

Neural adjustments to chromatic blur

MICHAEL A. WEBSTER *, YOKO MIZOKAMI,
LEEDJIA A. SVEC and SARAH L. ELLIOTT

Department of Psychology, University of Nevada, Reno, Nevada NV 89557, USA

Received 20 November 2004; accepted 18 June 2005

Abstract—The perception of blur in images can be strongly affected by prior adaptation to blurry images or by spatial induction from blurred surrounds. These contextual effects may play a role in calibrating visual responses for the spatial structure of luminance variations in images. We asked whether similar adjustments might also calibrate the visual system for spatial variations in color. Observers adjusted the amplitude spectra of luminance or chromatic images until they appeared correctly focused, and repeated these measurements either before or after adaptation to blurred or sharpened images or in the presence of blurred or sharpened surrounds. Prior adaptation induced large and distinct changes in perceived focus for both luminance and chromatic patterns, suggesting that luminance and chromatic mechanisms are both able to adjust to changes in the level of blur. However, judgments of focus were more variable for color, and unlike luminance there was little effect of surrounding spatial context on perceived blur. In additional measurements we explored the effects of adaptation on threshold contrast sensitivity for luminance and color. Adaptation to filtered noise with a $1/f$ spectrum characteristic of natural images strongly and selectively elevated thresholds at low spatial frequencies for both luminance and color, thus transforming the chromatic contrast sensitivity function from lowpass to nearly bandpass. These threshold changes were found to reflect interactions between different spatial scales that bias sensitivity against the lowest spatial grain in the image, and may reflect adaptation to different stimulus attributes than the attributes underlying judgments of image focus. Our results suggest that spatial sensitivity for variations in color can be strongly shaped by adaptation to the spatial structure of the stimulus, but point to dissociations in these visual adjustments both between luminance and color and different measures of spatial sensitivity.

Keywords: Blur; adaptation; color; contrast sensitivity.

INTRODUCTION

Blur represents an important and conspicuous property of spatial stimuli, and is a feature that the visual system appears to continuously calibrate for. A focused edge has an amplitude spectrum in which contrast varies inversely with spatial frequency,

*To whom correspondence should be addressed. E-mail: mwebster@unr.nevada.edu

or as $1/f$. Attenuating the contrast at higher frequencies biases the spectrum and causes the edge to appear blurred, while boosting the amplitude at high frequencies instead causes the stimulus to appear too sharp. This $1/f$ scaling also characterizes the average amplitude spectrum of natural scenes, and many authors have suggested that visual coding has been shaped by this characteristic (Atick, 1992; Simoncelli and Olshausen, 2001). For example, the center-surround antagonism in retinal receptive fields acts to discount the low-frequency bias in natural images, so that the neural response is effectively whitened (Atick and Redlich, 1992; Srinivasan *et al.*, 1982). Similarly, in the spatial-frequency tuning of cortical cells, the average bandwidth increases roughly in proportion to the preferred frequency (or as $\sim f/1$), so that the responses to $1/f$ spectra are more nearly equated across spatial scale (Field, 1987). A vivid illustration of this match is that $1/f$ noise appears to have salient structure at many spatial scales, while white noise (which has a physically flat spectrum) instead appears composed only of high frequency structure (Field and Brady, 1997).

The visual system also recalibrates for image blur at much shorter time scales. An obvious example of this is the accommodative changes of the eye's optics in order to focus the retinal image. Yet neural responses may also adjust continuously to the degree of blur or sharpness in the retinal image, through the processes of adaptation. For example, Webster *et al.* (2002) found that after adapting to a blurry image, a physically focused image appeared over-sharpened. They suggested that such short-term adjustments may be important for fine tuning the match between spatial sensitivity and the spatial statistics of images, since this match could otherwise be corrupted by properties of the observer (e.g. refractive errors or changes with development) or, perhaps to a lesser extent, by properties of the environment (e.g. in hazy conditions). The fact that these adjustments occur rapidly and lead to strong perceptual aftereffects suggests that they may play an important role in spatial vision, and in turn, suggest that precisely matching sensitivity to the spatial statistics of scenes may be functionally important for spatial coding.

In this study we asked whether similar adjustments occur when the spatial statistics are defined by variations in color rather than luminance. That is, to what extent is the visual system able to calibrate spatial sensitivity based on the chromatic contrast in images? Information about color can support many spatial judgments, and indeed color vision may primarily serve as another means to form perception (De Valois, 2003; Mullen and Kingdom, 1991). However, the spatial properties of color coding are in some cases very different from luminance coding, and this has drawn attention to the question of whether and to what extent these properties are also optimized for the spatial structure of the environment. For many images the amplitude spectra for color variations falls near $1/f$ and thus parallels the structure of luminance variations (Burton and Moorhead, 1987; Párraga *et al.*, 1998; Ruderman *et al.*, 1998; Webster and Mollon, 1997). Moreover, independent components analysis of images yields opponent-color functions with spatial properties that share comparable features with the

derived luminance components (Wachtler *et al.*, 2001). Yet retinal coding and psychophysical measures of contrast sensitivity at different scales are markedly different for color and luminance. While the luminance contrast sensitivity function (csf) is bandpass and extends to high spatial frequencies, sensitivity to color contrast shows little low-frequency attenuation and poorer spatial resolution (Mullen, 1985). The difference between the luminance and chromatic csf's has been accounted for by assuming that spatial color contrasts in images are noisier and thus cannot support discriminations at finer scales (Atick *et al.*, 1992), or by assuming that color is specialized for a particular subset of images with different structure. For example, Párraga *et al.* (2002) found that close-up images of colored objects like fruit tend to have steeper amplitude spectra for the chromatic contrast, and suggested that the low-pass csf for color may reflect an emphasis on encoding the low-frequency bias in such images.

The response of chromatic mechanisms to image blur remains unclear. Wuerger *et al.* (2001) found that the ability to discriminate changes in the magnitude of blur was very similar for luminance and chromatic patterns that were detected by the L and M cones, while very different for patterns that isolated S cones. This suggests that at least some types of color variation can support sensitive blur judgments. Yet the visual system may often 'ignore' this potential chromatic information in the perception of blur. For example, isoluminant stimuli are largely ineffective for driving the accommodative response (Switkes *et al.*, 1990; Wolfe and Owens, 1981), and in patterns with both luminance and chromatic contrast (i.e. stimuli characteristic of most natural scenes) the perceived blur may be strongly dominated by the luminance content of the scene. A striking example of this is illustrated in Wandell (1995, plate 7). Blurring only the light-dark variations in an image produced obvious changes in perceived image blur, yet when the same blur was applied only to the color variations the image remained perceptually well-focused.

We examined the responses to blur in chromatic stimuli by specifically asking whether the visual system can adapt to changes in the degree of blur or sharpening in chromatic images. Such adjustments might suggest that the spatial sensitivity for color is somehow matched to the spatial properties of the image, even if this match may not be important for the actual perception of blur. In previous studies we explored three different aspects of these adjustments for luminance-varying images. Webster and Miyahara (1997) measured how threshold contrast sensitivity is altered by adaptation to focused images or images with blurred or sharpened spectra, and found that adaptation produced pronounced and selective changes in the shape of the luminance csf. Webster *et al.* (2002) instead measured the actual perception of blur in stimuli after adapting to images that were blurred or sharpened, and again found strong after-effects. Finally, Webster *et al.* (2002) also observed strong changes in perceived blur when a focused image was presented within a blurred or sharpened surround. One goal of the present work was to test whether similar blur adaptation and blur induction effects occur for color-varying patterns, or whether these adjustments might reflect specialized processes within mechanisms

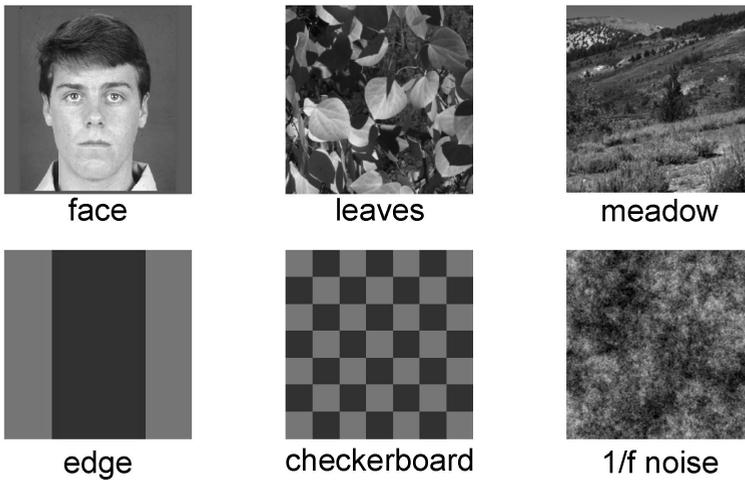


Figure 1. Images used to judge perceived focus when contrasts were defined by luminance or color variations.

sensitive to luminance. A second goal was to compare the pattern of adjustments for luminance and color to examine the extent to which the different blur adaptation and induction effects are functionally distinct.

METHODS

Stimuli consisted of images of natural objects or scenes, simple geometric patterns, or filtered noise, as described in Webster and Miyahara (1997) (Fig. 1). All images had an intensity resolution of 256 levels. For luminance images, these were used to define uniform gray-scale values corrected for the non-linearities of the display. For chromatic images, a look-up table was used to remap the luminance levels into chromatic contrasts. Chromaticities in the color images were varied along the two axes of the MacLeod-Boynton chromaticity diagram, which correspond to opposing signals in the long- and medium-wavelength sensitive cones (LM), or signals in the short-wavelength sensitive cones opposed by the combined signals in the L and M cones, (S-LM) (MacLeod and Boynton, 1979). These two axes are thought to be the principal axes underlying early post-receptoral color coding (Krauskopf *et al.*, 1982). The spatial capacities for the S axis are of further interest because the small number and sparse sampling by S cones severely restricts the spatial resolution of the S-cone pathways (Williams and Collier, 1983). For both axes we arbitrarily defined contrasts to equal 1.0 for the maximum complementary color excursions available on the monitor. The resulting stimuli had a mean chromaticity equivalent to Illuminant C (MacLeod-Boynton r, b coordinates of 0.6568, 0.01825) and maximum excursions of (0.7117, 0.01825) for the +L-M axis and (0.6568, 0.03388) for the +S axis. Isoluminance was defined photometrically based on calibrations of the display with a PR650 spectroradiometer.

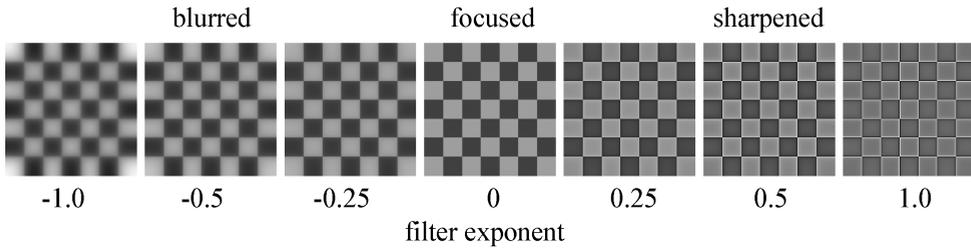


Figure 2. Examples of the image arrays, which varied the original spectrum ($s = 0$) in finely graded steps from moderately blurred ($s = -1$) to moderately sharpened ($s = +1$).

The images were filtered by multiplying the original amplitude spectrum by f^s , where f is the spatial frequency and s represented the change in the spectral slope of log amplitude *vs.* log frequency. Negative values of s steepened the original slope by reducing amplitude more at higher frequencies, and thus caused the image to appear blurred. Positive values instead flattened the slope by boosting the contrast at higher frequencies and thus sharpened the images. For most experiments we created an array of images by varying s from -1 to $+1$ in steps of 0.01 , providing a series that varied from moderately blurred to moderately sharpened in finely graded steps (Fig. 2). Each image was rescaled after filtering so that it had the same mean luminance and rms contrast as the original image.

Responses to blur were assessed at suprathreshold by measuring the perceived blur of images and at threshold by measuring contrast sensitivity for grating patterns. The two tasks involved different procedures and displays and were tested for different subsets of observers. The observers included the authors and 5 additional subjects who were unaware of the specific aims of the experiment.

Suprathreshold blur judgments

For measurements of perceived blur, the images were shown on a Sony 20SE monitor controlled by a standard VGA card. Observers viewed the display binocularly in a dark room from a distance of 135 cm. At this distance, the 256×256 images subtended 4 deg centered within a 11.7 by 15.7 gray background, and spanned a range of horizontal or vertical frequencies from 0.25 to 32 c/deg. The mean luminance of the display was ~ 10 cd/m². Perceived focus was measured with a forced-choice staircase procedure. On each trial a test image was shown for 500 ms, and the observer used a button box to respond whether the image appeared ‘too blurred’ or ‘too sharp’. The slope (s) of subsequent images was varied in two randomly interleaved staircases, with the estimate of ‘best focus’ based on the mean of the final 6 reversals from each staircase. Settings were made either before or after adaptation to blurred or sharpened versions of the images. In adapting runs, subjects viewed a single image of a specified slope for 3 minutes. The image was randomly repositioned within a 6 deg field every 250 ms in order to prevent local differences in light adaptation. Test images were then shown for 500 ms and interleaved with 6 s periods of readaptation prior to each presentation. A uniform

field was displayed for 500 ms between the adapting and testing images to prevent masking. In further experiments we also measured the effects on perceived blur of induction from a simultaneously presented surrounding field rather than adaptation from a prior stimulus. The stimulus configuration for these experiments is described below in the appropriate section of the results. Typically, 4 settings were made for each adaptation and induction condition, with the order counterbalanced for luminance and color and for different images.

Threshold contrast sensitivity

To measure contrast sensitivity functions following adaptation, stimuli were displayed on a Sony 20SE monitor controlled with a Cambridge Research Systems VSG graphics card, which allowed near threshold stimuli to be displayed with high resolution. Procedures and stimuli were similar to those used previously by Webster and Miyahara (1997). Adapting images in this case were all white noise filtered over a range of spectral slopes. These were adjusted for an rms luminance contrast of 0.35, or a nominal contrast of 1.0 for the chromatic patterns. They were shown at 8-bit resolution through the VSG framestore. The images subtended 5.6 deg and were delimited by a narrow black border from an 8 by 10.5 deg background of the same mean chromaticity and mean luminance (30 cd/m²). At the 200 cm viewing distance the images contained frequencies ranging from 0.149 to 19.1 c/deg. Testing began with an initial 5-minute period of adaptation. To control for light adaptation in these experiments, observers viewed a rapid succession of 16 different noise images that all had the same spectral slope. A new image from the set was chosen at random every 300 ms. Following adaptation, a horizontal test grating was shown in the display field for 700 ms, with contrast ramped on and off during the first and last 150 ms with a Gaussian envelope ($\sigma = 50$ ms). The test and adapt stimuli were separated by a 500 ms uniform field, and each test presentation was preceded by a 6 s readaptation interval. In pre-adapt baseline settings, the same sequence was followed but with uniform fields in place of the adapting images. The gratings were displayed using the VSG waveform generator which provided a contrast resolution of 14 bits/gun. Subjects used a button box to adjust the grating contrast until it was at the detection threshold. Settings were made for test frequencies ranging from 0.25 to 16 c/deg in 1 octave steps. Results reported are the average of between 6 and 12 settings for each frequency.

RESULTS

Perceived focus of luminance and chromatic images

As a prelude to examining the effects of adaptation and induction for chromatic blur, we first compared the ability to simply judge the focus of images defined by luminance or chromatic contrast. Subjects were shown the 6 images in Fig. 1 and

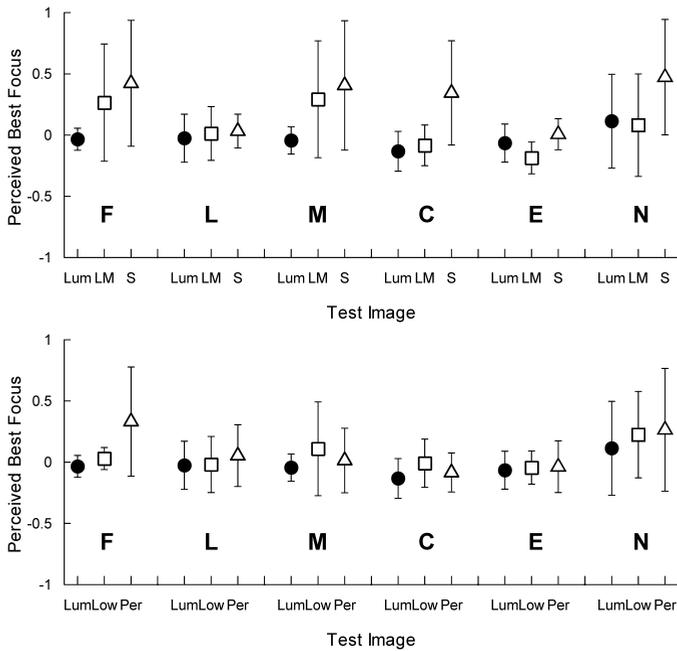


Figure 3. Slopes at which the images were judged to be best focused. Top panel: points plot the mean and standard deviations for 7 observers' settings when the same images were defined by luminance contrast (circles) or LM (squares) or S (triangles) chromatic contrast. Different triplets of settings correspond to the 6 images shown in Fig. 1. A setting of 0 corresponds to the original focused image, while a positive value means the original spectrum had to be sharpened in order for the image to appear focused. Bottom panel: settings for the original luminance images (circles) compared to settings when the luminance contrast was reduced by one-half (squares) or when the images were viewed at 7 deg in the periphery (triangles).

were asked to vary the spectral slope of each until they appeared physically focused. The mean settings for 7 observers are shown in Fig. 3. The top panel compares settings when the images varied in luminance (filled circles), in LM chromatic contrast (unfilled squares) or in S chromatic contrast (unfilled triangles). Values near zero indicate that the observers chose slopes close to the original, unfiltered spectra. For luminance, the chosen slopes were all close to the original images, and close to $1/f$ for the filtered noise. These results are similar to those reported previously by Tadmor and Tolhurst (1994) and Field and Brady (1997), and again show that subjects had accurate *a priori* knowledge of the image characteristics defining blur. Notably, settings for the luminance images were as consistent for the natural images as for the simple edges, and more consistent than for the filtered noise.

The settings for the chromatic images could differ from the settings for luminance-varying images in two ways. First, observers might be less sensitive to the slope of the amplitude spectra in the chromatic images, and thus their settings might be more variable. Second, the point of subjective best focus might differ for luminance-

Table 1.

Comparisons of the perceived focus settings for luminance and chromatic images, as plotted in Fig. 3

		Comparison	<i>F</i>	<i>p</i>
(a)	Mean	Luminance vs. LM −0.03 vs. 0.064	1.36	NS
	Variance	0.049 vs. 0.154	3.13	<0.001
(b)	Mean	Luminance vs. S −0.03 vs. 0.28	4.02	<0.001
	Variance	0.049 vs. 0.204	4.14	<0.001
(c)	Mean	High vs. Low Contrast −0.03 vs. 0.052	1.50	NS
	Variance	0.049 vs. 0.076	1.55	NS
(d)	Mean	Foveal vs. Peripheral −0.03 vs. 0.091	1.84	NS
	Variance	0.049 vs. 0.136	2.75	<0.001

F tests compare differences in the mean slope or in the variance of the settings for (a) luminance vs. LM varying images; (b) Luminance vs. S varying images; (c) high contrast vs. low contrast luminance images; or (d) luminance images presented in the fovea or the periphery. All comparisons are based on pooling the settings across the 6 different images and the 7 different observers.

varying and color-varying images. For example, if the original slope appeared blurred in the chromatic images, then observers might choose a shallower slope to set the focus. To examine this, we compared the mean and variance of the settings for the luminance and chromatic images (Table 1). This was done by pooling across the 6 different images and 7 observers. The variance in the settings was significantly higher for the LM and the S images compared to the luminance images. Moreover, the mean slope for the S images, but not the LM images, was significantly higher than for their luminance counterparts. As Fig. 3 suggests, these comparisons must be interpreted with caution since the differences between luminance and color were not consistent across the different images. (We do not know the bases for these differences.) Nevertheless, subjects in general were less consistent at judging the slopes in the chromatic images.

The differences between luminance and color could reflect properties of spatial coding that were specific to color, or more generally differences in the resolution or contrast sensitivity for the two types of stimuli. In the latter case we might be able to mimic the color results by displaying the luminance images at a lower contrast or under conditions that lower the resolution of the visual system. To assess this we repeated the measurements for the luminance patterns either at one-half the contrast or when they were viewed centered at 7 deg in the periphery. These comparisons are shown in the lower panel of Fig. 3. Reducing the contrast did not significantly affect the judgments, while with eccentric viewing variability increased while the mean settings remained similar to those for central fixation (Table 1). The latter is consistent with the compensation for blur in peripheral viewing reported by Galvin *et al.* (1997). Again, these differences are not conclusive, because they may

not mimic the actual changes in effective contrast or resolution for the chromatic patterns. However, they leave open the possibility that the changes in subjective focus judgments for the S images (but not the LM images) are not accounted for simply by the differences in relative contrast or acuity for these images.

Adaptation to blur

We next tested whether the judgments of focus could be biased by prior adaptation. As discussed above, Webster *et al.* (2002) found that viewing blurred or sharpened images shifted the perceived focus of subsequently viewed images so that they appeared sharper or blurrier, respectively. The present experiments examined whether adaptation could similarly alter the perception of chromatic patterns. Because sensitivity to blur in the chromatic patterns was poorer (as noted above), we first trained subjects to learn the original focus by repeating the blur settings with feedback. The same judgments were then made without feedback after adapting to blurred or sharpened versions of the image.

Figure 4 shows the settings for 4 observers tested with luminance or chromatic versions of the checkerboard image. In all cases there is a consistent bias in the focus judgments following adaptation. Specifically, adaptation to the blurred checkerboard caused the original to appear too sharp, so that the image that appeared properly focused was now physically blurred, while prior adaptation to the sharpened image induced the opposite bias. Moreover, in most cases the magnitude of these shifts was comparable for luminance and color, and for both types of chromatic contrast. Thus despite the poorer sensitivity to blur in the chromatic patterns, for both luminance and color the judgments of blur appear similarly affected by adaptation.

The measurements in Fig. 4 were for adapting and test images that had the same type of contrast (i.e. both images were luminance or both were chromatic). Were observers adapting to the general property of blur *per se*, or to the blur along specific axes of color space? To test this, we made further measurements when the contrast defining the test and adapting stimuli fell along the same or different axes. This experiment also used a different image (the ‘leaves’ image of Fig. 1) to ensure that the blur aftereffects for color were not specific to simple binary patterns like the checkerboard image.

In this case subjects made settings after adapting to either a sharpened ($s = +0.5$) or blurred ($s = -0.5$) level of the adapting image. Again, these two stimuli should induce opposite shifts in the perceived focus of the test stimulus, and we therefore used the difference between the slopes chosen under these two conditions in order to compare the magnitude of the aftereffects. These differences are shown in the three bar charts in Fig. 5. The three panels plot the changes in the settings after adapting to images defined by luminance contrast (left panel), LM contrast (middle panel), or S contrast (right panel), while the three bars within each panel show how adaptation to blur along each axis affected a test pattern defined by the same or different axes. A value of zero means that the focus settings were equal after

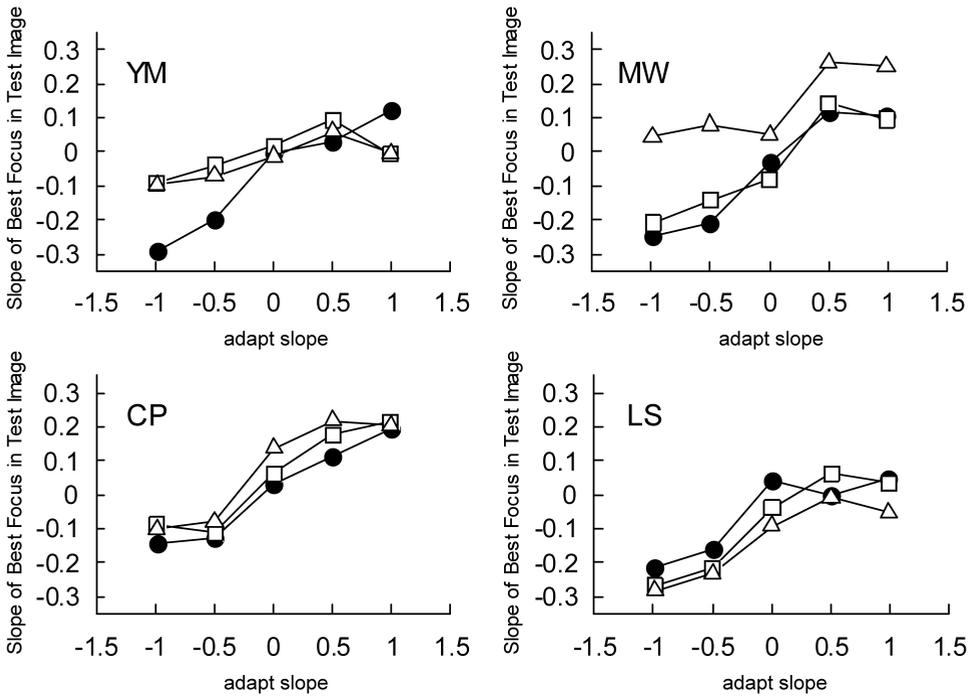


Figure 4. Changes in perceived blur following adaptation to blurred or sharpened images for luminance contrast (circles), LM chromatic contrast (squares) or S chromatic contrast (triangles). Each point plots the mean of 4 settings for the checkerboard pattern. The 4 panels show results for 4 different observers.

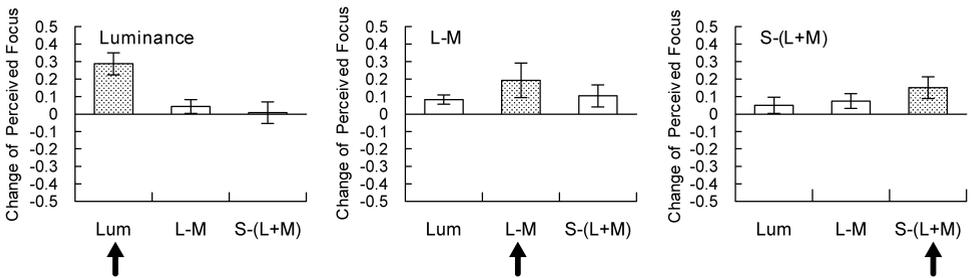


Figure 5. Changes in perceived blur when the adapting and test images both varied in luminance or along the same color axis (shaded bars), or when the adapt and test images varied along two different axes (unshaded bars). Bars show the difference in the blur settings after adaptation to a sharpened (+0.5) or blurred (-0.5) version of the 'leaves' image. Positive values indicate that the test image appeared more blurred after adapting to a sharp image than a blurred image. The three bars in each panel are for a luminance, LM, or S test image, each based on the mean settings for 5 observers (± 1 standard deviation). The 3 panels show results for luminance (left), LM (right), or S adaptation.

blurred or sharpened adaptation, while a positive value indicates that the test image appeared more blurred after adapting to a sharpened image than a blurred image, consistent with the after-effects shown in Fig. 4. Once again there is clear adaptation

for both luminance and color when the test and adapting images varied along the same axis (though in these settings it was generally stronger for luminance). Yet the biases are consistently weaker when the adapt and test axes differ. Thus the changes in blur involve changes in mechanisms that are selective for the luminance, LM, and S axes of color space. This selectivity also precludes the possibility that the adaptive shifts seen for color tests reflected judgments based on the luminance artifacts in the nominally chromatic patterns for, in that case, there should have been strong effects of luminance adaptation on the color tests. Instead, the color-selectivity indicates that the adaptation can adjust specifically to the blur carried by chromatic contrast.

Blur induction

As noted, Webster *et al.* (2002) also found that perceived blur is strongly influenced by the relative blur in the surrounding context. An example of these induction effects is illustrated in Fig. 6. The center segments of the bars are all square-wave edges, yet the luminance edge is perceptually sharpened by the blurred luminance surround while blurred by the sharpened surround. We used a similar stimulus arrangement to test for induction effects for chromatic contrast. The vertical edges of the test bars subtended 1 deg, and were shown within abutting surrounding edges that extended 3 deg above or below the test. To facilitate judging the test, a focused reference bar (without surrounding edges) was displayed 3 deg to the left, and observers adjusted the test edge until it appeared as sharp as the reference. Settings were made for surrounding edges that were either sharpened ($s = +0.5$) or blurred ($s = -0.5$), and we again compared the difference in the focus settings for the test edge under these two conditions.

Figure 7 plots the results for two observers. The three panels again correspond to inducing bars defined by luminance contrast (left), LM contrast (middle), or S contrast (right). For luminance, there is a strong simultaneous contrast interaction, consistent with the effects visible in the images in Fig. 6. However, when the center and surround edges were defined by either chromatic axis there was instead little induction. Thus, unlike the adaptation, for the conditions we tested color and luminance appeared to have different effects on the perception of relative spatial differences in blur. The weak induction for color again cannot be accounted for merely by the poorer acuity for color, because the induction effects for luminance actually become stronger when the images are viewed in the periphery (Webster *et al.*, 2001).

Figure 6. (See color plate IV) An illustration of blur induction for luminance or chromatic edges. Top: effect of luminance surrounds on luminance or S edges. The center row of luminance edges on the left are squarewave edges. However, these edges appear sharpened when the surround edges are blurred while blurred when the surround edges are sharpened. The same luminance surrounds induce an opposite aftereffect on S edges — the squarewave S edges at top right appear blurred (rather than sharpened) when surrounded by blurred luminance edges. Bottom: S surrounds instead have little effect on the luminance or S center squarewave, suggesting that there is little spatial blur induction from the S patterns.

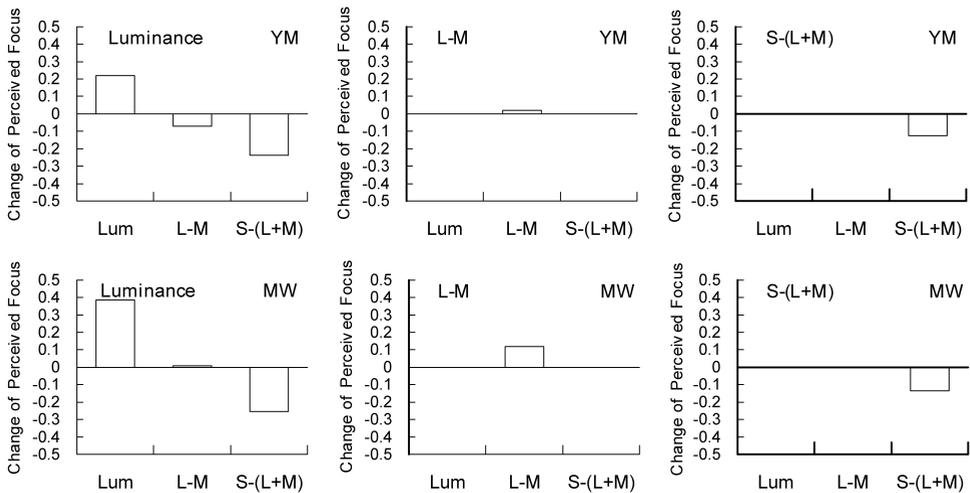


Figure 7. Blur induction for luminance or chromatic edges. Bars plot the change in perceived focus of a central edge in the presence of blurred (-0.5) or sharpened ($+0.5$) surround edges. A positive value indicates that the test edge appeared sharper when surrounded by the blurred edge. The three panels plot the results for luminance edges (left), LM edges (center) or S edges (right). The effects of luminance surrounds were tested for both luminance and color while, the color surrounds were tested only on the corresponding color test. The 2 rows show results for 2 observers.

The induction effects also revealed an asymmetric interaction between luminance and color. Specifically, surrounding luminance edges induced changes of opposite sign in the luminance and S chromatic test edges (Fig. 7, left column). That is, a blurred luminance surround caused the luminance test to appear sharper, yet the same surround caused an S edge to appear blurrier. The conditions yielding these opposite effects are illustrated by the images in Fig. 6. (In the converse case, shown in the lower image in Fig. 6, chromatic surrounds had no noticeable effect on a central luminance edge.) The luminance-induced blur in the S-cone pattern is reminiscent of the ‘capture’ of chromatic contrast by luminance edges (as in the blur illustration of Wandell, 1995), yet in this case the capture extended across a 1-deg gap at which there were no physical luminance edges.

Adaptation and threshold contrast sensitivity

In the next set of experiments we tested for adaptation to chromatic blur by examining how adaptation to blurred or sharpened images altered the shape of the contrast sensitivity function. Figure 8 shows measurements of contrast sensitivity as a function of spatial frequency before or after adapting to $1/f$ noise along the luminance axis or the LM or S chromatic axes. As Webster and Miyahara (1997) found previously for luminance-varying images, adaptation to the $1/f$ spectra characteristic of natural images induces a loss in contrast sensitivity at low and medium spatial frequencies, while sparing sensitivity at higher frequencies. Thus

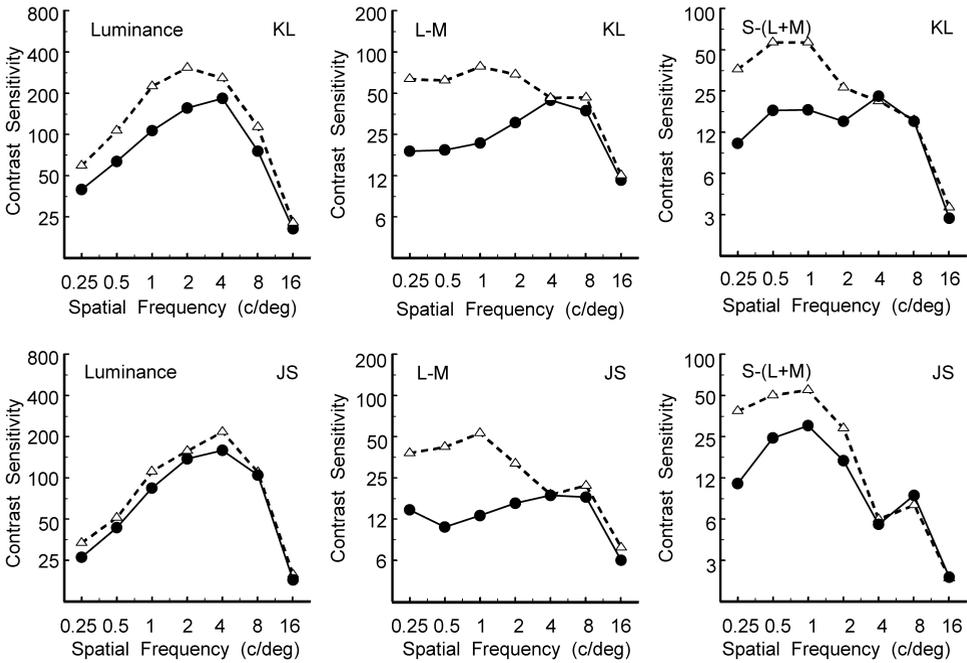


Figure 8. Contrast sensitivity functions measured before (triangles) or after (circles) adaptation to $1/f$ noise defined by luminance contrast (left), LM chromatic contrast (center), or S contrast (right). The 2 rows show results for 2 observers.

adaptation biases the overall sensitivity of the visual system toward higher spatial frequencies.

Under the present conditions these sensitivity changes turned out to be much stronger for chromatic contrast. Threshold elevations for both chromatic axes were pronounced at lower spatial frequencies, while again spared at the higher frequencies. Consequently, the chromatic csf switches from clearly lowpass before adaptation to weakly bandpass after adaptation. Figure 9 shows that the threshold changes for color also depend on the degree of blur in the adapting images. The different panels plot contrast sensitivity measured after adaptation to a range of LM noise images with amplitude spectral varying in slope from 0 (white noise) to -2.5 (strongly blurred; note that in this case slope values refer to the absolute slope and note the slope relative to $1/f$). As we found previously for luminance, white noise adaptation had relatively weak effects on sensitivity (Webster and Miyahara, 1997). But as the spectrum becomes more biased, there are progressively stronger and more selective changes in threshold at the lower frequencies, so that under adaptation to pronounced blur the chromatic csf is clearly bandpass. The shifts with the adapting spectrum reinforce the measurements of suprathreshold blur adaptation above, in showing that the visual system adaptively adjusts to changes in the spatial structure of the chromatic stimuli (though these adjustments may be much coarser than the

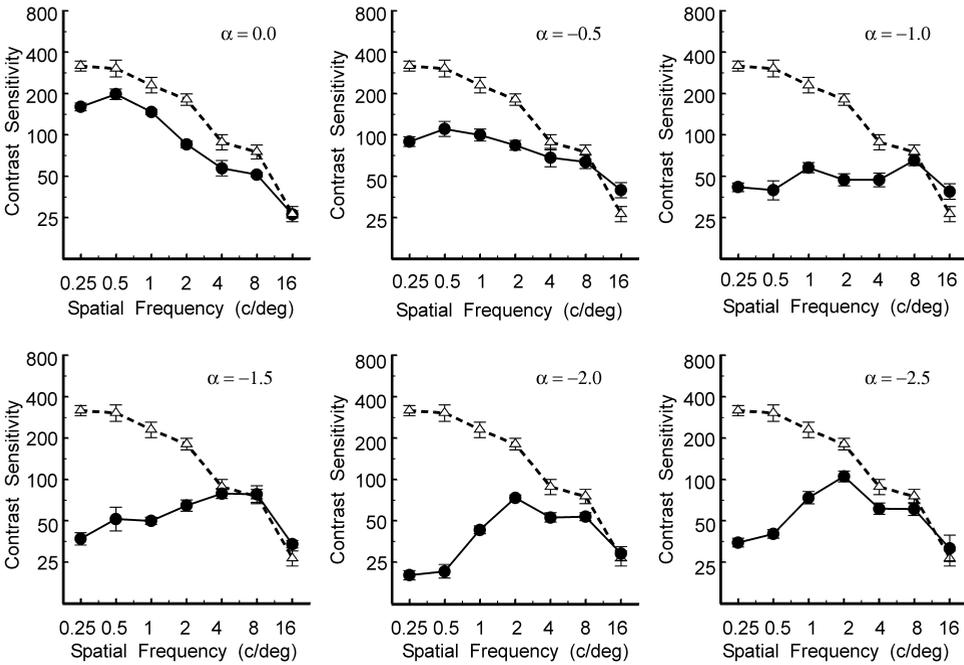


Figure 9. LM chromatic contrast sensitivity following adaptation to LM chromatic noise, for a single observer (MW) tested over a range of adapting slopes. Triangles plot the sensitivity before adaptation. Each panel plots the csf after adaptation to noise with the indicated spectral slope.

changes in surpathreshold blur, in the sense that much larger changes in adapting blur are required to produce a measurable change in the shape of the csf).

Again, for the conditions of our measurements the magnitude of these threshold changes was much larger for color than luminance. This is evident in Fig. 10, which plots the changes in contrast sensitivity (post-adapt/pre-adapt threshold) induced by the adaptation. The chromatic thresholds are taken from the plots in Fig. 9, while the luminance settings are from the study of Webster and Miyahara (1997) for the same observer and viewing conditions (their Fig. 10). For both luminance and color, the threshold changes clearly track the changes in the adapting spectra, but the selectivity and magnitude of these changes is more pronounced for color, with thresholds elevated by more than a log unit at the lowest frequencies.

The stronger adaptation effects for color are consistent with the higher intrinsic sensitivity of color mechanisms at low frequencies. That is, because the chromatic csf shows little low frequency attenuation, the effective contrast of natural spectra at low frequencies (i.e. the contrast after filtering by the csf) might be higher for the chromatic components than the luminance components. Thus we might expect more adaptation to the low frequencies for color. However, there are a number of complications with this simple interpretation. First, we made no attempt to equate the relative contrasts along the luminance and chromatic axes, and thus any differences could in part reflect differences in the overall contrast. To

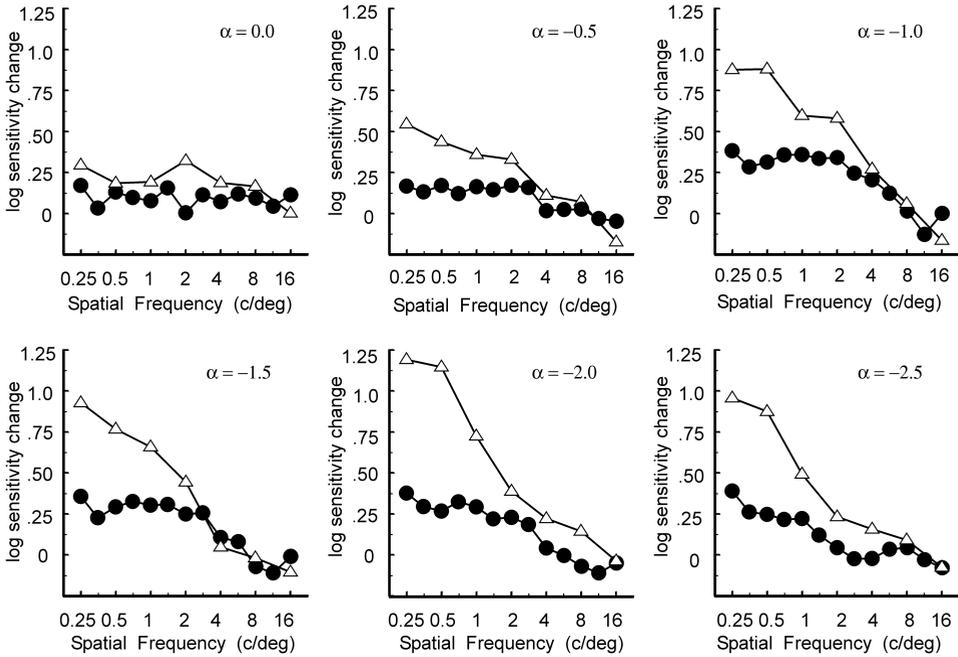


Figure 10. Change in log contrast sensitivity for LM gratings after adaptation to LM chromatic noise (triangles) or for luminance gratings after adaptation to luminance noise (circles). Chromatic results plot the change in pre- vs. post-adapt sensitivity for the settings in Fig. 9. Luminance results are for the same observer from the study of Webster and Miyahara (1997).

evaluate the relative adaptation states of color and luminance vision under natural viewing, it would be instructive to measure contrast sensitivity after adapting to actual images of natural scenes. A second complication is that at higher spatial frequencies the effects of optical chromatic aberrations become pronounced, so that these frequencies might be detected by the resulting luminance artifacts in the stimuli. We made no effort to correct for chromatic aberration, and thus it is possible that the adaptation for color is much less selective for spatial frequency than our results imply, because the thresholds at higher frequencies depend on detecting the encroaching luminance contrast. However, this does not alter the conclusion that sensitivity to chromatic variations in the stimulus may become more nearly bandpass under natural states of adaptation, nor that the shape of the chromatic csf can vary with the amount of blur in the image.

Threshold vs. suprathreshold adjustments to blur

The preceding results show that for both luminance and color, adaptation to blur can alter both the relative sensitivity to different spatial scales and the perceived blur in suprathreshold patterns. However, these two measures surprisingly point to different neutral states for the adaptation. Specifically, adaptation to a focused pattern does not alter perceived focus, as would be expected since this is the type of pattern we

are already routinely adapted to and thus presumably should be already matched for. Yet exposure to the same focused pattern has large selective effects on the threshold csf, biasing sensitivity against lower frequencies, as if the visual system is *not* already matched to natural image spectra. In the final experiment we explored why adaptation to an ‘*a priori* unselective’ stimulus like a $1/f$ spectrum leads to a selective change in thresholds. For these settings we restricted the stimuli to luminance images, since these provide a more sensitive measure of the adjustments and are less confounded by artifacts like chromatic aberration that might complicate the interpretation.

The failure of $1/f$ adaptation to influence thresholds at higher frequencies could result because of the paucity of physical contrast at those frequencies. By this account, the selective changes in the csf result simply because the intrinsic sensitivity of the visual system does not compensate for the low-frequency bias in the physical stimulus. However, an alternative possibility is that the adaptation cannot be predicted simply from the amplitude spectrum of the stimulus, because the visual system does not adapt independently to the contrast at different scales. This latter possibility is suggested by previous studies of adaptation to simple compound gratings. These studies have shown that the threshold changes following adaptation to a grating (e.g. of frequency $3f$) are reduced when the same adapting grating is presented in the presence of a lower fundamental frequency (e.g. of frequency f) (Klein and Stromeyer, 1980; Nachmias *et al.*, 1973; Tolhurst, 1972; Tolhurst and Barfield, 1978). That is, the lower frequency components in the stimulus appear to block adaptation to the higher frequency components.

We tested whether similar interactions occur for natural image spectra. To examine this, we again adapted to $1/f$ noise images but this time filtered out frequencies below a given cutoff. The cutoff frequencies ranged from 0.5 to 16 c/deg. The filtering removed all frequencies below the cutoff and did not rescale contrast, so that frequencies above the cutoff remained at the same amplitude as in the original unfiltered image. Observers again adapted to a random sequence of noise images with the same spectra, and as before set thresholds for a range of frequencies before or after adaptation. We also increased the viewing distance so that the stimuli subtended 4 deg, so that in this case frequencies in the images ranged from 0.25 to 32 c/deg.

Figure 11 plots the change in sensitivity to a fixed test frequency as a function of the cutoff frequency of the adapting stimuli. Thus the individual curves do not show the effects of individual adapting spectra as in previous figures, but rather directly show how the sensitivity at a given test frequency varied with changes in the adapting spectrum. The two curves plot the results for two observers. Lowering the cutoff frequency always resulted in an increase in the physical contrast of the adapting stimuli. Yet the largest threshold changes consistently occurred when the test frequency corresponded to the cutoff frequency — or in other words to the lowest frequency component in the adapting stimulus. In particular, there are clear threshold changes at the highest frequencies (8 and 16 c/deg) when the

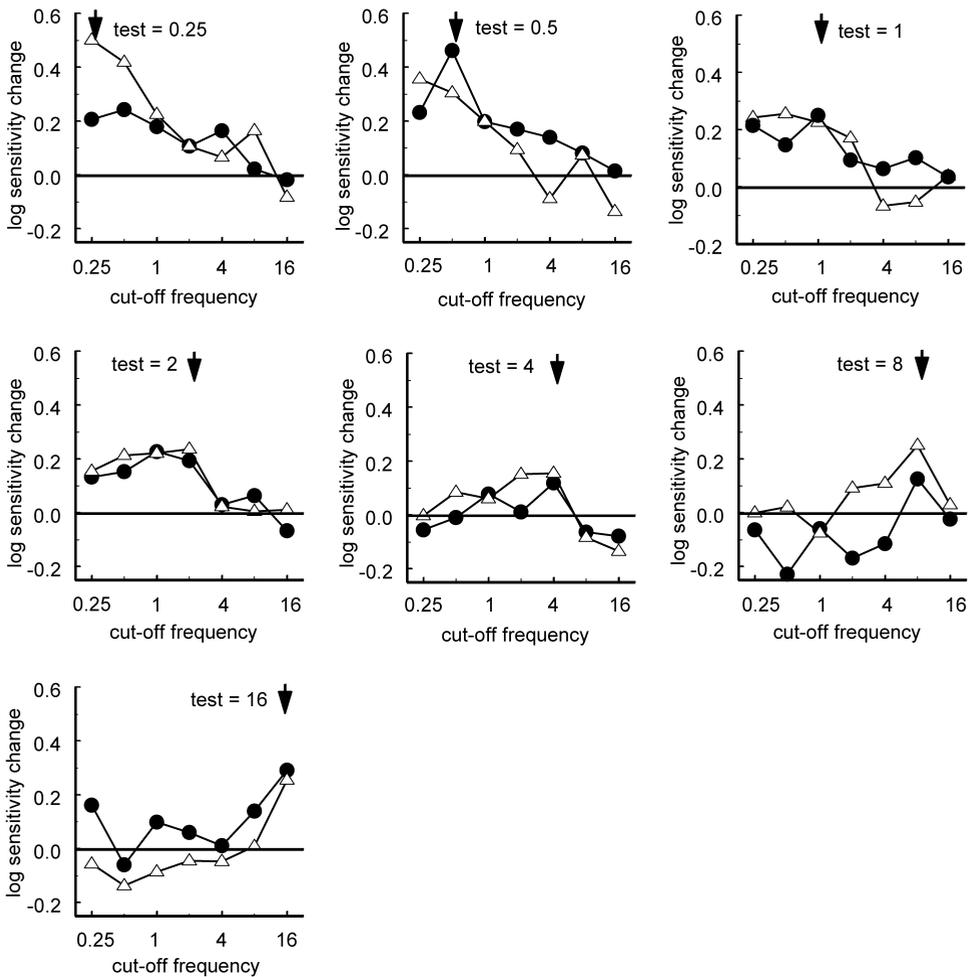


Figure 11. Changes in thresholds for test gratings as a function of the cutoff frequency of the adapting spectra. Each panel plots the results for the single test frequency indicated as a function of the lowest frequency in the adapting image. The 2 curves plot the results for 2 different observers.

adaptation was restricted to those frequencies, even though sensitivity at these same frequencies remained largely unaffected when the adapting images were broadened in bandwidth. These results are thus consistent with the adaptation effects reported previously for compound gratings. They suggest that the biases induced in contrast sensitivity arise, not because visual sensitivity is otherwise mismatched to natural image spectra, but because the effects of adaptation at different spatial scales are not independent. In particular, the contrast changes appear to reflect adaptation to the largest scale or 'size' in the adapting stimulus.

Webster *et al.* (2002) similarly concluded that the effects of adaptation on blur perception could not be accounted for by the overall amplitude spectrum. They found that how adaptation transferred across different images depended

on the actual physical focus of the images and not on the average contrast at different spatial scales (which can vary across physically focused images because of differences in the density of structure at different scales (Field and Brady, 1997)). Thus, like judgments of image blur (Field and Brady, 1997; Tadmor and Tolhurst, 1994), the adaptation is controlled by the actual blur in the image and not by the global spectrum.

This leaves unanswered the question of why adaptation-induced changes in the csf are not manifest in the judgments of image focus. One possibility is that the pattern of the sensitivity changes is different at high test contrasts (Snowden and Hammett, 1992), such as those examined in our blur task. However, Webster and Miyahara (1997) found similar selective changes in perceived contrast in suprathreshold gratings of moderate contrast. This suggests that the difference may instead be due to the nature of the test stimuli. The visual cues to blur are surprisingly poorly defined, and as the preceding paragraph suggests, may depend on attributes that are not readily captured by the amplitude spectrum. Thus sensitivity to blur and to sine wave gratings may tap very different processes. Consistent with this, Wuerger *et al.* (2001) found that the differences in the luminance and chromatic csf's could not predict performance in their blur discrimination task.

DISCUSSION

Color vision provides a useful context for exploring the match between spatial coding and the visual environment, for it provides the visual system with additional sources of information about the world, and thus the chance to test whether design principles developed in one context have general validity (Atick, 1992; Simoncelli and Olshausen, 2001). There are many clear cases where the encoding of color seems strongly driven by the properties of the environment, as for example in the variations in spectral sensitivity with environmental niche (Lythgoe, 1979). Recently, MacLeod and von der Twer (2003) explored the match between post-receptoral color coding and the distribution of colors in the natural environment. They showed that contrast coding for color can be closely predicted from natural color distributions and from the principle that the visual system is designed to minimize the overall error in the representation of different levels in these distributions. This match makes sense, for clearly a fundamental function of our color vision is to provide us with information about color.

However, chromatic variations in images also carry information about the spatial properties of objects. In this study we examined the extent to which spatial sensitivity based on color reflect the characteristic spatial structure of natural images. The role of color in this case is less certain. On the one hand, color is clearly a useful cue for spatial vision, and supports spatial discriminations that are nearly as fine as those supported by luminance (Krauskopf and Farell, 1991; Webster *et al.*, 1990). Yet on the other hand, it is clear that some aspects of spatial vision, such as visual acuity, are markedly degraded for chromatic contrast. Moreover, there are

a number of visual judgments that become impoverished at isoluminance, in part because the visual system fails to encode information that is potentially available in the chromatic content of the stimulus (Mullen and Kingdom, 1991). As noted in the Introduction, this may specifically occur in the case of blur, since color can support fine blur discriminations (Wuerger *et al.*, 2001) yet does not appear important for accommodation (Switkes *et al.*, 1990; Wolfe and Owens, 1981) or for judgments of blur in images that also vary in luminance (Wandell, 1995).

Regardless of their potential functional role, the present results suggest that the spatial properties of chromatic mechanisms are shaped by the chromatic spatial structure of images. The primary evidence for this is the changes we observed in perception and sensitivity to color patterns when observers adapted to images with altered spectra. Changes in perceived blur and threshold sensitivity varied in systematic ways as the adapting image spectra were progressively blurred, and the adaptation affected perceived blur selectively for luminance and chromatic contrast. Our results thus parallel the evidence for spatial- and color-selective adaptation reported previously from measures of grating adaptation (Bradley *et al.*, 1988). The qualitative similarity between the adaptation effects for luminance and color suggest that at least some aspects of the mechanisms encoding blur are functionally similar for luminance and chromatic contrast, as also suggested by the work of Wuerger *et al.* (2001).

Yet we also observed important differences in blur perception for color. First, observers were generally much less sensitive to the absolute blur in the chromatic patterns, and for the S stimuli tended to perceive the chromatic images as blurrier than their luminance counterparts. Secondly, we found little evidence for blur induction for the chromatic patterns, suggesting that color cannot be used to adjust for differences in relative blur across the visual field. The blur induction for luminance may be related to contrast gain control, in which the perceived contrast of a central region is reduced in the presence of a higher contrast surround (Chubb *et al.*, 1989). However, strong contrast induction is also observed at isoluminance, and these contrast changes show some selectivity for the spatial properties of the stimuli (D’Zmura and Singer, 1999). Thus it is surprising that it is specifically the feature of blur that fails at isoluminance in induction.

Again, these differences are unlikely to result simply from the lower acuity for color, and may reflect characteristics of spatial vision that are somehow unique to color. What are these characteristics? One possibility is that they reflect the representation of borders or edges in chromatic images. Chromatic patterns — and particularly S-cone mediated patterns — are poor at mediating the perception of well-defined spatial transitions (Boynton *et al.*, 1977). In fact, one common method for empirically defining isoluminance is to vary the relative luminance of two colors until they form a ‘minimally distinct border’ (Boynton, 1978). This does not reflect poor resolution alone, for color also exhibits an active filling-in process which may be held in check by luminance edges (Pinna *et al.*, 2001). For example, adding luminance contrast often facilitates the ability to discriminate a difference in color

between two regions (Eskew *et al.*, 1991; Montag, 1997; Switkes *et al.*, 1988), for without it the regions tend to 'bleed' together, as in the classic observation of the limited hues distinguishable in the spectrum (Smeulders *et al.*, 1994). This capture of color by luminance may underlie the failure to perceive chromatic blur when luminance components of the image are in focus (Wandell, 1995) and may account for the blurring of S-cone patterns induced by blurred luminance surrounds (Figs 6 and 7). Thus it may be the failure of color to support the perception of edges, rather than a failure to encode spatial structure, that accounts for the differences we observed.

Our results also highlight the different effects of adaptation on threshold sensitivity and suprathreshold blur perception. Observers were highly sensitive to blur in most luminance images and rapidly adapted to modest changes in the blur or sharpness of the adapting images. In contrast, the changes in detection thresholds showed a comparatively weak dependence on the specific adapting slope and strong sensitivity changes even to the $1/f$ patterns to which the visual system is normally exposed and thus presumably matched. Conversely, sensitivity and adaptation to blur in the chromatic patterns were weaker even though the threshold changes were substantially larger than for luminance. Thus it was generally not possible to predict the changes in blur perception from the ways in which adaptation did or did not alter the threshold contrast sensitivity function. This is consistent with our finding that the changes in the csf with adaptation cannot be accounted for by independent gain changes at different spatial scales. Instead, they appear to reflect an adjustment to the lowest spatial 'grain' in the image. The csf is routinely used to characterize the spatial sensitivity of the visual system for luminance and chromatic stimuli. However, our results show that the shape of the csf may change substantially under states of adaptation that are likely to characterize natural viewing conditions, even to the extent that the lowpass spatial sensitivity that is considered a hallmark of color vision can give way to a bandpass function more typical of luminance coding. Perhaps more importantly however, these differences in threshold sensitivity do not readily translate into differences in other perhaps more ecologically important spatial judgments, such as the perception of blur. This suggests that in relating visual coding to natural images it may be important to choose a dependent measure that is itself natural and functionally important.

Acknowledgement

This research was supported by National Eye Institute Grant EY-10834.

REFERENCES

- Atick, J. J. (1992). Could information theory provide an ecological theory of sensory processing? *Network* **3**, 213–251.
- Atick, J. J. and Redlich, A. N. (1992). What does the retina know about natural scenes? *Neural Computation* **4**, 196–210.

- Atick, J. J., Li, Z. and Redlich, A. N. (1992). Understanding retinal color coding from first principles, *Neural Computation* **4**, 559–572.
- Boynton, R. M. (1978). Ten years of research with the minimally distinct border, in: *Visual Psychophysics: Psychophysics and Physiology*, Armington, J. C., Krauskopf, J. and Wooton, B. (Eds). Academic Press, New York.
- Boynton, R. M., Hayhoe, M. M. and MacLeod, D. I. A. (1977). The gap effect: chromatic and achromatic visual discrimination as affected by field separation, *Optica Acta* **24**, 159–177.
- Bradley, A., Switkes, E. and De Valois, K. K. (1988). Orientation and spatial frequency selectivity of adaptation to color and luminance gratings, *Vision Research* **28**, 841–856.
- Burton, G. J. and Moorhead, I. R. (1987). Color and spatial structure in natural scenes, *Applied Optics* **26**, 157–170.
- Chubb, C., Sperling, G. and Solomon, J. A. (1989). Texture interactions determine perceived contrast, *Proc. Nat. Acad. Sci. USA* **86**, 9631–9635.
- De Valois, K. K. (2003). The role of color in spatial vision, in: *The Visual Neurosciences*, Chalupa, L. M. and Werner, J. S. (Eds), Vol. 2, pp. 924–935. MIT Press, Cambridge.
- D’Zmura, M. and Singer, B. (1999). Contrast gain control, in: *Color Vision: From Genes to Perception*, Sharpe, L. T. and Gegenfurtner, K. R. (Eds), pp. 369–385. Cambridge University Press, Cambridge.
- Eskew, R. T., Stromeyer, C. F., III., Picotte, C. J. and Kronauer, R. E. (1991). Detection uncertainty and the facilitation of chromatic detection by luminance contours, *J. Optic. Soc. Amer. A* **8**, 394–403.
- Field, D. J. (1987). Relations between the statistics of natural images and the response properties of cortical cells, *J. Optic. Soc. Amer. A* **4**, 2379–2394.
- Field, D. and Brady, N. (1997). Visual sensitivity, blur, and the sources of variability in the amplitude spectra of natural images, *Vision Research* **37**, 3367–3383.
- Galvin, S. J., O’Shea, R. P., Squire, A. M. and Govan, D. G. (1997). Sharpness overconstancy in peripheral vision, *Vision Research* **37**, 2035–2039.
- Klein, S. and Stromeyer, C. F., III. (1980). On inhibition between spatial frequency channels: adaptation to complex gratings, *Vision Research* **20**, 459–466.
- Krauskopf, J. and Farell, B. (1991). Vernier acuity: Effects of chromatic content, blur and contrast, *Vision Research* **31**, 735–749.
- Krauskopf, J., Williams, D. R. and Heeley, D. W. (1982). Cardinal directions of color space, *Vision Research* **22**, 1123–1131.
- Lythgoe, J. N. (1979). *The Ecology of Vision*. Clarendon Press, Oxford.
- MacLeod, D. I. A. and Boynton, R. M. (1979). Chromaticity diagram showing cone excitation by stimuli of equal luminance, *J. Optic. Soc. Amer.* **69**, 1183–1186.
- MacLeod, D. I. A. and von der Twer, T. (2003). The pleistochrome: optimal opponent codes for natural colours, in: *Colour Perception: Mind and the Physical World*, Mausfeld, R. and Heyer, D. (Eds), pp. 155–184. Oxford University Press, Oxford.
- Montag, E. D. (1997). Influence of boundary information on the perception of color, *J. Optic. Soc. Amer. A* **14**, 997–1006.
- Mullen, K. T. (1985). The contrast sensitivity of human colour vision to red-green and blue-yellow chromatic gratings, *J. Physiol.* **359**, 381–409.
- Mullen, K. T. and Kingdom, F. A. A. (1991). Colour contrast in form perception, in: *Vision and Visual Dysfunction 6: The Perception of Colour*, Gouras, P. (Ed.), pp. 198–217. Macmillan, London.
- Nachmias, J., Sansbury, R., Vassilev, A. and Weber, A. (1973). Adaptation to square-wave gratings: in search of the elusive third harmonic, *Vision Research* **13**, 1335–1342.
- Párraga, C. A., Brelstaff, G., Troscianko, T. and Moorehead, I. R. (1998). Color and luminance information in natural scenes, *J. Optic. Soc. Amer. A* **15**, 563–569.
- Párraga, C. A., Troscianko, T. and Tolhurst, D. J. (2002). Spatiochromatic properties of natural images and human vision, *Current Biology* **12**, 483–487.

- Pinna, B., Brelstaff, G. and Spillmann, L. (2001). Surface color from boundaries: a new 'watercolor' illusion, *Vision Research* **41**, 2669–2776.
- Ruderman, D. L., Cronin, T. W. and Chiao, C.-C. (1998). Statistics of cone responses to natural images: implications for visual coding, *J. Optic. Soc. Amer. A* **15**, 2036–2045.
- Simoncelli, E. P. and Olshausen, B. A. (2001). Natural image statistics and neural representation, *Ann. Rev. Neurosci.* **24**, 1193–1216.
- Smeulders, N., Campbell, F. W. and Andrews, P. R. (1994). The role of delineation and spatial frequency in the perception of colours in the spectrum, *Vision Research* **34**, 927–936.
- Snowden, R. J. and Hammett, S. T. (1992). Subtractive and divisive adaptation in the human visual system, *Nature* **355**, 248–250.
- Srinivasan, M. V., Laughlin, S. B. and Dubs, A. (1982). Predictive coding: a fresh view of inhibition in the retina, *Proc. Roy. Soc. London B* **216**, 427–459.
- Switkes, E., Bradley, A. and De Valois, K. K. (1988). Contrast dependence and mechanisms of masking interactions among chromatic and luminance gratings, *J. Optic. Soc. Amer. A* **5**, 1149–1162.
- Switkes, E., Bradley, A. and Schor, C. (1990). Readily visible changes in color contrast are insufficient to stimulate accommodation, *Vision Research* **30**, 1367–1376.
- Tadmor, Y. and Tolhurst, D. J. (1994). Discrimination of changes in the second-order statistics of natural and synthetic images, *Vision Research* **34**, 541–554.
- Tolhurst, D. J. (1972). Adaptation to square-wave gratings: inhibition between spatial frequency channels in the human visual system, *J. Physiol.* **226**, 231–248.
- Tolhurst, D. J. and Barfield, L. P. (1978). Interactions between spatial frequency channels, *Vision Research* **18**, 951–958.
- Wachtler, T., Lee, T.-W. and Sejnowski, T. J. (2001). Chromatic structure of natural scenes, *J. Optic. Soc. Amer. A* **18**, 65–77.
- Wandell, B. A. (1995). *Foundations of Vision*. Sinauer, Sunderland, MA.
- Webster, M. A. and Miyahara, E. (1997). Contrast adaptation and the spatial structure of natural images, *J. Optic. Soc. Amer. A* **14**, 2355–2366.
- Webster, M. A. and Mollon, J. D. (1997). Adaptation and the color statistics of natural images, *Vision Research* **37**, 3283–3298.
- Webster, M. A., De Valois, K. K. and Switkes, E. (1990). Orientation and spatial-frequency discrimination for luminance and chromatic gratings, *J. Optic. Soc. Amer. A* **7**, 1034–1049.
- Webster, S. M., Webster, M. A., Taylor, J., Jaikumar, J. and Verma, R. (2001). Simultaneous blur contrast, *Proc. SPIE* **4299**, 414–422.
- Webster, M. A., Georgeson, M. A. and Webster, S. M. (2002). Neural adjustments to image blur, *Nature Neurosci.* **5**, 839–840.
- Williams, D. R. and Collier, R. J. (1983). Consequences of spatial sampling by a human photoreceptor mosaic, *Science* **221**, 385–387.
- Wolfe, J. M. and Owens, D. A. (1981). Is accommodation colorblind? Focusing chromatic contours, *Perception* **10**, 53–62.
- Wuerger, S. M., Owens, H. and Westland, S. (2001). Blur tolerance for luminance and chromatic stimuli, *J. Optic. Soc. Amer. A* **18**, 1231–1239.