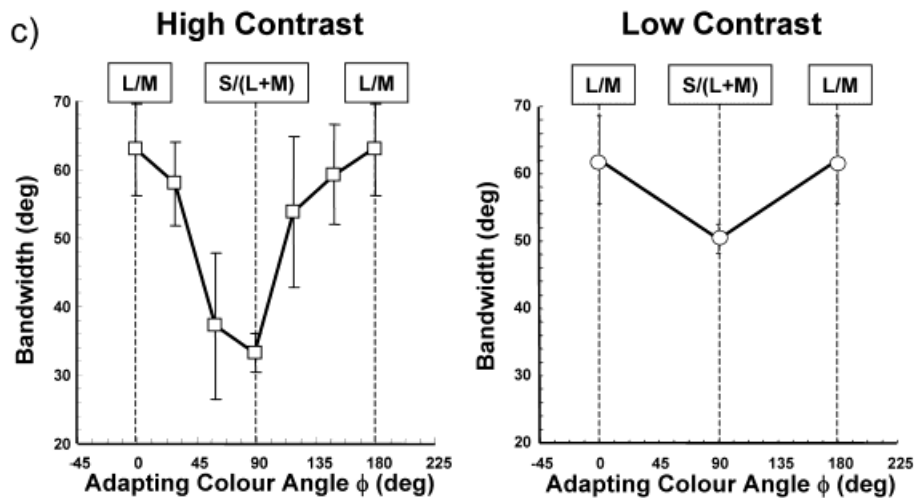
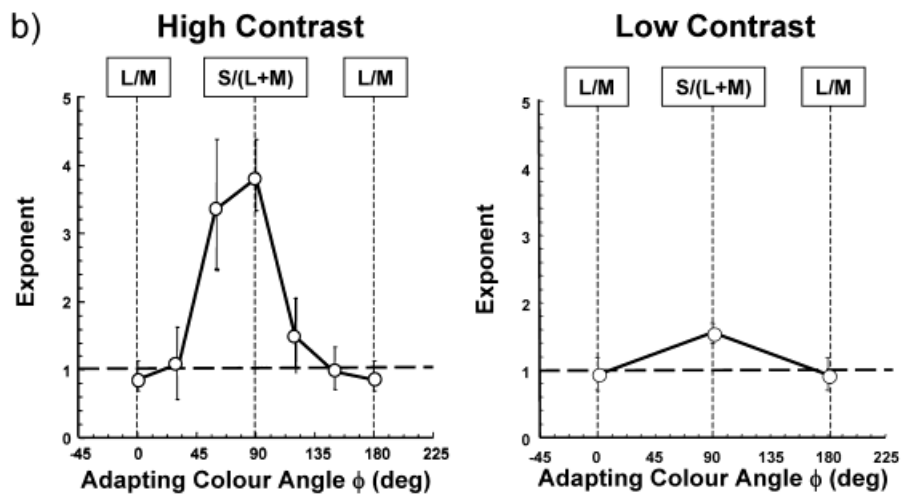
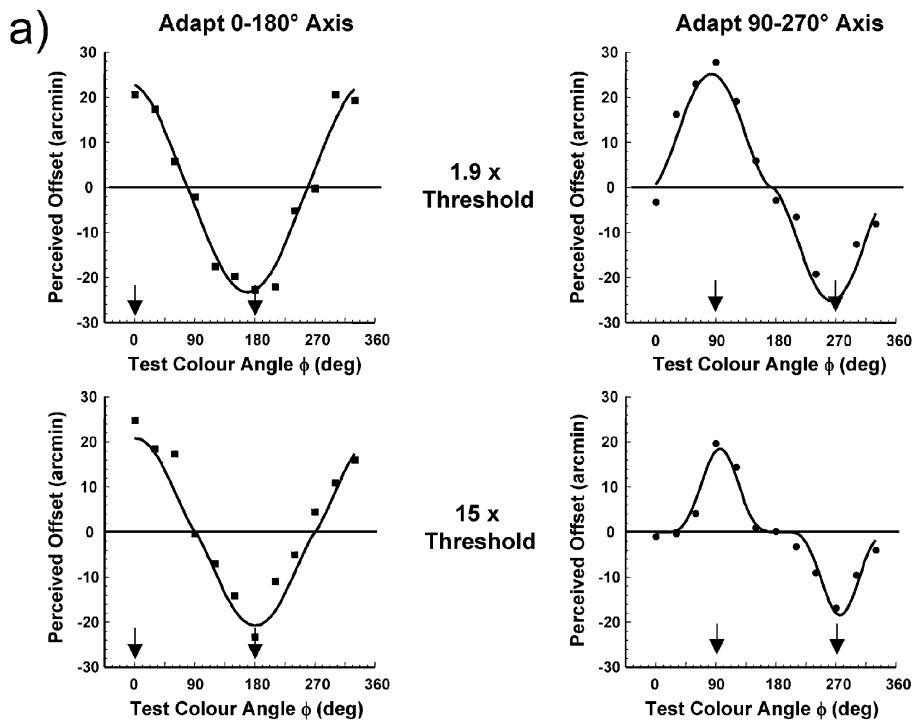
Adaptation to chromatic stimuli that modulate along different axes in color space generates misperceptions in the spatial localization of chromatic test stimuli. The magnitude of the positional shifts is highly dependent upon the chromatic composition of the adapting and test stimuli. The largest positional shifts are always produced

when the adapting and test stimuli lie along the same axis in color space, regardless of whether it is a cardinal or an intermediate axis. As the color angle between the test and adapting stimuli increases, the magnitude of the effect decreases, revealing the chromatic selectivity of these mechanisms.

Adaptation to low-contrast chromatic stimuli of any orientation in color space generates positional shifts that are well described by sinusoidal functions. This indicates the operation of chromatic mechanisms with a high degree of linearity, where the perceived offsets can be predicted by the position of the centroid generated by a linear combination of cone contrasts present within the after-image of the adapting stimulus and the test stimulus. The chromatic bandwidths of the functions generated by adaptation to low-contrast stimuli are broad, ranging from 52 deg for S/(L+M) adaptation to 64 deg for L/M adaptation. Such linear, broadband functions are consistent with the properties of neurons found in the LGN and would seem to be reflecting properties consistent with precortical chromatic mechanisms.

Adaptation to high-contrast stimuli, specifically those that lie on or close to the S/(L+M) axis, generates positional shifts that cannot be accounted for by simple linear combinations of contrast. The offsets measured under these conditions can only be fitted by sinusoids raised to exponents greater than unity. As a result of this nonlinear behavior, the bandwidths of these functions are significantly narrowed falling to a minimum of 30 deg for S/(L+M) adaptation. The bandwidths of the functions generated by L/M adaptation by comparison do not appear to undergo similar degrees of compression, remaining in excess of 60 deg. The nonlinear behavior exhibited following S/(L+M) adaptation seems distinctly at odds with the highly linear, broadband tuning properties exhibited by chromatic neurons in the LGN. However, it does have a strong resonance with, and suggest the involvement of, neuronal activity in V1. DeValois et al. (2000b) have described what they term as “an expansive nonlinearity” in the responses of chromatically sensitive neurons in macaque V1. This nonlinearity, like that demonstrated in this study, increases with the extent of S-cone involvement and has the effect of narrowing chromatic bandwidth. A complete description as to how this nonlinearity operates is, as yet, unclear. But the fact that we have demonstrated that its effects are more manifest at high contrasts may indicate a connection with the push–pull inhibitory models that have been invoked in order to explain the maintenance of narrow orientation selectivity in cat cortical neurons when exposed to stimuli of increasing contrast (Troyer et al., 1998; Ferster & Miller, 2000). This link remains highly speculative at present, but whatever the basis for this narrowing of chromatic bandwidth, its operation may provide the basis for the increases in color selectivity exhibited by cortical neurons in V1 and extrastriate areas (e.g. Vautin & Dow, 1985; Kiper et al., 1997). Furthermore, the restriction of this nonlinear behavior to S/(L+M) stimuli would appear to be consistent with the view of S-cones playing an important role in the transformation away from cone opponency to more perceptually relevant mechanisms (DeValois & DeValois, 1993; DeValois et al., 2000a).

The foregoing discussion considers a cortical locus for the nonlinearity that brings about compression of the S/(L+M) tuning function, but contributions from precortical mechanisms cannot be completely ruled out. We have shown elsewhere that the positional offset effect exhibits little intraocular transfer and has a decay constant of less than 2 s (McGraw et al., 2004). Both of these properties strongly implicating retinal-based mechanisms, although do not completely rule out cortical involvement. More problematical for a precortical explanation is the fact that previous



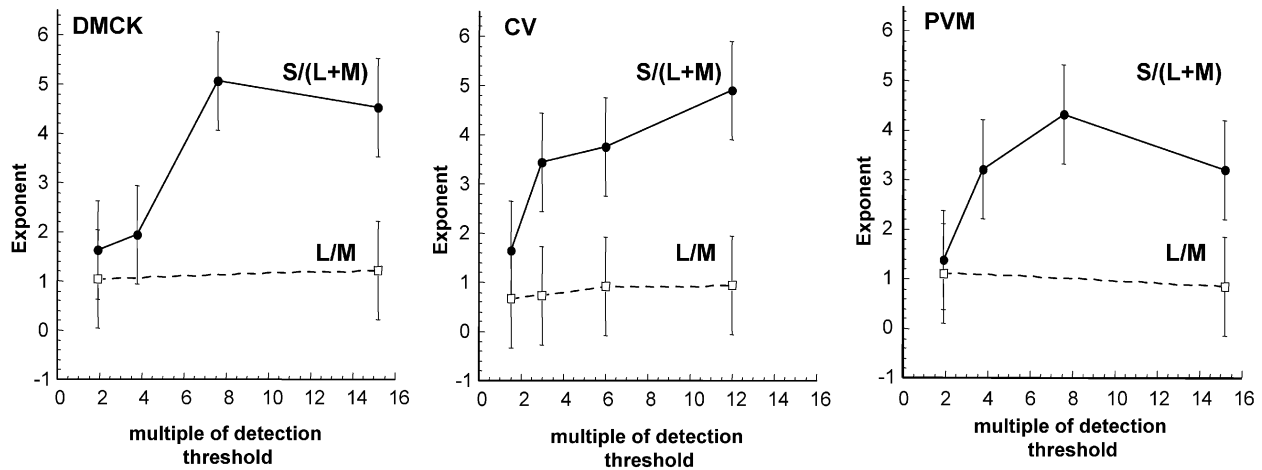


Fig. 4. The value of the best-fitting exponent required to fit the positional offset data generated by S/(L+M) and L/M adaptation, plotted as a function of stimulus contrast. Data are shown for three observers PVM, DMCK, and CV. Error bars represent standard deviations of the mean.

electrophysiological studies consistently show that summation of cone contrast takes place in a linear fashion for both L/M and S-cone information (Derrington et al., 1984; DeValois et al., 2000b). Therefore in terms of the centroid extraction model, a precortical locus would imply the existence of complex, nonlinear interactions between the after-images produced by S-cone stimuli and their combination with real images. A potential source of such interactions might arise as a result of the various adaptation anomalies that are known to selectively involve the short-wavelength system (see Mollon, 1982).

In the context of psychophysical studies that have attempted to assess the bandwidths of chromatic mechanisms, the results presented here would suggest that it might be an attribute that is not contrast invariant, particularly for mechanisms on or close to the S/(L+M) axis. Close to detection threshold there seems to be a degree of uniformity across color space, with mechanisms displaying largely broadband and linear characteristics. This picture is consistent with the results of D'Zmura and Knoblauch (1998) who examined chromatic detection thresholds in the presence of chromatic noise masking. At high suprathreshold contrasts, there is a loss of this uniformity across color space with mechanisms revealed by S/(L+M) adaptation exhibiting distinctly nonlinear, narrowband properties. Interestingly, the notion of narrowly tuned, nonlinear mechanisms concur with the findings of Goda and Fujii (2001), who suggested bandwidths of the order of 40 deg for the mechanisms revealed in their experiments. However, our results

diverge from theirs in one important aspect—we have made no assumptions regarding the uniformity of chromatic mechanisms across color space. In fact, we find evidence for the existence of chromatic mechanisms of variable bandwidth in suprathreshold vision across color space.

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Fig. 3. (a) Plots showing the variation in the perceived shifts generated in test stimuli of varying chromaticity (color angle, ϕ) following adaptation to two different color axes (L/M) (0–180 deg) and S/(L+M) (90–270 deg). Data obtained at two contrast levels 1.9 and 15 times detection threshold (adapt/test ratio = 1 in both cases) are illustrated and have been fitted by exponentiated sinusoidal functions (solid lines). Observer DMCK. (b) Mean values of the exponents required to fit data of the kind shown in Fig. 3. The data are plotted as a function of the axis of adaptation for observers PVM, DMCK, and CV. For adaptation to high-contrast stimuli, the highest exponents are required to fit the perceived shifts measured following adaptation to S/(L+M) stimuli, whilst an exponent close to unity (i.e. a sinusoidal function) adequately describes the effects of adaptation to L/M stimuli. For low contrasts, the increase in exponent for S/(L+M) adaptation is greatly reduced and closer to the unitary values obtained for the L/M data. Error bars represent standard deviations of the mean. (c) The mean bandwidths (half-height-half-bandwidths) of the tuning functions plotted as a function of the adapting stimulus chromaticity for high- and low-contrast stimuli. Error bars represent standard deviations of the mean.

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