

Contrast adaptation and the spatial structure of natural images

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Natural images have a characteristic spatial structure, with amplitude spectra that decrease with frequency roughly as $1/f$. We have examined how contrast (pattern-selective) adaptation to this structure influences the spatial sensitivity of the visual system. Contrast thresholds and suprathreshold contrast and frequency matches were measured after adaptation to random samples from an ensemble of images of outdoor scenes or of synthetic images formed by filtering the amplitude spectra of noise over a range of spectral slopes. Adaptation selectively reduced sensitivity at low-to-medium frequencies, biasing contrast sensitivity toward higher frequencies. The pattern of aftereffects was similar for different natural image ensembles but varied with large changes in the slope of the noise spectra. Our results suggest that adaptation to the spatial structure in natural scenes may exert strong and selective influences on perception that are important in characterizing the normal operating states of the visual system. © 1997 Optical Society of America [S0740-3232(97)02009-7]

1. INTRODUCTION

Visual perception is adjusted continuously by adaptation processes that alter sensitivity to match the properties of the ambient stimulus. Retinal mechanisms of light adaptation adjust sensitivity to the average luminance and color in the scene, whereas cortical mechanisms of contrast (pattern-selective) adaptation adjust instead for the patterns of spatial, temporal, and chromatic variations relative to the average.¹ Exposure to adapting patterns induces a variety of related aftereffects. Thresholds for detecting similar patterns are elevated,^{2,3} the apparent contrast of suprathreshold patterns appears lower,⁴⁻⁶ and test stimuli may be biased to appear less similar to the adapting pattern (as in tilt,⁷ motion,⁸ or color-contrast⁶ aftereffects). These adaptation effects have been attributed either to independent response changes in channels tuned to the adapting stimulus,⁹ or to adaptation-dependent interactions between channels.^{10,11} In either case, the aftereffects reflect losses in sensitivity that are selective for the structure of the adapting pattern. Even brief exposures to an adapting stimulus are sufficient to induce strong aftereffects, which suggests that contrast adaptation plays a fundamental role in regulating our perception.

In this study we have examined how the properties of our form perception might be influenced by adaptation to the spatial structure of the natural visual environment. The intensities at different locations within natural images exhibit strong correlations. Several studies¹²⁻¹⁷ have shown that this spatial redundancy has a characteristic form: The amplitude spectra of natural images tend to fall off with frequency roughly as $1/f$, so that on a log-amplitude versus log-frequency plot the spectra tend to follow a straight line with a slope (α) near -1 . Similar amplitude spectra have been found for a diverse array of images of both natural and carpentered environments. This characteristic signature of natural images is often

assumed to reflect in real-world scenes the preponderance of edges (which have $1/f$ spectra). However, Ruderman¹⁸ has recently argued that the scaling property of natural images may instead arise because real-world scenes are typically composed of objects present at many different scales, with strong correlations within objects and weaker correlations between objects.

We asked whether the characteristic spatial structure found in natural images might lead to characteristic states of spatial contrast adaptation. One of the cardinal features of pattern adaptation is that it appears selective for the spatial-frequency content of the adapting stimulus. Thus adaptation to a single sine-wave grating elevates thresholds most for test gratings with similar frequencies and has little effect on test stimuli far removed from the adapting frequency.² Studies of spatial-frequency adaptation are one of the principal sources of psychophysical evidence for multiscale models of spatial vision based on multiple channels that are each responsive to, and adapted by, the variations at different spatial scales in the image.¹⁹⁻²¹ The ubiquitous low-frequency bias in natural scenes might therefore be expected to adapt primarily the subset of channels sensitive to lower frequencies and consequently to maintain the visual system in a state of reduced sensitivity at lower frequencies.

However, predicting how the visual system might adapt to natural stimuli is complicated for two reasons. First, the effective adapting stimulus will depend not only on the physical contrast in the image but also on the observer's sensitivity to different spatial scales. The spatial contrast sensitivity function (CSF) is typically band-pass, so that both low- and high-frequency components in the stimulus are attenuated. Low-frequency attenuation arises from lateral inhibition in the retina, which may in fact be designed to remove the spatial correlations in the image.²²⁻²⁴ Retinal filtering alone may therefore compensate for much of the low-frequency bias in images, so

that the neural image reaching the cortex (the probable locus of contrast adaptation) is effectively whitened. Moreover, the bandwidth of spatial-frequency channels and individual striate cells increases with frequency (remaining approximately constant in octaves). This increasing bandwidth may be designed to compensate for the falloff in stimulus amplitude with frequency, so that for natural scenes the total power in each channel remains approximately constant (though again the effective stimulus for cortical cells will depend on any visual filtering that occurs prior to the cortex).¹⁴

A second problem in predicting adaptation to natural images is that most previous studies have examined contrast adaptation effects only with relatively simple spatial patterns (e.g., gratings). It has proved difficult to predict, from the results for single gratings, the adaptation effects that occur even for simple combinations of gratings (e.g., for compound gratings composed of two different frequencies or orientations). For example, adaptation to a square-wave grating (whose amplitude spectrum follows $1/f$) may produce less adaptation at the third harmonic than when the $3f$ component is presented in isolation.^{25,26} Such results have suggested that channels tuned to different frequencies or orientations may mutually inhibit one another and thus lower the effective adapting contrast,²⁵⁻²⁷ though alternative accounts have been proposed.²⁸ In any case, these results suggest that in complex stimuli observers may not adapt independently to the energy at different spatial scales. Relative to the component contrasts, the adaptation effects for complex patterns like natural images might be substantially weakened, and, in the extreme, patterns with very complicated or unbiased spectra (e.g., random dot patterns) may prove largely ineffective.²⁹ One goal in our work was therefore to assess the actual magnitude and form of adaptation effects for natural images.

A second goal in our study was to examine how specific the sensitivity changes might be to the specific statistical structure of the images. Not all scenes have amplitude spectra that follow f^{-1} . Instead, the slopes for different images may vary between roughly -0.5 and -1.5 (e.g., Refs. 16 and 17). We asked whether this range is large or narrow with regard to visual adaptation. Specifically, we examined whether for contrast adaptation the pattern of sensitivity losses depends critically on the spectral slope of the adapting stimuli. Our results suggest that adaptation to natural scenes may induce pronounced and selective changes in sensitivity at lower frequencies and that the pattern of these sensitivity changes does not vary greatly for different image ensembles or within the range of slopes reported for natural amplitude spectra. Adaptation to the natural visual environment may therefore tend to maintain the visual system in characteristic operating states that may profoundly influence our form perception.

2. METHODS

Contrast adaptation effects were measured for two types of adapting stimuli: outdoor scenes that lacked obvious human influence, and synthetic images derived from filtered noise. In both cases we were interested in the av-

erage aftereffects induced by ensembles of scenes rather than in effects that might reflect unique properties of individual images. Thus the adaptation was always to a group of images, and aftereffects were compared across groups. We measured how adaptation to the images affected both detection thresholds and suprathreshold matches for test frequencies ranging from 0.25 to 16 cycles per degree (c/deg).

A. Apparatus and Calibration

Stimuli were presented on a Sony Trinitron Multiscan 20se monitor controlled by a Cambridge Research Systems VSG (visual stimulus generator) graphics board. The adapting images were presented through a framestore with 8-bit resolution. Test stimuli were horizontal sine-wave gratings and were presented through a waveform generator windowed by the framestore. Grating contrast could be specified with a resolution of 14 bits. Outputs of the framestore and the waveform generator were linearized through separate gamma corrections and were closely matched for mean luminance (12 cd/m^2 for the natural images or 30 cd/m^2 for the noise images) and chromaticity (equivalent to Illuminant C). The calibrations were based on measurements with a PhotoResearch PR650 spectroradiometer.

B. Adapting Stimuli

1. Natural Images

Outdoor scenes were recorded with a Kodak DCS420IR monochrome digital camera (with added IR filter). The images were taken in the Sierra mountains near Reno, Nevada, at the Whittell Forest and Wildlife Area (a field station maintained by the University of Nevada) and at Tahoe Meadows. Rather than attempt a representative sampling of scenes, we tested whether the adaptation effects depended on the specific adapting ensemble by comparing three classes of images that differed in subject matter and viewing distance. The image groups were (a) meadows: distant views of meadows and mountains, often with sky visible; (b) forest: images taken within a pine forest and dominated by trees, with viewing distances ranging from a few to several meters; and (c) close-ups: images of rocks, bark, leaves, and ground cover, taken at a distance of between 1 and 2 m. Each of the 3 groups consisted of 16 different images. Figure 1 shows examples from each image group.

Images acquired by the camera had a resolution of 1012×1524 pixels and 256 gray levels. Each pixel subtended 1 arcmin^2 . Adapting stimuli were taken from the central 763×763 pixels, corresponding to a visual angle of 12.7 deg in width and height. Pixel luminances were linearized by an empirically defined gamma correction and then were averaged over 3×3 blocks to form a 256×256 pixel image. The reduced resolution was necessary to store and display multiple images during the adaptation sequence. All the images were adjusted to have the same mean pixel value (51, equal to 12 cd/m^2). The low mean luminance was necessary because pixel distributions for natural images are strongly skewed toward luminances higher than the mean.³⁰ The mean was chosen to allow a maximum luminance on our monitor of

60 cd/m² (for 255). Only images with fewer than 0.5% truncated pixels (both before and after adjustment of the mean luminance) were included as adapting stimuli.

For each of the resulting 48 images we calculated the rms contrast (defined by the standard deviation of all the pixel intensities relative to the mean image intensity) and the slope (α) of the amplitude spectrum (obtained from a line fitted to log amplitude versus log frequency after averaging of the amplitude at each frequency over all the orientations). Values for both parameters are plotted for each image in Fig. 2. The rms contrast averaged 0.784,

while the mean α value was -1.13 . Both the mean and the range of the values are comparable with previous estimates. The mean values for the three different image groups (i.e., meadows, forest, and close-ups) are listed in Table 1. While each group appears characteristic of previous estimates, differences across the three groups in both rms contrast and α values were found in Kruskal-Wallis tests to be significant ($\chi^2 = 15.36$, $df = 2$, $p < 0.001$ for rms contrast; and $\chi^2 = 11.67$, $df = 2$, $p < 0.003$ for α). Moreover, it is evident from Fig. 2 that the variance in the slopes is substantially greater for

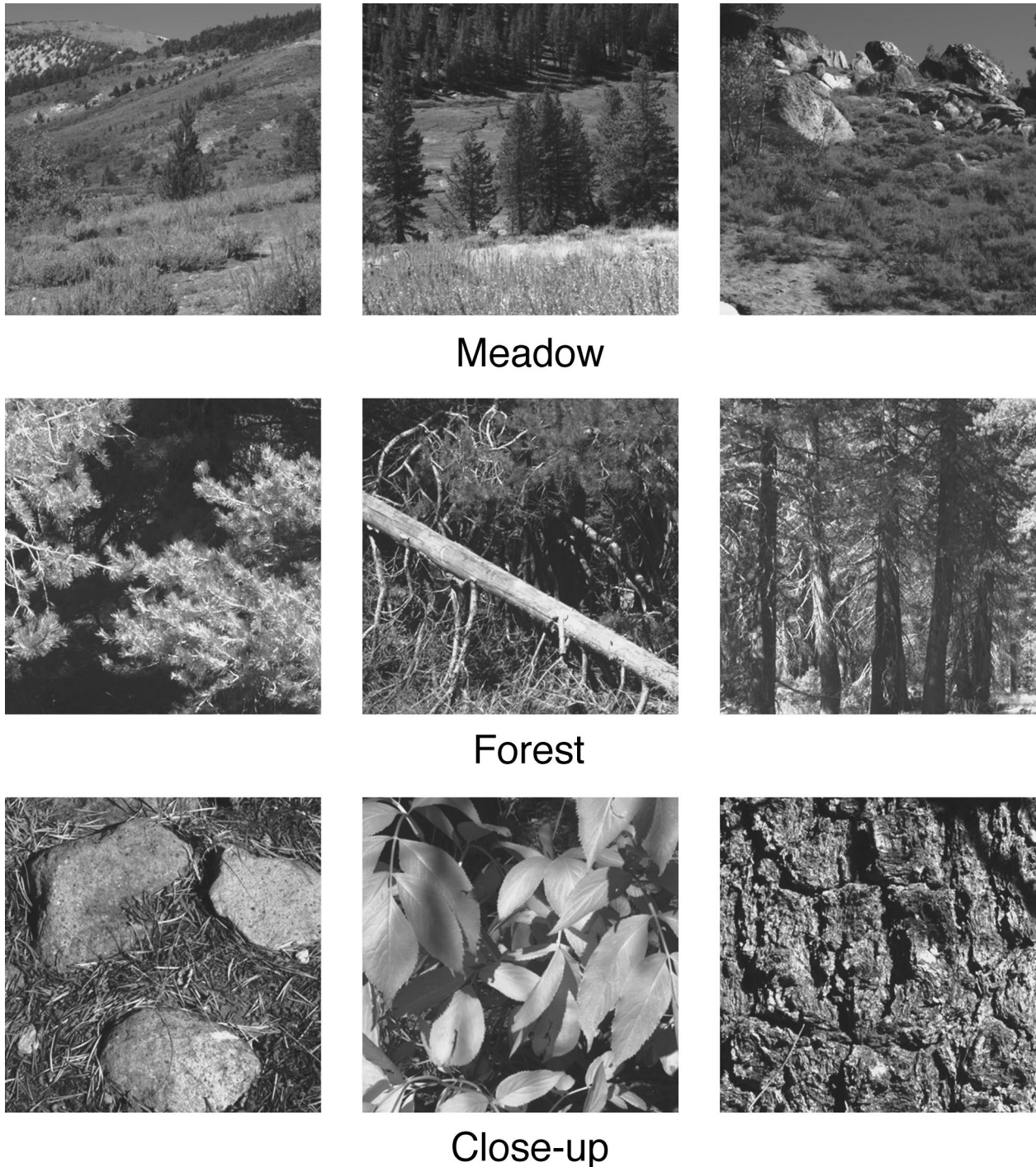


Fig. 1. Examples of the natural image stimuli for the three image groups of meadows, forests, and close-ups.

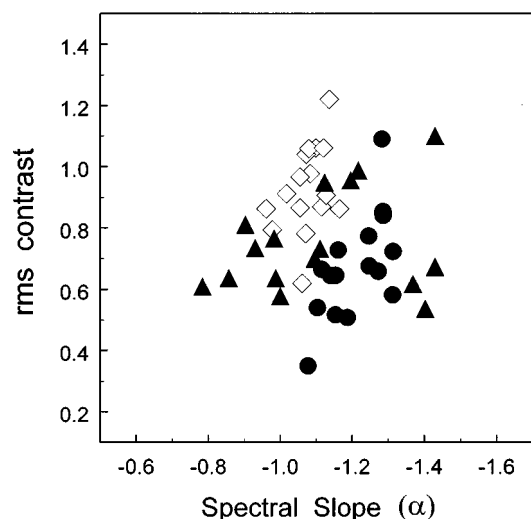


Fig. 2. Scatterplot of the spectral slope (α) and the rms contrast of the natural image stimuli. The circles are for images of meadows, the diamonds are for forest, and the triangles are for close-ups.

Table 1. Spectral Slope (α) and the Rms Contrast of the Natural Images

Group	Spectral Slope (α)		Rms Contrast	
	Mean	SD ^a	Mean	SD
Meadows	-1.209	0.080	0.675	0.170
Forest	-1.075	0.055	0.928	0.143
Close-ups	-1.114	0.211	0.751	0.165

^aSD, standard deviation.

close-ups, which in visual inspection appeared to include a much more heterogeneous class of images.

2. Filtered Noise

As a second set of adapting stimuli, we created synthetic images that were constructed to vary over a wide range of α values. Similar stimuli have been used previously by Knill *et al.*³¹ and by Tadmor and Tolhurst.³² 256 \times 256 pixel white-noise images were generated from random normal deviates. Each image was defined by a different sequence. The image amplitude spectrum was multiplied by f^α , with the value of α ranging from 0 to -2.5 in 0.5 steps (Fig. 3). All the filtered images were adjusted to a mean value of 128 (corresponding to 30 cd/m²) and were scaled to have a rms contrast of 0.35 (near the limit for avoiding significant pixel truncation). Only images with fewer than 0.5% truncated pixels were included. For each α value 32 images were created to form 2 different adapting sets, each with 16 images. Examples of the filtered noise stimuli are shown in Fig. 4.

C. Procedure

1. Contrast Thresholds

Stimuli were presented in a square 5.6-deg field (corresponding to 428 pixels) in the center of the display. Narrow black borders demarcated the field from a background (8 \times 10.5 deg) of the same mean luminance. Filling the display field with an adapting image required magnifying each image twofold (from 256 to 512 pixels),

though only a 428-pixel block could be displayed at any one time. The position of the displayed block within the image was chosen at random for each presentation. The resulting image contained frequencies ranging from 0.149 to 19.1 c/deg and, because of the zooming, had a minimum element size of 2 \times 2 pixels. This quantization was not visible from the subject's viewing distance. Test gratings were presented in cosine phase with the center of the field and were weighted vertically by a fixed Gaussian envelope with a SD of 1.6 deg.

The observer viewed the display binocularly in an otherwise dark room from a distance of 200 cm. Each run began with an initial 5-min period of adaptation. During adaptation the observer viewed a rapid and random sequence of 16 images drawn from one of the three sets of natural images, from a grating of either 0.25 or 2 c/deg with randomized phase, or from a set of filtered noise images with a common α value. The displayed image was resampled at random every 300 ms. This simulates the pattern of local stimulation that might arise from rapid and random eye movements within the image ensemble. The high resampling rate was chosen in an attempt to minimize local light adaptation to individual images. After the initial 5-min adaptation, the field returned to zero contrast for 500 ms, and then a test grating was presented for 700 ms, with contrast ramped on and off during the first and the last 150 ms by a temporal Gaussian with a SD of 50 ms. After the test a zero-contrast field was

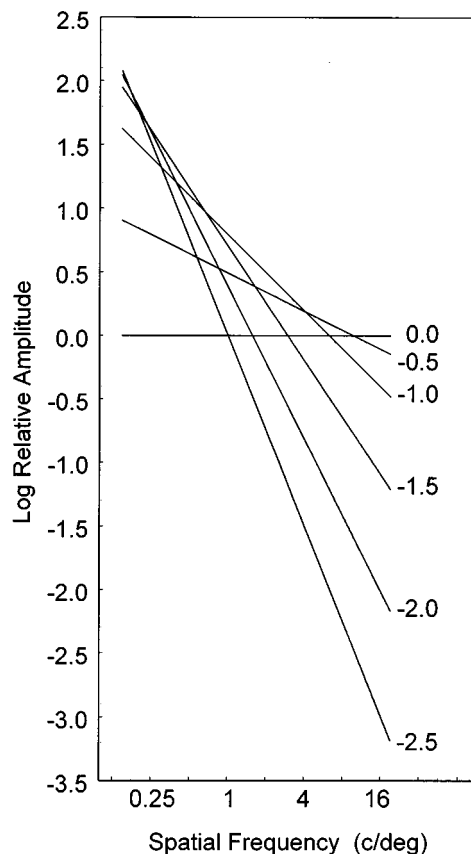


Fig. 3. Relative amplitude spectra for filtering the noise images. Slopes (α) of the spectra are indicated to the right. Images with different slopes had the same rms contrast (0.35) and thus the same total power.

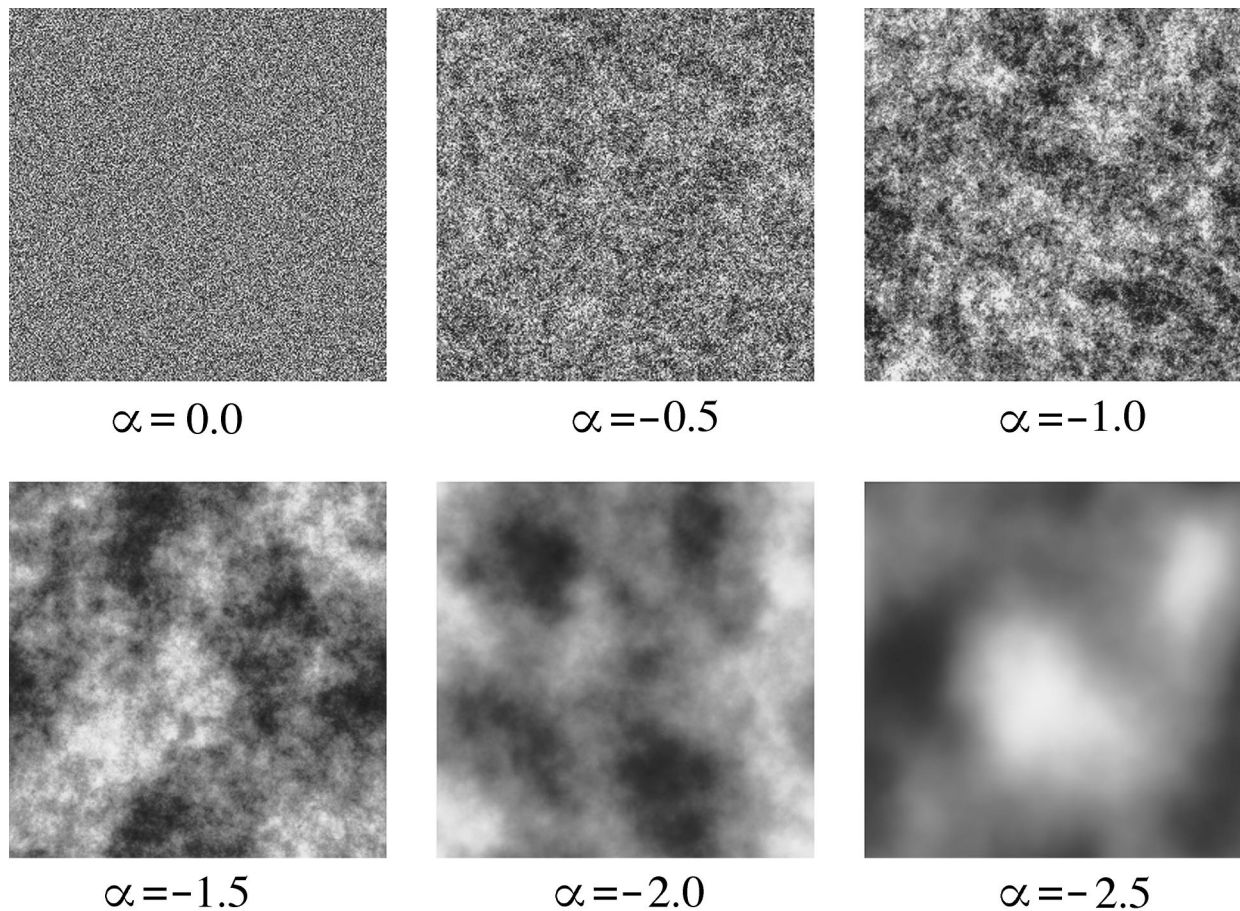


Fig. 4. Examples of the filtered noise stimuli. The slopes of the image amplitude spectra (α) vary from 0 to -2.5 .

presented for 500 ms, and then a 6-s period of readaptation was given. The sequence of tests interleaved with 6-s readaptation continued throughout the run. The observer set thresholds by using a button box to adjust the contrast of the test grating. During a run thresholds were set once for each test frequency, in counterbalanced order. The postadapt results presented are each based on the average of six settings per frequency. Each session also included two initial runs in which preadapt thresholds for each frequency were measured. For these runs the adapting field remained at zero contrast, but the testing sequence remained otherwise identical to postadapt trials. The results presented for the preadapt contrast sensitivity are based on the mean of 10 or 12 runs averaged across the different sessions.

2. Suprathreshold Matches

To examine how adaptation affected the appearance of suprathreshold gratings, the adapt and the test stimuli were confined to a 3.9-deg vertical \times 6.7-deg horizontal field above a fixation cross. The observer adapted to a 5-min random sequence of images. (The 6.7-deg field equaled the full width of the zoomed image, and thus in this case only the vertical placement of an individual image was free to vary.) Test gratings and the adapting sequence followed the same time course as in the threshold measures. The gratings were windowed in space only by the adapting field. A matching grating was presented si-

multaneously with the test, but in a neutral (zero-contrast) field placed symmetrically below fixation. The observer used separate pairs of buttons to adjust the matching grating to equate both the perceived contrast of the test and matching stimuli and their perceived spatial frequency. Individual frequencies were again run in counterbalanced order, with an average of six settings taken for each frequency.

D. Observers

Observers included the two authors (MW and EM) and a paid, naïve observer (VR). The observers had normal (MW) or corrected-to-normal (EM and VR) visual acuity.

3. RESULTS

A. Natural Images

1. Contrast Thresholds

Figure 5 shows how adaptation to the different natural image groups affected threshold contrast sensitivity. Unfilled symbols plot the CSF for neutral (zero-contrast) adaptation, while filled symbols in each panel plot sensitivity after adaptation to each ensemble. For neutral adaptation the CSF exhibits characteristic bandpass tuning, with peak sensitivity near 2 c/deg.¹⁹ Adaptation produced large losses in sensitivity at low spatial frequencies but had little effect at higher frequencies, in qualitative

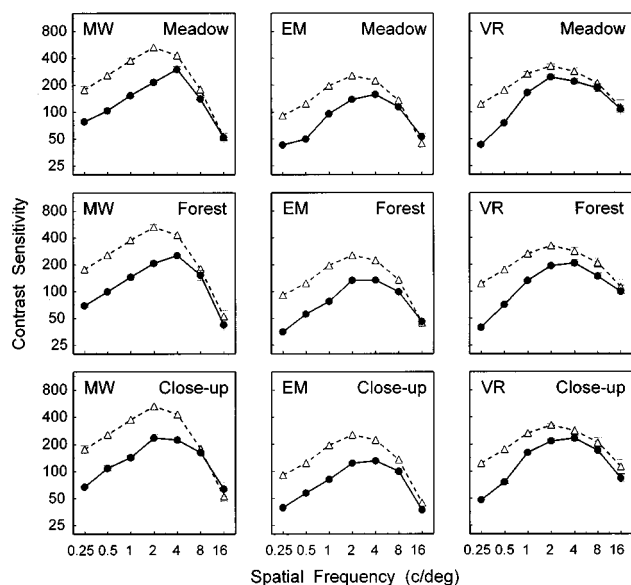


Fig. 5. CSF's before and after adaptation to the three groups of natural images for the three observers. The triangles show sensitivity for neutral adaptation. The circles show the contrast sensitivities following adaptation to the natural image sets. The error bars are the standard errors of the means.

agreement with the low-frequency bias of the adapting stimulus. The selective losses in low-frequency sensitivity alter the shape of the CSF by shifting peak sensitivity toward higher frequencies and by slightly decreasing the bandwidth of the tuning. [From these results one cannot rule out the possibility that measurable adaptation might have occurred at 16 c/deg had our adapting stimuli extended to frequencies higher than 19 c/deg, since this falls far short of the bandwidth for a channel tuned to 16 c/deg. However, a similar limitation occurs at the lowest frequency, where the sensitivity losses are largest (for tests of 0.25 c/deg versus a lowest image frequency of 0.15 c/deg). Moreover, in subsequent control runs with higher-resolution images (38 c/deg) there was again little effect on the thresholds for the 16-c/deg tests.]

The threshold changes for the three different image groups were similar in both magnitude and form. This is illustrated in Fig. 6, which plots the change in contrast sensitivity for each adapting condition. The consistency in adaptation across the three groups is consistent with the general similarities in their average spatial structure (Fig. 2). However, the threshold changes are very different from the changes produced by adaptation to unnatural stimuli, such as a single grating (shown in Fig. 7 and by the unfilled symbols in Fig. 6). For this comparison observers adapted to horizontal sine-wave gratings of 0.25 or 2.0 c/deg, with Michelson contrasts of 0.5 (rms contrast, 0.35). As with the natural images, the phase was randomized every 300 ms. Adaptation to the 2-c/deg grating altered sensitivity most at the adapting frequency, with little threshold change at either higher or lower frequencies.² Adaptation to the 0.25-c/deg grating produced the largest threshold change at 0.25 c/deg but exhibited sharper frequency tuning than the adaptation for natural images. (See Fig. 6. This tuning difference is consistent with the results for the different noise im-

ages, as shown in Fig. 10 below.) Thus the sensitivity losses observed for the natural images do reflect selectivity for specific properties of the images. (In contrast to our results, early studies of grating adaptation suggested that low adapting frequencies might induce the largest threshold changes at higher test frequencies, implying

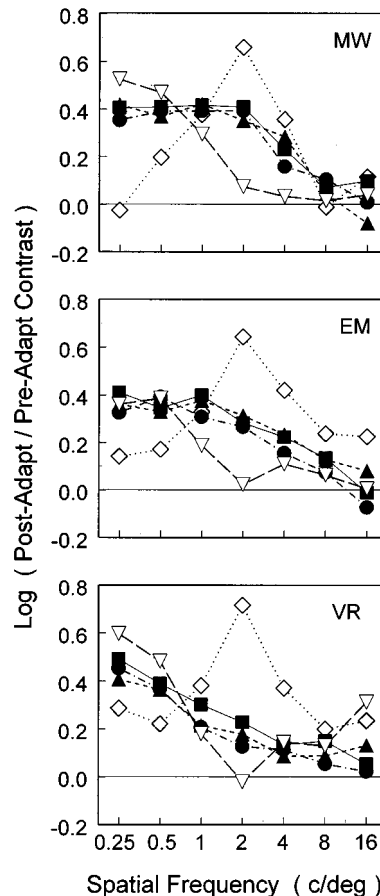


Fig. 6. Change in contrast sensitivity after adaptation to each image ensemble. Each curve plots the log difference between the neutral-adaptation and the image-adaptation CSF. Circles, meadows; squares, forest; filled triangles, close-ups; diamonds, 2-c/deg gratings; open triangles, 0.25-c/deg gratings.

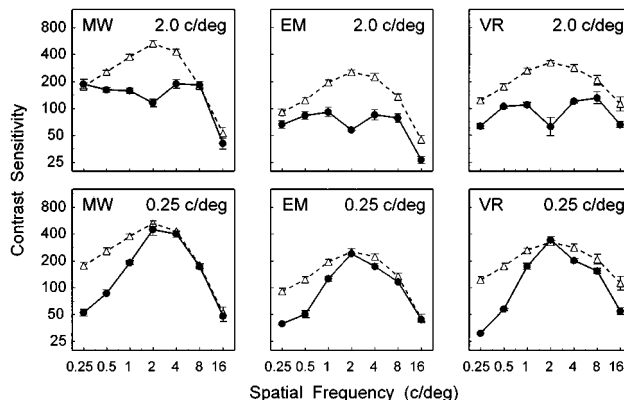


Fig. 7. CSF's before and after adaptation to 2- or 0.25-c/deg gratings for the three observers. The triangles show the sensitivity for neutral adaptation. The circles show the contrast sensitivities following adaptation to the gratings. The error bars are the standard errors of the means.

the presence of a “lowest adaptable channel.”^{2,33} However, more recent studies have demonstrated selective adaptation for frequencies roughly as low³⁴ or lower³⁵ than those we examined.)

2. Suprathreshold Matches

Figure 8 shows that the adaptation induced similar losses in the sensitivity to suprathreshold patterns. The figures plot for each adapting set the changes in perceived contrast of test frequencies that had a Michelson contrast of 0.05. Again the adaptation was characterized by large and selective losses in sensitivity at low frequencies, with very similar results across the three image sets, while very different results for the 2-c/deg grating adaptation (which are again largest at the adapting frequency). For these test gratings the contrast for neutral adaptation was 12–20 times the threshold contrast for medium spatial frequencies but only 2–3 times threshold for the 16-c/deg grating. We chose relatively low contrasts because adaptation tends to have only weak effects on high-contrast test patterns.^{5,6} However, similar results were obtained in pilot measurements (not shown) by use of a test contrast of 0.10.

Our results reveal that exposure to natural images can lead to pronounced sensitivity losses at low frequencies, with the magnitude of the bias changing gradually but progressively across much of the several-octave range of frequencies that we examined. This pattern of sensitivity loss predicts a further possible aftereffect of the adaptation. Exposure to a single spatial frequency not only alters the perceived contrast of gratings but can also alter the perceived size of similar frequencies so that they appear shifted away from the adapting frequency.³⁶ A conventional account of such aftereffects is that perceived size depends on the distribution of activity across multiple channels, each being responsive to a narrow but overlapping range of frequencies.⁹ Adaptation reduces sensitivity in the subset of channels that respond to the adapting frequency, thus skewing the distribution of responses to test stimuli away from the distribution to the adapt stimulus.

We therefore examined whether, for natural image adaptation, the systematic skewing of sensitivity toward higher frequencies might bias the perceived size of test stimuli toward higher frequencies. To test this observers matched not only the perceived contrast of the test gratings but also their perceived frequency. The resulting matches are plotted in Fig. 9. For the lowest frequency (0.25 c/deg), we found for our conditions that it was difficult to judge perceived frequency and that (accurate) settings instead appeared to be based on perceived symmetry in the display. Measurements at the lowest frequency were therefore excluded. For observer MW adaptation to each natural image set induced consistent biases in low to medium frequencies, increasing perceived frequency by 10–20%. This bias is comparable in magnitude with the aftereffects induced by single adapting gratings.³⁶ The shift toward high frequencies is again consistent with the pattern of the contrast sensitivity change induced by the adaptation. However, these shifts are less evident in EM’s results. When adaptation was instead to the 2-c/deg grating, both observers appeared to

show a shift toward high frequencies at 4 c/deg but surprisingly did not show the converse effect at 1 c/deg. We do not know the basis for this asymmetry. (Blakemore and Sutton³⁶ found similar but opposite shifts above and below the adapting frequency, with no bias in test grat-

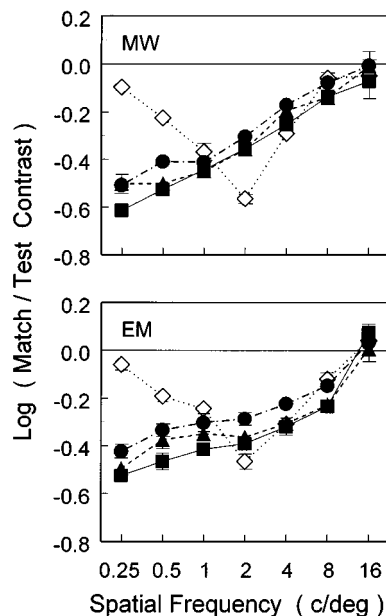


Fig. 8. Results of contrast matching for suprathreshold gratings (Michelson contrast of 0.05) for the two observers. The changes in perceived contrast of the grating are plotted as a function of the spatial frequency of the test grating. The diamonds show the changes after adaptation to the 2-c/deg grating; circles, meadows; squares, forest, and triangles, close-ups. The error bars are the standard errors of the means.

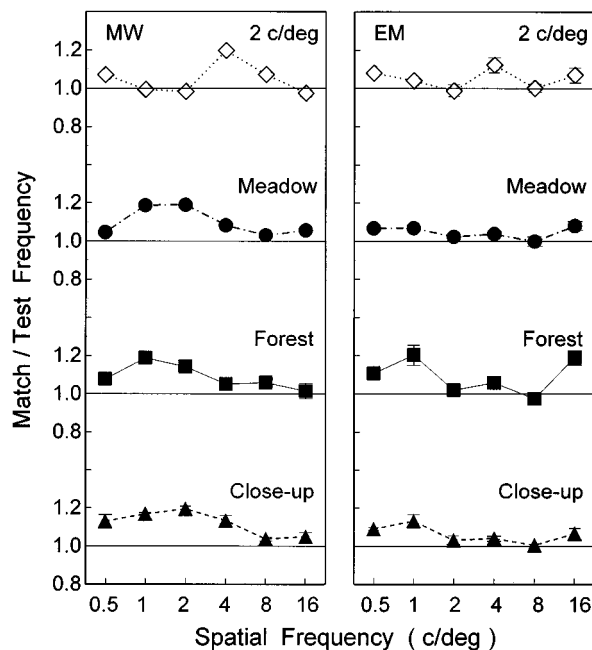


Fig. 9. Results of spatial-frequency matching for the suprathreshold gratings (Michelson contrast of 0.05) for the two observers. The changes in perceived spatial frequency of the grating are plotted as a function of the spatial frequency of the test grating. The error bars are the standard errors of the means.

ings that differed from the adapting grating by roughly 2 or more octaves. However, they did not examine adapting frequencies lower than 3.5 c/deg.)

B. Filtered Noise

1. Contrast Thresholds

The natural image sets that we examined appear to have a common property that leads to similar adaptation effects. The pattern of aftereffects is consistent with the notion that this property is the characteristic amplitude spectra of the images. But how selective are the sensitivity changes to the specific image spectra? As we have noted, the spectra for individual images have been found to vary over a range of slopes from roughly -0.5 to -1.5 . We therefore asked whether differences of this magnitude are sufficient to yield significantly different adaptation states. This question is of interest not only for assessing how different natural contexts might vary the observer's adaptation but also for examining more generally whether the amplitude spectrum is in fact a critical property underlying the adaptation. To test this we used as adaptation stimuli synthetic noise images that all shared the same mean luminance (30 cd/m^2) and rms contrast (0.35) but whose spectra were filtered over a wide range of slopes.

Figure 10 shows the CSF's measured before or after adaptation to noise images defined by slopes (α) varying from 0 (white noise) to -2.5 (highly blurred). In each case the postadapt thresholds were measured for two different image sets (16 images each). Thresholds for the two sets were similar and therefore have been averaged in the figure. For both observers the change in α leads to systematic changes in the form of the sensitivity losses. White noise produced only a weak and nonselective change in thresholds. However, as the spectra are biased toward lower frequencies, the adaptation begins to selectively reduce sensitivity at low to medium frequencies, and the range of the aftereffects shifts progressively toward the lower frequencies as the filtering increases [producing at medium frequencies the largest sensitivity changes for intermediate α values, a trend that roughly mirrors the trends in the adapting spectra (Fig. 3)]. As a result, the postadapt CSF for natural spectra (e.g., $\alpha = -1$) differs substantially from the CSF's for unnatural spectra (e.g., $\alpha = 0, -2.5$). Moreover, for the 1/f adapting images the spatial selectivity of the changes in the CSF appear qualitatively similar to the changes measured for the actual natural images (though in the present case the adaptation effects are weaker and the CSF peaks at slightly higher frequencies, consistent with the lower adapt contrast and higher mean luminance in the present experiment). However, while the amplitude spectra clearly affect the form of the adaptation, the selectivity for the specific spectral slope appears weak. For both observers the -0.5 spectra produced weaker sensitivity changes than more strongly biased spectra, but the differences between the CSF's when the adapting α values ranged from -1 to -2 are not compelling. Thus our results suggest that the small differences in average α that might be encountered in different natural contexts are unlikely to lead to large differences in the spatial dependence of the adaptation.

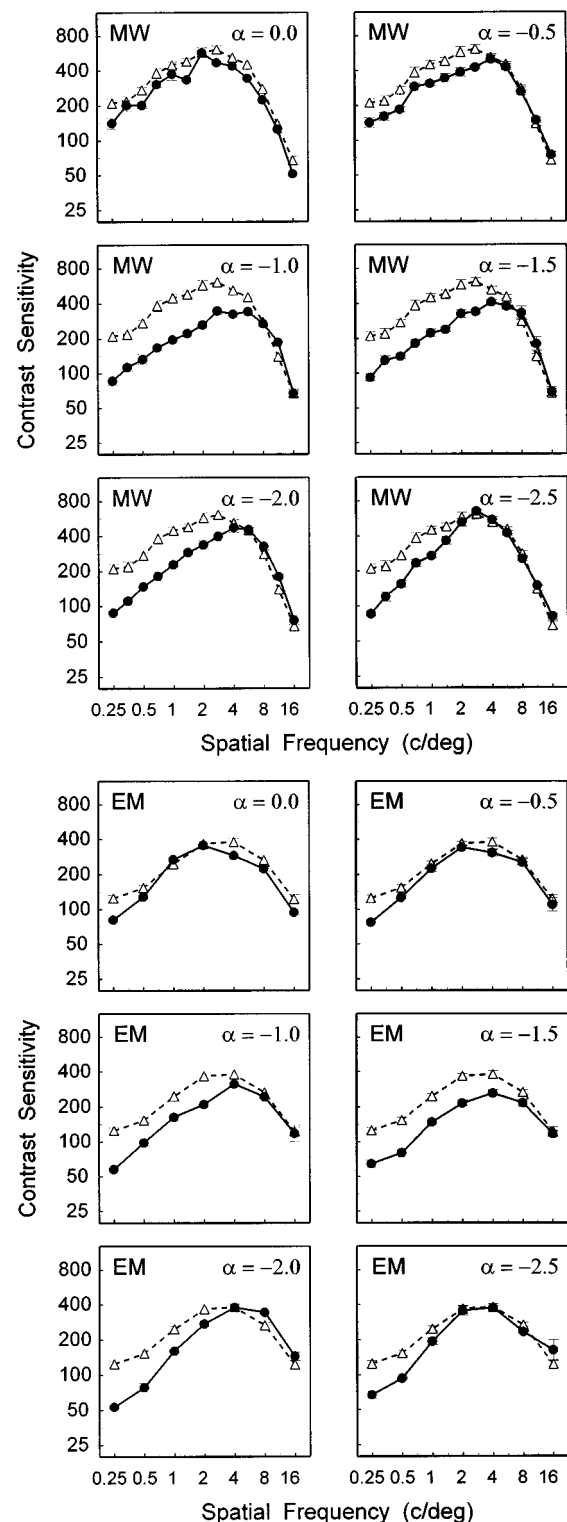


Fig. 10. CSF's after adaptation to the filtered noise images for two observers. The triangles show the contrast sensitivities after neutral adaptation. The circles show the contrast sensitivities after adaptation to the filtered noise. The error bars are the standard errors of the means.

2. Suprathreshold Matches

Once again these threshold results are largely parallel by the pattern of aftereffects at suprathreshold contrasts. Figure 11 plots the changes in both the apparent contrast

and the perceived spatial frequency of the test stimuli for each set of filtered noise stimuli. Test stimuli again had a physical contrast of 0.05. Losses in perceived contrast become progressively more selective for low frequencies as the filtering of the adaptation increases. However, for the -0.5 stimuli there is for both observers more adapta-

tion at the high frequencies than would be predicted from the threshold changes, and, for EM, contrast changes may actually become biased toward high frequencies for the least filtered stimuli. (While weak, this bias was replicated in additional runs by EM.) The aftereffects again appear very different when large differences in the adapting α are compared but do not differ markedly for small changes in the spectral slopes, and the aftereffects for the $1/f$ spectra are qualitatively similar to the contrast changes induced by adaptation to the natural image sets. Finally, the results for the filtered noise spectra again suggest that the selective sensitivity losses at low frequencies may result in biases in perceived size toward higher frequencies. For both observers these biases become progressively more evident as the slope of the adapting spectra increases.

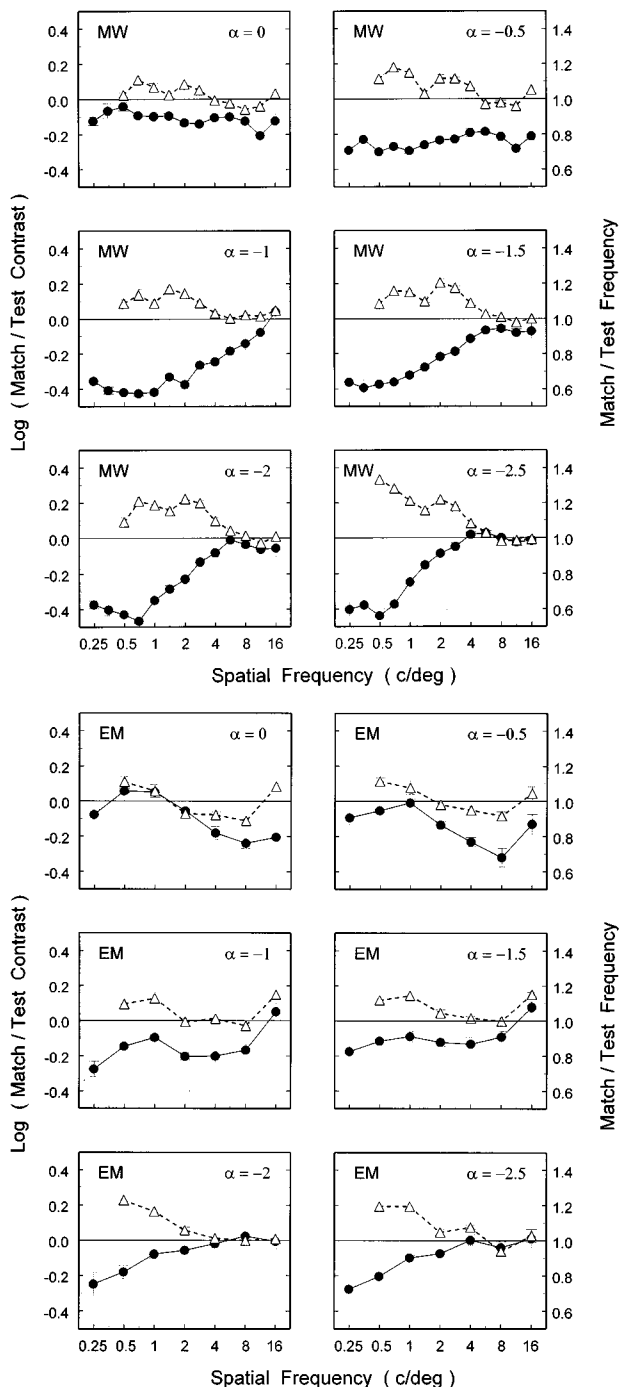


Fig. 11. Results of contrast and spatial-frequency matching for the suprathreshold gratings for two observers after adaptation to the filtered noise stimuli. The circles show the changes in perceived contrast on a logarithmic scale (left-hand Y axis), and the triangles show the changes in perceived spatial frequency in a linear scale (right-hand Y axis), respectively, as a function of the spatial frequency of the test grating. The error bars are the standard errors of the means.

4. DISCUSSION

In summary, we have found that exposure to natural images induces pronounced changes in contrast sensitivity. The aftereffects are characterized by selective losses in sensitivity at lower spatial frequencies, consistent with the characteristic amplitude spectra of natural images. In normal viewing contrast adaptation may thus exert a ubiquitous influence on spatial sensitivity, markedly altering the spatial filtering characteristics of our form perception. We have shown that this influence is manifest both at threshold and in suprathreshold appearance at different spatial scales.

A. Adaptation and Natural Viewing

While our goal was to assess the states of spatial contrast adaptation that are likely to arise in the natural visual environment, there are obviously many ways in which our paradigm fails to mimic natural viewing conditions. It therefore remains important to assess the magnitude of contrast adaptation effects under conditions more natural than most psychophysical experiments have accommodated. For example, we resampled the adapting images at a rapid rate that was designed to minimize local changes in light adaptation and to expose observers to the average contrast both across different scenes and within different parts of the same scene. Thus our procedure does not simulate the temporal sequence or fixation biases (e.g., to specific objects or parts of the image) that are likely to occur for natural patterns of eye movements. However, we have found for uniform flickering fields that contrast adaptation extends over a wide range of temporal frequencies, and the effects of light adaptation and contrast adaptation appear to be largely separable.^{37,38} This suggests that the form of the aftereffects that we observed is not critically dependent on the sampling rate. (A variant of the present experiments that may allow for more natural temporal patterns of stimulation was explored previously in experiments by Atick,³⁹ who examined adaptation induced by viewing video sequences.)

A related example of how our stimuli departed from normal viewing is that we constrained all the adapting images to have the same mean luminance. We imposed this constraint to test specifically the adaptation effects that arise from the spatial structure in the images. How-

ever, differences in the average light level across individual scenes (e.g., for areas in sun or shadow) may often be substantial. If in normal viewing there are large and frequent modulations of the dc (zero-frequency) luminance, then the sensitivity changes may in fact be much more pronounced and selective for low frequencies than those we have measured.

B. General Versus Image-Specific Patterns of Adaptation

In the present experiments we adapted to ensembles of images to explore the general properties of the spatial aftereffects. We assume that this simulates more closely the pattern of stimulation underlying spatial adaptation in natural viewing, which should depend on the average characteristics of scenes built up over multiple fixations. Our results suggest that the low-frequency biases common to virtually all natural scenes conspire to induce a consistent, general pattern of sensitivity loss at low-to-medium spatial frequencies. It remains possible that there are other general properties of natural image structure—including aspects of image structure that have yet to be defined—that may play an important role in defining the adaptation. For example, we measured the sensitivity changes only in horizontal test gratings. However, the average amplitude spectra of natural images are anisotropic, with more power at vertical and horizontal orientations.^{17,40} If these differences are preserved in the retinal ensemble (despite frequent changes in the observer's orientation), then the adaptation effects may also exhibit an orientation bias (though our results suggest that weak biases in the adapting spectrum are unlikely to produce large changes in spatial sensitivity).

Because we always adapted to groups of images our current procedure does not readily reveal properties of individual images (e.g., the phase spectrum) that may be important in determining the form of the spatial adaptation. Individual images can produce strong and idiosyncratic aftereffects, and if contrast adaptation serves a functional role then it is the changes in sensitivity across different images or contexts that are important.^{1,10,11} For example, Webster, MacLin, and colleagues^{41,42} examined figural aftereffects in natural stimuli by using images of human faces (for which small configural changes are highly discriminable). Adaptation to a distorted face leads to strong and selective changes in the appearance of normal faces, yet such aftereffects cannot be accounted for by the amplitude spectra of the stimuli. Moreover, in a study analogous to the present research, Webster *et al.*⁴³ and Webster and Mollon⁴⁴ examined how color perception is affected by adaptation to the natural environment. In their studies they focused on the aftereffects that might arise from exposure to the color gamuts defining individual scenes. They found that the distribution of colors across different scenes varied substantially and that adaptation to individual distributions induced changes in color appearance that were selective for the specific adapting distribution.

One difference across images that our results do address is in the specific slope of the amplitude spectra. For the range of slopes that have been reported for natural scenes we found only modest changes in the spatial se-

lectivity of the adaptation, though more extreme slopes outside the range of naturally occurring spectra produced clearly different aftereffects. If the state of adaptation normally depends on the average characteristics across many samples, then large deviations (within the naturally occurring range) from $1/f$ in the average adapting spectrum may be infrequent. This suggests that the characteristic spatial structure of the natural world will tend to maintain the visual system in characteristic states of spatial contrast adaptation. A similar argument applies to color vision. As we noted, the color distributions across individual scenes are large enough to induce markedly different changes in sensitivity.^{43,44} However, the range of color distributions within the natural environment is nevertheless limited, and thus the natural states of color contrast adaptation may similarly be limited.

In addition to the spectral slope, a second obvious source of variation in the spatial statistics of natural images is in rms contrast, which varies widely across images. (See Fig. 2.) Changes in ambient contrast may more strongly modulate the state of adaptation than differences in α , for it is evident that, while the latter is considered a relatively stable property of natural scenes, contrast can change markedly with viewing conditions (e.g., in fog or rain). In fact, an important proposed function of contrast adaptation or contrast gain control is to adjust sensitivity to match the prevailing contrast gamut.⁴⁵ In the present study we have not explored whether the changes in spatial adaptation are substantial over the range of luminance contrasts that we are likely to encounter, but the magnitude of sensitivity changes typically increases monotonically with adapting contrast,^{5,46} and Webster and Mollon⁴⁴ have shown clear changes in sensitivity that depend on adaptation to the different chromatic and luminance contrasts across scenes. One variant on the present experiments would be to group natural images according to high or low rms contrast or high or low α values and then test whether the natural variations within either dimension are sufficient to change significantly the pattern of adaptation.

C. Contrast Adaptation and Spatial Vision

The states of contrast adaptation induced by natural images are important to quantify because they determine the natural operating states of our spatial vision and are thus the most relevant for understanding our form perception (in the same way that the light-adapted retina is more relevant for understanding photopic vision than is the dark-adapted visual system). The specific pattern of adaptation effects that we found therefore has a number of implications for form perception. These are illustrated in the following three examples.

(1) The CSF is fundamental to models of spatial vision and for characterizing the spatial filtering properties of our vision. The adaptation induced by natural viewing may significantly alter both the shape and the peak frequency of the CSF, and these changes may be important to include to more accurately model the encoding of spatial patterns.

(2) While the spectral slopes of natural images may not vary enough to alter substantially the pattern of adaptation, as we noted, the effective adapting stimulus will depend on both the stimulus spectrum and the observer's CSF. Thus natural images might induce very different sensitivity changes under conditions that vary the CSF. Several factors are known to strongly affect the shape of the CSF, including temporal frequency, mean luminance level, eccentricity, and whether the stimulus variations are luminance or chromatic.^{19,47} A particularly relevant factor is the state of accommodation, since the effects of changing α are roughly similar to the effects of blurring the image.³² Since much of the visual field is often out of focus, the primary stimulus for natural adaptation may be further biased toward lower frequencies. An intriguing possibility is that associated with refractive errors there may tend to be different characteristic states of contrast adaptation, for the sensitivity losses owing to blur will tend to shield the visual system from sensitivity losses owing to the adaptation.

(3) At suprathreshold contrasts our results show that adaptation strongly biases the apparent contrast of low frequencies relative to higher frequencies. The CSF fails to predict visual performance at suprathreshold levels, where perceived contrasts across different frequencies tend to follow the physical contrast (rather than multiples of threshold contrast).^{48,49} This compensation for the sensitivity differences at different spatial scales is thought to allow for contrast constancy, for example, as the size of objects changes. Yet under natural states of adaptation the bias against low frequencies may influence contrast constancy and could even cause perceived contrast at higher frequencies to appear overcompensated. However, our present results are restricted to low contrasts, and the adaptation effects at higher contrast levels are likely to be weaker. It thus remains important to further assess the extent to which contrast coding might be affected by the adaptation.

D. Contrast Adaptation and Coding Efficiency

A number of studies have argued that the spatial sensitivity of the visual system is well matched to the spatial statistics of natural images. One can successfully predict the receptive-field characteristics of both retinal²²⁻²⁴ and cortical¹⁴ cells by characterizing the properties of natural images and then asking how stimuli with such properties can be represented efficiently.^{50,51} Psychophysically, Knill *et al.*³¹ and Tadmor and Tolhurst³² examined whether visual performance was matched to the spatial structure of natural images by testing how well observers could discriminate between different images on the basis of differences in the amplitude spectra. Contrast adaptation may similarly provide a potential empirical test for probing the match between visual coding and the stimulus. For example, the visual system might be regarded as well matched to stimuli that produce a nonselective adaptation effect, for in this case the visual responses at all the points along the relevant stimulus dimension are given equal weight. In this regard, it is notable that the adaptation effects that we observed are stronger at lower spatial frequencies, which suggests that the distribution of energy is not uniform across the spatial channels un-

derlying the adaptation. Contrast adaptation may therefore play an important role in whitening the neural image. Moreover, the very existence of pattern-selective adjustments emphasizes that the statistics of the visual world are not static and points to the need to change coding to match sensitivity specifically to the prevailing stimulus.^{1,10,11} Our results suggest that such adjustments are a prevalent component in the visual response to natural stimuli.

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REFERENCES

1. M. A. Webster, "Human color perception and its adaptation," *Network Comput. Neural Syst.* **7**, 587-634 (1996).
2. C. Blakemore and F. W. Campbell, "On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images," *J. Physiol. (London)* **203**, 237-260 (1969).
3. A. S. Gilinsky, "Orientation-specific effects of patterns of adapting light on visual acuity," *J. Opt. Soc. Am.* **58**, 13-17 (1968).
4. C. Blakemore, J. P. J. Muncey, and R. M. Ridley, "Perceptual fading of a stabilized cortical image," *Nature* **233**, 204-205 (1971).
5. M. A. Georgeson, "The effect of spatial adaptation on perceived contrast," *Spatial Vis.* **1**, 103-112 (1985).
6. M. A. Webster and J. D. Mollon, "The influence of contrast adaptation on color appearance," *Vision Res.* **34**, 1993-2020 (1994).
7. J. J. Gibson and M. Radner, "Adaptation, after-effect and contrast in the perception of tilted lines. I. Quantitative studies," *J. Exp. Psychol.* **20**, 453-467 (1937).
8. A. Wohlgenuth, "On the after-effect of seen movement," *Bri. J. Psychol. Monogr. Suppl.* **1**, 1-117 (1911).
9. O. Braddick, F. W. Campbell, and J. Atkinson, "Channels in vision: basic aspects," in *Handbook of Sensory Physiology VIII*, R. Held, H. W. Leibowitz, and H. Teuber, eds. (Springer-Verlag, Berlin, 1978), pp. 3-38.
10. J. J. Atick, Z. Li, and A. N. Redlich, "What does post-adaptation color appearance reveal about cortical color representation?" *Vision Res.* **33**, 123-129 (1993).
11. H. B. Barlow, "A theory about the functional role and synaptic mechanism of visual after-effects," in *Vision: Coding and Efficiency*, C. Blakemore, ed. (Cambridge U. Press, Cambridge, 1990), pp. 363-375.
12. G. J. Burton and I. R. Moorhead, "Color and spatial structure in natural scenes," *Appl. Opt.* **26**, 157-170 (1987).
13. D. W. Dong and J. J. Atick, "Statistics of time-varying images," *Network Comput. Neural Syst.* **6**, 345-358 (1995).
14. D. J. Field, "Relations between the statistics of natural images and the response properties of cortical cells," *J. Opt. Soc. Am. A* **4**, 2379-2394 (1987).
15. D. L. Ruderman and W. Bialek, "Statistics of natural images: scaling in the woods," *Phys. Rev. Lett.* **73**, 814-817 (1994).
16. D. J. Tolhurst, Y. Tadmor, and T. Chao, "Amplitude spectra of natural images," *Ophthalmic Physiol. Opt.* **12**, 229-232 (1992).
17. A. van der Schaaf and J. H. van Hateren, "Modelling the power spectra of natural images: statistics and information," *Vision Res.* **36**, 2759-2770 (1996).
18. D. L. Ruderman, "Origins of scaling in natural images," in *Human Vision and Electronic Imaging*, B. E. Rogowitz and J. P. Allebach, eds., *Proc. SPIE* **2657**, 120-131 (1996).

19. R. L. De Valois and K. K. De Valois, *Spatial Vision* (Oxford U. Press, Oxford, 1988).
20. N. Graham, *Visual Pattern Analyzers* (Oxford U. Press, Oxford, 1989).
21. L. A. Olzak and J. P. Thomas, "Seeing spatial patterns," in *Handbook of Perception and Human Performance*, K. R. Boff, L. Kaufman, and J. P. Thomas, eds. (Wiley, New York, 1986), Vol. 1, pp. 7-1-7-56.
22. J. J. Atick and A. N. Redlich, "What does the retina know about natural scenes?" *Neural Comput.* **4**, 196-210 (1992).
23. M. V. Srinivasan, S. B. Laughlin, and A. Dubs, "Predictive coding: a fresh view of inhibition in the retina," *Proc. R. Soc. London Ser. B* **216**, 427-459 (1982).
24. J. H. van Hateren, "Spatiotemporal contrast sensitivity of early vision," *Vision Res.* **33**, 257-267 (1993).
25. J. Nachmias, R. Sansbury, A. Vassilev, and A. Weber, "Adaptation to square-wave gratings: in search of the elusive third harmonic," *Vision Res.* **13**, 1335-1342 (1973).
26. D. J. Tolhurst, "Adaptation to square-wave gratings: inhibition between spatial frequency channels in the human visual system," *J. Physiol. (London)* **226**, 231-248 (1972).
27. M. W. Greenlee and S. Magnussen, "Interactions among spatial frequency and orientation channels adapted concurrently," *Vision Res.* **28**, 1303-1310 (1988).
28. S. Klein and C. F. Stromeyer, "On inhibition between spatial frequency channels: adaptation to complex gratings," *Vision Res.* **20**, 459-466 (1980).
29. K. K. De Valois and E. Switkes, "Spatial frequency specific interaction of dot patterns and gratings," *Proc. Natl. Acad. Sci. USA* **77**, 662-665 (1980).
30. S. B. Laughlin, "Form and function in retinal processing," *Trends Neurosci.* **10**, 478-483 (1987).
31. D. C. Knill, D. Field, and D. Kersten, "Human discrimination of fractal images," *J. Opt. Soc. Am. A* **7**, 1113-1123 (1990).
32. Y. Tadmor and D. J. Tolhurst, "Discrimination of changes in the second-order statistics of natural and synthetic images," *Vision Res.* **34**, 541-554 (1994).
33. D. J. Tolhurst, "Separate channels for the analysis of the shape and the movement of a moving visual stimulus," *J. Physiol. (London)* **231**, 385-402 (1973).
34. A. Bradley, E. Switkes, and K. K. De Valois, "Orientation and spatial frequency selectivity of adaptation to color and luminance gratings," *Vision Res.* **28**, 841-856 (1988).
35. C. F. Stromeyer, S. Klein, B. M. Dawson, and L. Spillmann, "Low spatial-frequency channels in human vision: adaptation and masking," *Vision Res.* **22**, 225-233 (1982).
36. C. Blakemore and P. Sutton, "Size adaptation: a new aftereffect," *Science* **166**, 245-247 (1969).
37. M. A. Webster, V. E. Raker, and J. A. Wilson, Department of Psychology, University of Nevada, Reno, Nev. 89557 (personal communication, 1997).
38. M. A. Webster and J. D. Mollon, "Colour constancy influenced by contrast adaptation," *Nature* **373**, 694-698 (1995).
39. J. J. Atick, Computational Neuroscience, Rockefeller University, New York, N.Y. 10021 (personal communication, 1995).
40. E. Switkes, M. J. Mayer, and J. A. Sloan, "Spatial frequency analysis of the visual environment: anisotropy and the carpentered environment hypothesis," *Vision Res.* **18**, 1393-1399 (1978).
41. M. A. Webster, O. H. MacLin, A. L. Rees, and V. E. Raker, "Contrast adaptation and the spatial structure of natural images," *Perception (Suppl.)* **25**, 47 (1996).
42. O. MacLin, H. A. Nelson, and M. A. Webster, "Figural after-effects in the perception of faces," *Invest. Ophthalmol. Visual Sci. (Suppl.)* **37**, S193 (1996).
43. M. A. Webster, A. Wade, and J. D. Mollon, "Color in natural images and its implications for visual adaptation," in *Human Vision and Electronic Imaging*, B. E. Rogowitz and J. P. Allebach, eds., *Proc. SPIE* **2657**, 144-152 (1996).
44. M. A. Webster and J. D. Mollon, "Adaptation and the color statistics of natural images," *Vision Res.* (to be published).
45. R. O. Brown and D. I. A. MacLeod, "Induction and constancy for color saturation and achromatic contrast variance," *Invest. Ophthalmol. Visual Sci. (Suppl.)* **27**, 75 (1991).
46. M. W. Greenlee, M. A. Georgeson, S. Magnussen, and J. P. Harris, "The time course of adaptation to spatial contrast," *Vision Res.* **31**, 223-236 (1991).
47. D. H. Kelly and C. Burbeck, "Critical problems in spatial vision," *Crit. Rev. Biomed. Eng.* **10**, 125-177 (1984).
48. N. Brady and D. J. Field, "What's constant in contrast constancy? The effects of scaling on the perceived contrast of bandpass patterns," *Vision Res.* **35**, 739-756 (1995).
49. M. A. Georgeson and G. D. Sullivan, "Contrast constancy: deblurring in human vision by spatial frequency channels," *J. Physiol. (London)* **252**, 627-656 (1975).
50. J. J. Atick, "Could information theory provide an ecological theory of sensory processing?" *Network Comput. Neural Syst.* **3**, 213-251 (1992).
51. D. J. Field, "What is the goal of sensory coding?" *Neural Comput.* **6**, 559-601 (1994).