

Pattern-Selective Adaptation in Color and Form Perception

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... I used to think that the aftereffects of persisting stimulation of the retina obtained by prolonged fixation of a display could be very revealing. Besides ordinary afterimages there are all sorts of perceptual aftereffects, some of which I discovered. But I no longer believe that experiments on so-called perceptual adaptation are revealing, and I have given up theorizing about them. . . .

J. J. Gibson, *The Ecological Approach to Visual Perception* (1979, p. 248)

J. J. Gibson was among the most influential perceptual psychologists of the twentieth century. Early in his career he reported a striking visual illusion—the tilt aftereffect (Gibson and Radner, 1937). After tilted lines are viewed for a brief period, a vertical line appears tilted in a direction opposite to the adapting orientation (Fig. 60.1). There are many similar examples of visual aftereffects. For example, to experience the motion aftereffect or *waterfall illusion*, stare at the water pouring down a fall for a few moments and then shift your gaze to the side. The static rocks will briefly appear to ooze upward. Such aftereffects are a consequence of perceptual adaptation. The visual system adapts or reduces its sensitivity in response to the currently viewed stimulus. These sensitivity changes are normally selective—they adjust to specific properties or patterns of the image—and thus the aftereffects are usually experienced as a bias toward the opposite or more novel image properties. The resulting illusions attest to the malleability of perception and have provided one of the most commonly used tools for probing visual coding. Indeed, adaptation is often referred to as the *psychologist's electrode*, for it is routinely used to try to detect and characterize visual mechanisms by measuring how their sensitivities change following adaptation.

However, while pattern adaptation has been central to the study of vision, it is less often thought to be important to the actual act of seeing and has even been regarded as an anomaly of perception, arising when the visual system is fatigued by exposure to situations it was never designed to handle. In later years, Gibson went on to found an entire school of perception that emphasized the importance of understanding vision within the context of the rich patterns of information provided by actively exploring the natural visual environment (Gibson, 1979). From this perspective, adaptation was no longer useful as a tool, because the very notion of intervening processes became irrelevant. But as the

quote above implies, he also felt that maintaining fixation on a tilted line (a typical procedure for inducing aftereffects) was itself an unnatural task, and thus was irrelevant to understanding the normal dynamics of perception. And in his final major treatise on vision, the aftereffects he helped reveal were relegated to a footnote.

The aim of this chapter is instead to emphasize the importance of adaptation, both as a method for understanding the processes mediating perception and as a principle for understanding why things look the way they do. Even brief exposures to a pattern can dramatically alter perception, and this is one reason adaptation remains such a popular paradigm. The following sections review the nature of these perceptual aftereffects and illustrate how they have been used to uncover the visual mechanisms encoding color and form. But if we can recast vision so easily in the lab, how is it being molded by the patterns we are routinely exposed to on the outside, as you walk through a forest or sit reading this page? The final sections take up this question by considering how visual perception is influenced by adaptation to the natural visual environment. The visual world is not random. Natural images have characteristic properties, and exposure to these *persisting patterns of stimulation* may therefore hold the visual system in specific states of adaptation. These states provide the relevant contexts for understanding natural vision.

Pattern adaptation and visual channels

What can an orientation-selective aftereffect tell us about the visual processes underlying form perception? Figure 60.2A shows the kinds of measurements one might record in a study of orientation adaptation. In this plot the angle corresponds to the pattern orientation, while the distance from the origin corresponds to the pattern contrast. Note that we could represent any stimulus within the plane by taking only two “measurements” (e.g., of the component contrasts along the horizontal and vertical axes) and that these could sample contrasts along any pair of axes within the plane. But how many measurements are actually used, and along which axes do they lie?

Adaptation experiments address this question by exploring how responses to stimuli are altered after observers are

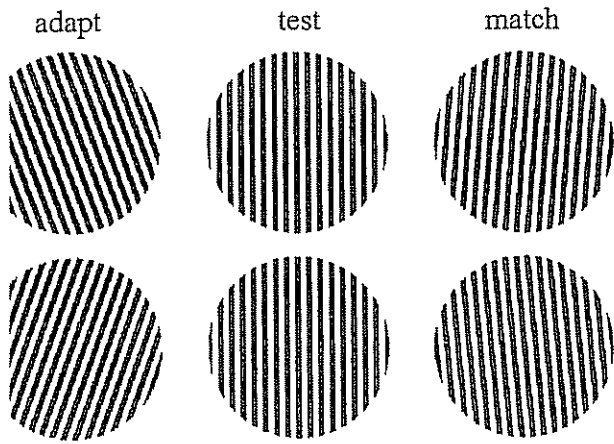


FIGURE 60.1. The tilt aftereffect. Adapting to a counterclockwise tilted line causes a vertical line to appear tilted clockwise, and vice versa.

posed to and thus adapted by different stimuli. To induce a new state of adaptation, subjects typically view the adapting stimulus for a few minutes and then make judgments about a set of briefly presented test stimuli. Two common measures of judgments are used. In one case, sensitivity is probed by finding the threshold for detecting or discriminating the test stimulus. In the second, the subjective appearance of the test is assessed. One way to do this would be to match the apparent orientation of the test by physically adjusting the orientation of a nearby comparison stimulus presented to a part of the retina maintained under neutral adaptation. This *asymmetric matching* task assumes that the effects of adaptation are confined to the regions of the retina (or their associated pathways) that were exposed to the stimuli. A second approach is to vary the test stimulus physically in order to elicit a perceptual change. For example, the orientation of a test could be adjusted so that it always appears vertical. This *nulling* method assumes that any response changes

induced by adaptation are equivalent to the responses induced by a physical stimulus. Still other common measures include rating the perceived magnitude of an aftereffect or its perceived duration.

Figure 60.2A plots an idealized set of results after adapting to a bar tilted at a clockwise angle. Measures of sensitivity to different orientations would show that adaptation increases the threshold for detecting patterns that have orientations similar to the adapting pattern (Gilinsky, 1968). Measures of appearance would show that after adaptation a vertical line appears tilted counterclockwise. Both aftereffects are consistent with a selective loss in sensitivity to the adapting orientation, and thus imply that adaptation is altering the responses in something that can be selectively tuned for orientation. Results of this kind are usually explained in terms of visual channels—the notion that the visual system encodes information within a bank of *filters* that respond to different but overlapping ranges along the stimulus continuum (e.g., to different orientations, hues, or directions of motion). Any stimulus is thus represented by the distribution of activity across the set of channels. A further common assumption is that these channels are *labeled* for particular sensations, so that which stimulus is perceived (e.g., vertical or red) depends on which channels respond, while the magnitude of the stimulus (e.g., contrast or saturation) is encoded by the size of the response (Braddick et al., 1978).

Figure 60.2B shows one possible account of the tilt aftereffect based on changes in the distribution of activity across multiple channels. Suppose that adaptation reduces a channel's sensitivity according to how strongly the channel responded to the adapting stimulus. This would reduce the channel's responses to a subsequent test stimulus. The test orientations to which it is tuned would become harder to detect, and patterns that are above threshold would appear to have lower contrast. Moreover, the diminished signals

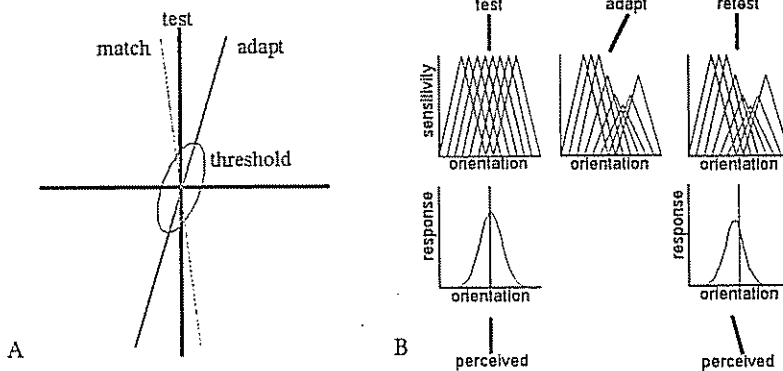


FIGURE 60.2. Multichannel accounts of the tilt aftereffect. *a*, Measurements of detection thresholds (elliptical contour) or perceived tilt of a vertical test after adapting to a clockwise bar. *b*, Both effects can be accounted for by adaptation in orientation-selective chan-

nels that reduces sensitivity in channels tuned to the adapter and thus skews the distribution of responses to the test away from the distribution of responses to the adapter.

would reduce its contribution to the collection of channel responses, and thus for nearby test orientations would skew the mean of the distribution away from the mean for the adapting orientation, inducing the perceived aftereffect. (However, this leaves the problem of how distortions in the pattern's features can be reconciled with their perceived retinal location; Meese and Georgeson, 1996.)

Often the studies using adaptation have not been interested in the processes of adaptation itself, but rather in the properties of the channels implied by the adaptation. One question of interest is the bandwidths or profiles of the channels. For example, an adaptation effect that influenced only a narrow range of orientations would imply that the channels are highly selective for orientation. A second commonly asked question concerns the number of channels. If the response changes are selective for the adapting axis, that implies a channel tuned to that axis. If selective aftereffects can be found for many axes, then that might imply many channels. We could thus repeat the measurements of Figure 60.2A for many adapting and test orientations in order to characterize how orientation is represented at the level at which the adaptation alters sensitivity. The results of such studies have shown that sensitivity changes appear selective for any orientation, suggesting that orientation is encoded effectively by a continuum of channels, with bandwidths (orientation range at which sensitivity falls to half the peak) on the order of roughly ± 10 degrees (Blakemore and Nachmias, 1971).

However, the interpretation of these results is complicated, precisely because any inferences about the underlying channels depends on assumptions about the nature of the adaptation. For instance, the model in Figure 60.2B assumes that each channel adapts independently. Yet suppose that adaptation instead reflects an interaction between channels (Barlow, 1990; Wilson, 1975). For example, Barlow suggested that adaptation involves reciprocal inhibition between two channels that builds up whenever their outputs are correlated. The effect of this mutual repulsion is to bias the channels' responses until they are statistically independent. An account of the tilt aftereffect based on this principle is shown in Figure 60.3. (For a comprehensive model, see Clifford et al., 2000.) In this example, orientation is encoded by pair of channels that, under neutral adaptation, are tuned to horizontal and vertical. Exposure to the clockwise adapter would produce covarying responses in both channels, leading to inhibition between them. This alters the response within each channel by subtracting a fraction of the response in the second channel. In turn, this reduces the responses to the adapting axis and tilts the tuning function for each channel away from the adapting axis, spherizing the response distribution. Thus, an important feature of this model is that adaptation could induce a selective change in sensitivity even to stimulus directions to which neither channel is tuned.

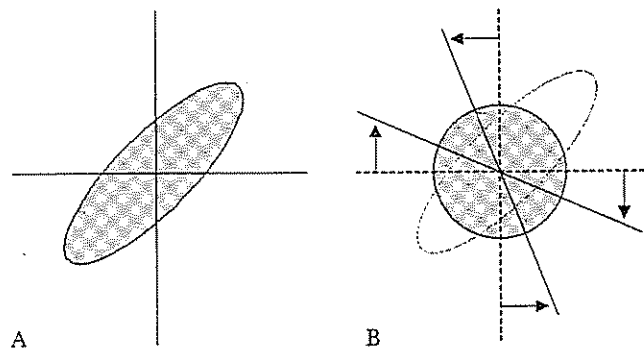


FIGURE 60.3. An alternative account of tilt aftereffects based on mutual inhibition between channels. *a*, Signals along an oblique axis produce correlated responses in channels tuned to horizontal and vertical. *b*, Inhibition between the channels leads to an oblique rotation of their response axes, decorrelating their outputs.

Consequently, adaptation effects alone do not conclusively reveal the specific channel structure.

The actual neural mechanisms underlying pattern-selective adaptation remain unresolved, though it is clear that the channels defined psychophysically do not reflect passive habituation in a neuron's responses. Physiological measurements of contrast adaptation in the cortex suggest that the response changes result from a tonic hyperpolarization imposed on a separate stimulus-driven response that is unaffected by adaptation (Carandini and Ferster, 1997). At least some components of the adaptation are extremely rapid (Muller et al., 1999), and can selectively adjust to the co-occurrence or contingencies between pairs of stimuli (Carandini et al., 1997) and alter the shape of an individual neuron's tuning curve (Movshon and Lennie, 1979; Muller et al., 1999).

The fact that very different models can lead to very similar explanations of visual aftereffects shows that the implications of contrast adaptation must be interpreted with caution. On the other hand, the models illustrated share important features. Both assume that stimuli are encoded by a set of channels that are (or can be) selectively tuned to many different directions, and that adaptation alters perception by altering the distribution of responses within these channels. Thus, the presence of a pattern-selective aftereffect remains a powerful source of evidence about the nature of visual representations.

The sites of adaptation

As Gibson noted, there are all sorts of perceptual aftereffects. Indeed, we can see the signs of adaptation literally everywhere we look. Neural adjustments begin at the earliest stages in the retina, where processes of light adaptation adjust sensitivity in order to match the ambient light level (Hood, 1998). At the other extreme, some perceptual adap-

tations are actually perceptual-motor adjustments, because they involve recalibration of sensorimotor signals. For example, many studies have examined the visual and behavioral changes that result when observers wear prisms that distort or even invert the visual field (Welch, 1986). Subjects show a remarkable capacity to adjust to these distortions so that they can move about and reach for objects appropriately. This relearning is distinct from a purely visual change because it requires active exploration of the world and primarily reflects changes in perceived body position.

At intermediate stages, the visual system adjusts not merely to the average light level, but also to the patterns of light or contrasts in the image (Webster, 1996). These patterns may be stimulus variations in space, time, or color. Classic examples include not only the tilt and motion aftereffects (Mather et al., 1998), but also numerous figural or size-selective aftereffects, in which adaptation to a particular shape or size biases the apparent shape or size of other images (Kohler and Wallach, 1944). Pattern adaptation can also selectively adjust to specific combinations or conjunctions of visual attributes, and in this case is known as *contingent adaptation* (Stromeyer, 1978). For example, color aftereffects can be induced that are contingent on the spatial orientation or direction of motion of a pattern, or vice versa. Contingent aftereffects are sometimes distinguished from simple pattern aftereffects by their long persistence and by the possibility that they must be actively extinguished rather than passively decaying, characteristics that have blurred the distinction between adaptation and learning.

The aftereffects of pattern adaptation primarily reflect sensitivity changes originating in visual cortex. Three lines of evidence support this. First, what is being affected is sensitivity to patterns—to tilted lines, tinted bars, or drifting gratings—and neurons in the primate visual system do not appear to have the requisite selectivity until striate cortex. For example, tuning for orientation, direction of motion, and spatial frequency are properties that first clearly emerge in striate cortex (De Valois and De Valois, 1988). The second source of evidence is that most visual aftereffects show substantial interocular transfer (Blake et al., 1981). That is, an adapting pattern that is viewed only by the right eye can influence a test pattern that is presented only to the left eye. Because signals from the two eyes first converge in the cortex, this is the earliest plausible site at which a sensitivity change could lead to binocular interactions. Finally, direct recordings from neurons along the visual pathway have shown that cortical cells are strongly adapted by patterns, while response changes in geniculate and retinal cells are weaker (Maffei et al., 1973; Ohzawa et al., 1982) though still substantial (Brown and Masland, 2001; Chander and Chichilnisky, 2001; Smirnakis et al., 1997).

While striate cortex may therefore be an important site of pattern adaptation, this does not preclude sensitivity changes

at higher levels. A number of aftereffects point to multiple cortical sites in pattern adaptation. For example, distinct motion aftereffects have been found for static versus dynamic test patterns and for simple gratings versus two-dimensional plaids, and these have been attributed to sensitivity changes at different sites or pathways (Mather et al., 1998). Moreover, functional magnetic resonance imaging (fMRI) studies have demonstrated response changes correlated with the motion aftereffect that are strongest in area MT, an extrastriate area specialized for motion (Tootell et al., 1995). Studies of orientation adaptation have provided intriguing clues about the sites of the sensitivity changes controlling the tilt aftereffect. Asymmetrical tilt aftereffects occur between real and illusory contours, and these may reflect differences between striate cortex and area V2 in the representation of subjective contours (Paradiso et al., 1989). Distinct tilt aftereffects can also be demonstrated for oriented contours versus oriented textures, with the former affecting sensitivity changes at relatively high levels of shape coding (Suzuki, 2001). Surprisingly, tilt aftereffects can also be induced by patterns that cannot be consciously perceived because they are too fine to be resolved (He and MacLeod, 2001). This suggests that at least some of the aftereffects arise at relatively early cortical levels before visual awareness.

Adaptation and color vision

We can readily distinguish distinct and qualitatively different stages of light adaptation and pattern adaptation in color vision, and can use these effects to characterize how information about color is transformed and represented at successive visual levels. Figure 60.4 shows a standard model of human color vision. At the first stage, light is encoded by the responses in three types of cone that have peak sensitivities at short, medium, or long wavelengths (S, M, or L). Subsequently the signals from the cones are combined to form postreceptoral channels. These channels may draw on receptor signals of the same sign to form luminance-sensitive or nonopponent channels, or may receive antagonistic inputs from different cones to form color-sensitive or opponent channels. The two color channels shown receive opposing signals from the L and M cones (L-M) or S opposed by both L and M cones (S-LM). These combinations represent the preferred color directions of cells in the retina and geniculate, and thus are thought to characterize postreceptoral color coding at precortical stages in the visual system (Derrington et al., 1984).

One could evaluate a model like Figure 60.4 by asking how a response change in the different channels might alter color perception. Alternatively, we could approach the question from the opposite direction, by measuring the effects of adaptation to a stimulus and then asking what set of channels is consistent with the observed aftereffects. For example,

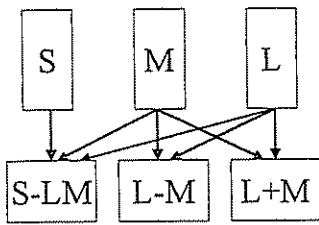


FIGURE 60.4. A standard two-stage model of color vision based on three classes of cones transformed into a luminance channel and two cone-opponent color channels.

Figure 60.5A shows a distribution of colors plotted in a space defined by the signals within the L-M and S-LM channels. In this plot different angles correspond to different hues, and saturation or contrast increases with the distance from the white origin. Note that this is very similar to the representation of contrast and orientation in Figure 60.2A. The stimulus distribution in Figure 60.5 is biased in two ways: the average color is not centered on white, and there is greater variance or contrast along the diagonal axis than along other axes of the space. Processes of light adaptation and contrast (pattern) adaptation selectively adjust to each of these properties (Webster and Mollon, 1995).

LIGHT ADAPTATION Light or chromatic adaptation induces dramatic changes in color vision that are easily demonstrated by the afterimages that are experienced when we fixate a pattern and then switch our gaze to a uniform field. The afterimages arise from lingering sensitivity changes that adjust each location of the retina according to the average light and color it is exposed to. In the example of Figure 60.5A the mean color would look purplish under neutral adaptation. However, adaptation readjusts sensitivity so that the average color appears more achromatic, producing corresponding shifts in the appearance of all colors in the distribution (Fig. 60.5B). To a large extent, the color appearance changes reflect multiplicative gain changes that occur independently within the cones or cone-specific pathways, a process known as *von Kries adaptation* (Chichilnisky and Wandell, 1995; Webster and Mollon, 1995; Wuerger, 1996). Thus, they represent adjustments at the first stage of color processing and, indeed, at the very beginning of vision.

In a classic series of experiments, Stiles (1959) examined the number and color selectivities of the mechanisms underlying chromatic adaptation. Thresholds for detecting a test light were measured in the presence of a uniform adapting background. As the background intensity increases, the processes that respond to the background become less sensitive or light adapt, so that performance follows a characteristic threshold versus intensity curve (Fig. 60.6). The test is detected by the mechanism(s) that are most sensitive on a given adapting background, with a switch between mechanisms revealed by separate branches in the curve. By varying

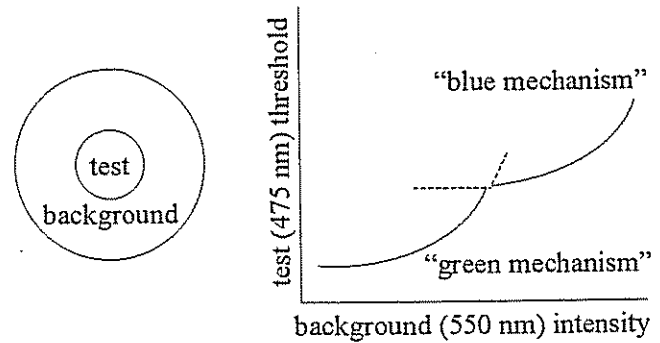


FIGURE 60.5. The two-color threshold method of Stiles. Thresholds for detecting a blue (475 nm) test on a yellow-green (550 nm) background follow two branches reflecting light adaptation in two different color mechanisms.

the wavelength of the test and adapting lights, Stiles showed that sensitivity was limited by a small number of discrete *pi* mechanisms with different sensitivities to wavelength, each adjusting independently to the adapting background.

The spectral sensitivities of the *pi* mechanisms are similar but not equivalent to those of the cones. Moreover, Stiles' work revealed more than three distinct mechanisms under different adapting conditions. These discrepancies have been resolved by showing that chromatic adaptation also depends on *second-site* adjustments in postreceptoral channels (Pugh and Mollon, 1979). One example of these is *transient tritanopia*, a loss in sensitivity to a short-wavelength test after turning off a long-wavelength background that is invisible to S cones (Mollon and Polden, 1977). Extinguishing the background should dark-adapt all of the cones and make them more sensitive, yet thresholds for an S cone detected test are temporarily elevated because the rebound from the yellow background saturates responses at a cone-opponent site. Such aftereffects provided an important source of evidence for color opponency. Second-site adjustments in light adaptation can also be seen in the ways that backgrounds influence sensitivity and appearance (Shevell, 1978; Walraven et al., 1990). A background light sets the gain of the visual mechanisms detecting a superimposed test but also physi-

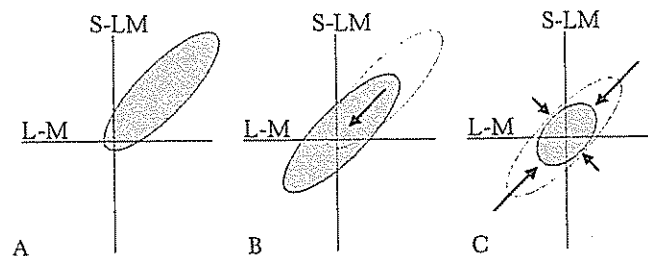


FIGURE 60.6. Adaptation in color vision. *a*, An elliptical distribution of colors plotted in terms of the two cone-opponent axes. Light adaptation adjusts the mean of the distribution so that the average color appears white (*b*). Contrast adaptation instead adjusts to the variations in color around the average (*c*).

cally adds light to the test. However, this added light often has little effect on the test's appearance, because spatial and temporal filtering subtract the signals from the background, leaving the visual system to respond primarily to spatial and temporal transients. Differences in the time course of sensitivity changes suggest that chromatic adaptation may in fact depend on several sites of both multiplicative and subtractive adjustments (Fairchild and Reniff, 1995; Hayhoe et al., 1987).

CONTRAST ADAPTATION As Figure 60.5B shows, even if we renormalize for the average color in an image, there may often remain a bias in the variance or contrasts in the distribution. Visual mechanisms also adjust to these "patterns" of color through contrast adaptation. This produces changes in color vision that are very different from the effects of light adaptation. Chromatic adaptation in the cones is largely a process that readjusts the white point. Contrast adaptation instead alters the perceived contrasts relative to the average color and thus has very little effect on the mean color itself (Webster and Wilson, 2000). Many studies have examined color adjustments by measuring only the stimulus that looks achromatic. This is perhaps the best setting for detecting chromatic adaptation, but it is the least likely to reveal the presence of contrast adaptation.

The first investigators to explicitly study adaptation to color contrast were Guth (1982) and Krauskopf et al. (1982), both by measuring how color vision is affected by adapting to a background that flickered between two colors. An advantage of this approach is that the flickering field did not change the time-averaged luminance or chromaticity of the adapting field, and thus bypassed the early stages of chromatic adaptation to alter sensitivity at more central sites. In fact, like other forms of pattern adaptation, adaptation to color contrast primarily reflects sensitivity changes in the cortex (e.g., Engel and Furmanski, 2001; Lennie et al., 1990). Studies of contrast adaptation thus allow direct measurements of color coding at cortical levels.

Krauskopf et al. (1982) used contrast adaptation to explore the spectral sensitivities of cortical color channels and, in particular, to ask which directions in color space they are tuned for. To do this, they measured thresholds for detecting a color change from white after adapting to fields that were sinusoidally modulated in color along different axes within the plane of Figure 60.5. These threshold changes revealed two important properties of the adapted color channels. First, aftereffects were primarily selective for three *cardinal directions*: an achromatic axis and the L-M and S-LM chromatic axes. For example, after adaptation to an L-M modulation, an L-M test was much harder to see, while sensitivity to an S-LM or luminance-varying test remained largely unaffected. This suggested that the adapted channels are organized in terms of these dimensions, and not in terms

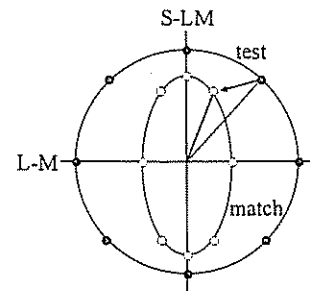


FIGURE 60.7. Contrast adaptation in color vision. Adaptation to flicker along the L-M axis reduces responses along this axis, compressing the circle of test stimuli into an ellipse. This biases the perceived hue of tests away from the adapting axis and toward the orthogonal axis.

of the red-green and blue-yellow dimensions predicted by subjective color experience. However, weak selectivity was also observed for adapting directions intermediate to the L-M and S-LM axes, suggesting the presence of additional channels tuned to these directions (Krauskopf et al., 1986). This raised the possibility that—like the representation of spatial patterns—the representation of color is elaborated in the cortex. Consistent with this, cells in striate cortex show a much wider range of preferred color directions than geniculate cells (Lennie et al., 1990).

Webster and Mollon (1994) extended this paradigm to examine how contrast adaptation alters color appearance. In their studies, subjects viewed adapting and test lights in a field above fixation and then matched the perceived color of the tests by adjusting the physical color in a comparison field presented below fixation. Color changes in the tests were strongly selective for the color axis of the adapting flicker, as illustrated schematically in Figure 60.7 by the matches made after adaptation to the L-M axis. This collapses perceived contrast along the L-M axis, and thus biases the perceived hue of test stimuli away from the L-M axis and toward the orthogonal (S-LM) axis (with a change in contrast but not hue along the adapting and orthogonal axes). Color shifts away from the adapting axis could be induced in any test direction, including the achromatic axis, suggesting that there is no axis that isolates a single type of channel (since the shifts presumably reflect a change in the distribution of responses across channels). These biases in perceived hue are analogous to the biases in perceived orientation in the tilt aftereffect and thus can be thought of as tilt aftereffects in color space. However, compared to orientation the hue shifts are many times larger, exceeding 30 degrees in some cases (compared to 5 degrees or less for typical tilt aftereffects). This difference may result because, when compared in a common metric like Figures 60.2 and 60.5, the color channels are much more broadly tuned than the channels coding orientation, so that the mean of the distribution shifts more with adaptation. The bandwidths of the color aftereffects

are in fact well fit by assuming that the channels are defined by different linear combinations of the cones.

Like orientation, these selective adjustments to color contrast could be achieved by very different routes. Specifically, to account for the selectivity for multiple directions, we could modify the second-stage mechanisms in Figure 60.4 either by adding many color channels that adapt independently or by allowing for adaptive interactions between them. Models based on each of these assumptions have been developed, and both provide a good fit of the observed color changes (Atick et al., 1993; Clifford et al., 2000; Lennie, 1999; Webster and Mollon, 1994; Zaidi and Shapiro, 1993). Thus, again, adaptation alone does not define the intrinsic number of color channels. However, other experimental approaches point to the presence of many chromatic mechanisms even in a single state of adaptation (Webster, 1996). This supports the idea that the cortex does encode color—like orientation—in a large number of channels, though it does not imply that these adapt independently.

Further adaptation effects have revealed a number of additional properties of cortical color channels. For example, adaptation to sawtooth modulations suggests that different populations of channels encode the opposite poles of luminance or chromatic axes (Krauskopf et al., 1982), and the axes may be even further subdivided into channels that code different ranges of contrast (Webster and Wilson, 2000). A number of studies have also explored a simultaneous analog of contrast aftereffects. The perceived contrast of a pattern can be strongly attenuated by embedding the pattern in a high-contrast surround (Chubb et al., 1989). This contrast induction again adjusts selectively to different chromatic axes (Brown and MacLeod, 1997; Singer and D'Zmura, 1994; Webster et al., 2002).

Adaptation has also proven useful for probing the spatial selectivities of color mechanisms. For example, adaptation to color spatial patterns (e.g., a red-green edge) makes color patterns with similar orientation and spatial frequency harder to detect (Bradley et al., 1988) and can induce tilt aftereffects in color patterns (Elsner, 1978). Moreover, the tilt aftereffects show selectivity for multiple color directions (Flanagan et al., 1990). Such results show that the affected channels can be tuned to both the color and the spatial properties of stimuli. A classic demonstration of this is the McCollough effect (McCollough, 1965). After viewing a red-vertical grating alternated in time with a green-horizontal grating, an achromatic-vertical grating looks greenish, while an achromatic-horizontal grating looks reddish. Thus, the color changes are contingent on the orientation of the adapting patterns. If we think of the bright-red adapting grating as an oblique direction within the color-luminance plane and the achromatic test as vertical, then this aftereffect can again be accounted for by a bias away from the adapting axis. That is, the color change in the test is a tilt

aftereffect in color-luminance space that is selective for spatial orientation (Webster and Malkoc, 2000).

The functions of adaptation

The preceding sections show that adaptation can exert a powerful hold over our perception. But if this influence reflects function rather than fatigue, then we should see tangible signs that it is helping us to see better in everyday contexts. The benefits of light adaptation seem clear. The response range of neurons is very limited, but must be used to encode visual signals over a staggering range of light intensities. Adjusting to the average light level allows the retina to use its full dynamic range to encode the information carried by stimulus contrasts (Craik, 1940; Walraven et al., 1990). Multiplicative adjustments within the cones further allow the visual system to maintain lightness and color constancy by factoring out changes in the mean illumination. Compared to light adaptation, the effects of pattern adaptation appear more subtle, and it has proven much more difficult to demonstrate improvements in visual performance. However, there are several potential benefits.

GAIN CONTROL One possibility is that adaptation protects against saturation in cortical responses in the same way that light adaptation protects retinal responses. Recordings in striate cells show that prior adaptation tends to center the cells' contrast response functions around the adapting contrast, and this can allow cells to respond differentially to stimuli that before adaptation led to saturated and thus indistinguishable responses (Albrecht et al., 1984; Sclar et al., 1989). However, psychophysically, only a minority of studies have found that contrast adaptation can improve contrast discrimination (Greenlee and Heitger, 1988; Wilson and Humanski, 1993).

GAMUT MATCHING A related possibility is that contrast adaptation functions to match visual responses to the contrast gamut of the ambient environment to provide contrast constancy (Brown and MacLeod, 1997; Zaidi et al., 1998). In the case of color vision, an interesting example is provided by anomalous trichromats, who have M and L pigments with very similar spectral sensitivities. Because of this, the chromatic signal defined by the L-M difference is very weak, but adaptation might adjust the gain of postreceptoral channels to fill the available range (though whether this occurs in the retina or cortex is uncertain; MacLeod, 2002; Regan and Mollon, 1997).

NORMALIZATION The idea of gamut matching suggests that the visual system tends to settle around special states that may reflect expectations about the properties of the visual environment. Examples of these states include *white* for color

or *static* for motion. Many aftereffects can be seen as a consequence of renormalizations for these states, especially when the adapting stimulus itself appears more "neutral" over time. For example, with adaptation a background color appears less saturated, drifting patterns seem to slow down, and tilted bars may appear more vertical. These adjustments might compensate for mean biases in the world or correct for errors or distortions in the visual system of the observer (Andrews, 1964), thus providing a form of perceptual constancy. For example, we will see below that adaptive renormalizations could maintain constancy for image structure despite variations in retinal image blur.

DECORRELATION Pattern adaptation could plausibly improve not only coding within a channel but also coding across channels by removing redundancies between channel responses to provide more efficient representations (Barlow, 1990). Stimuli will often lead to correlated responses within a set of channels. By removing these correlations, adaptation could increase efficiency by allowing each mechanism to code independent information. Recent analyses of adaptation in cortical cells in fact support the role of adaptation in reducing redundancy (Carandini et al., 1997; Muller et al., 1999).

LEARNING Finally, by adjusting to the correlations between image properties, adaptation provides a mechanism for representing the stimulus associations in the environment and for learning about new ones (Barlow, 1990). This aspect of adaptation is considered further in the concluding section.

Adaptation and the natural visual environment

Whether adaptation is important to visual function hinges on whether it actually occurs in natural contexts. Again, there is no question of this for light adaptation. It is universally recognized that these adjustments are both a critical and an intrinsic part of the visual response to any stimulus. In fact, it would be meaningless to try to describe visual responses without assuming a particular state of light adaptation. But what of adaptation to tilted lines and waterfalls? Do the adjustments they reflect hold a similar status in perception? To assess this, it is important to ask how patterns of luminance and color vary within the kinds of natural images we normally encounter, and whether adaptation to these patterns can influence natural visual judgments.

EVOLUTIONARY ADAPTATIONS OF VISION Before exploring the rapid visual adjustments implied by visual aftereffects, it is worth remembering that the very structure of the visual system evolved as a long-term adaptation to the animal's visual environment. Recent studies have provided powerful insights into visual coding by characterizing statistical prop-

erties of natural images and then asking how these could best be represented by the visual system. For example, color opponency can be seen as a means of removing redundancies across the different cones (Buchsbaum and Gottschalk, 1983), while the spatial structure of receptive fields removes redundancies across space (Srinivasan et al., 1982). In visual cortex, individual cells respond to different scales or spatial frequencies in the image. The response bandwidths increase roughly in proportion to the preferred frequency (e.g., as f), while the amplitude spectra of natural images instead characteristically vary as the inverse of frequency (e.g., as $1/f$) (Field, 1987). The tuning of cortical cells therefore compensates for the low-frequency bias in natural scenes so that response levels in the cortex are independent of spatial scale (see Chapter 70).

SHORT-TERM ADAPTATIONS TO VARYING ENVIRONMENTS However, the visual environment is not fixed and thus cannot be represented optimally by a visual system with fixed properties. Moreover, the visual system itself undergoes pronounced anatomical and physiological changes during development and aging. Some adjustments in the tuning are therefore important in order to match the system to the ambient environment and to provide stable perceptions despite variations in the observer. Exactly what kinds of natural stimulus patterns the visual system might adjust to is an intriguing but still largely unexplored question. Yet it is clear that natural images provide a powerful stimulus for pattern adaptation.

Webster and Mollon (1997) examined changes in color appearance induced by adaptation to the color contrasts characteristic of natural outdoor scenes. Color in natural images is highly constrained and tends to vary along a limited range of axes in color space, from blue-yellow for arid scenes to a greenish S-LM axis for lush scenes. In the former case there is often a very high correlation between the signals along the cardinal chromatic axes, so that color in these scenes is not efficiently represented in the geniculate. However, contrast adaptation might adjust to this bias in the cortex, and observers in different environments should then be adapted by the prevailing colors in different ways. Figure 60.8 shows tests of this by measuring color appearance after adaptation to a succession of colors drawn at random from a natural scene. Light adaptation adjusts to the average color, while contrast adaptation induces large, selective changes in sensitivity to the blue-yellow axis of the adapting distribution.

As noted above, natural images have characteristic amplitude spectra to which the visual system might normalize spatial sensitivity. However, image spectra are not entirely constant, but vary because of differences in both scenes and the observer. For example, optical blur steepens the spectrum by reducing finer details in the retinal image, and thus there

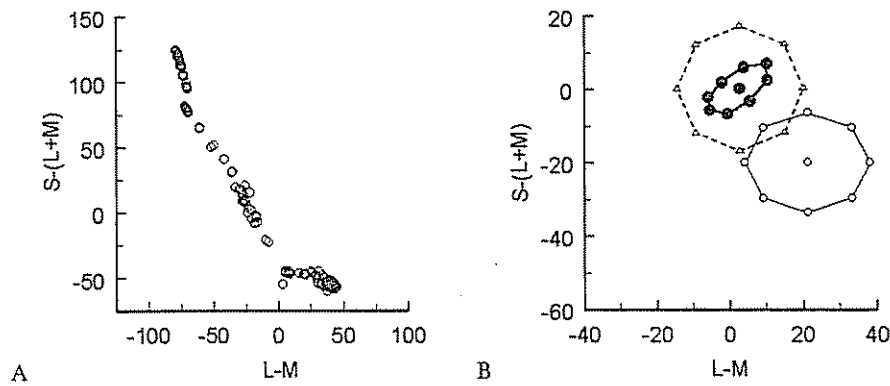


FIGURE 60.8. Adaptation to natural color distributions. Adaptation to the blue-yellow color variations in an arid scene (a) produces changes in color appearance that are strongly selective for the adapting axis (b). Test colors (unfilled circles) centered on the biased mean of the distribution are matched by colors centered around

white and compressed along the blue-yellow axis of the distribution (filled circles), showing the imprint of both light adaptation to the mean and contrast adaptation to the variations in the distribution. (Unfilled triangles plot the matches predicted by light adaptation alone.)

may be characteristic states of pattern adaptation associated with refractive errors. Visual acuity in fact increases after observers adapt for a period to optical defocus (Mon-Williams et al., 1998). Adaptation can also strongly affect the actual appearance of blur (Webster et al., 2002). Exposure to a blurred (sharpened) image causes a focused image to appear too sharp (blurred) (Fig. 60.9). Moreover, the blurred or sharpened adapting images themselves looked better focused the longer they are viewed, suggesting that adaptation is renormalizing perception of image focus. Figure 60.9 also shows a spatial analog of these effects induced by blurred or sharpened surrounds. Similar adaptation and induction effects also influence other judgments of the spatial statistics of images, such as the perception of texture density (Durgin and Huk, 1997). While these effects can be

very rapid, there may also be adjustments at much longer time scales. Fine et al. (2002) recently examined a subject who had had cataracts for decades. Even months after surgery, the world through his new lenses appeared overly sharpened.

The perceptual changes in blur adaptation are dramatic, possibly because the natural consequences of adaptation are best revealed by probing them with stimuli and tasks that are natural and relevant to the observer. Human face perception provides a clear example of such tasks. Observers are remarkably adept at recognizing and judging faces based on subtle differences in their configural properties and thus should be highly sensitive to any changes in configuration induced by adaptation. In fact, adaptation to a distorted face alters the appearance of subsequent faces (Webster and

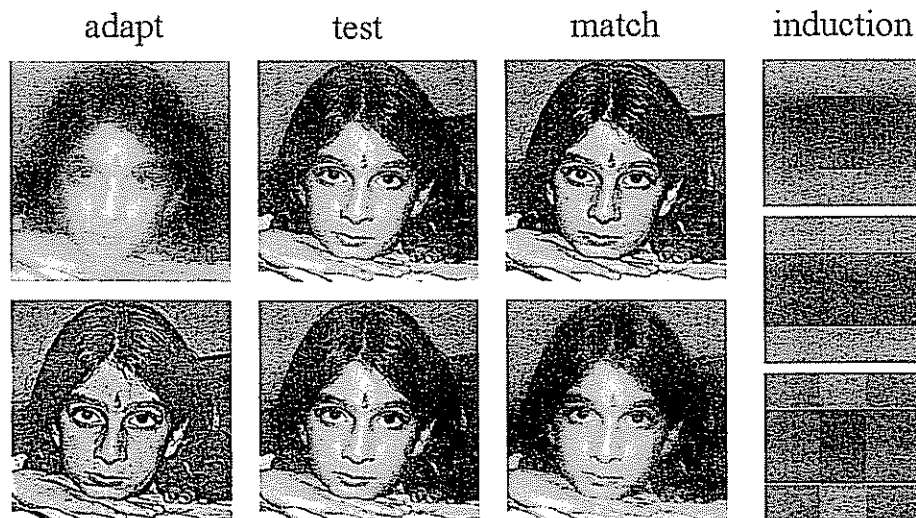


FIGURE 60.9. Adaptation to blur. A blurry adapting image causes a focused image to appear sharpened, or vice versa. Bars to the right show similar effects for induction. In each block the central

column of bars are all square edges. Yet the bars abutting the blurred edges appear too sharp, while the bars adjoining sharpened edges appear blurred.

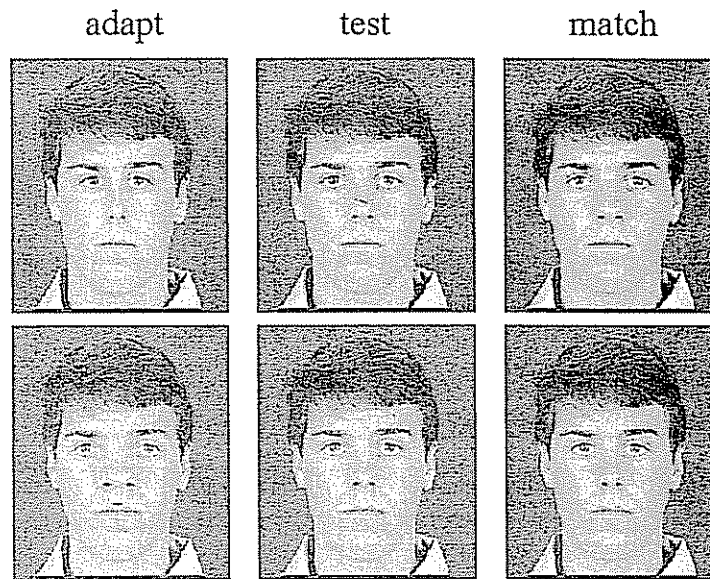


FIGURE 60.10. Adaptation to faces. Adaptation to a contracted face causes the original face to appear expanded, while an expanded face induces the opposite aftereffect.

MacLin, 1999) (Fig. 60.10). Large biases in recognition also occur for adapting and test images that are defined by the configurations characterizing real faces (Kaping et al., 2002; Leopold et al., 2001). Given that we are all exposed to a different diet of faces that are naturally “distorted” relative to the average human face, it seems likely that these adaptation effects influence many aspects of face recognition in everyday viewing. Recent studies have shown that face aftereffects are surprisingly unaffected by large changes in size or location between the adapting and test images (Leopold et al., 2001; Zhao and Chubb, 2001). This strongly suggests that the adaptation involves adjustments to the configural properties of the face, rather than to local, low-level features, and thus supports the possibility that the sensitivity changes reflect processes specialized for face coding. It seems probable that many other aspects of higher-level object recognition are similarly shaped by adaptation.

Adaptation and the phenomenology of perception

What are the implications of such adaptation effects for the subjective experience of seeing? One possible implication concerns whether we have shared or distinct perceptions (Webster, 2002). A long-standing philosophical question is what the world might look like if we could see it through the eyes of another. The private nature of our conscious experience may preclude a complete answer, but it is tempting to speculate that any answer will be constrained in important ways by the processes of adaptation. As the preceding sections illustrate, adaptation normalizes our perception according to properties of—or expectations about—the physical world. To the extent that two observers are adapted

to different environments, their visual systems will be normalized in different ways and their subjective experience should differ. For example, if you and I are exposed to a different population of faces, our perception (and not just our judgments) of the same physical facial characteristics are unlikely to agree. To the extent that two observers are exposed to a common environment, adaptation will tend to normalize their perception toward a convergent experience. For example, even if you and I have different refractive errors, our perceptions of image focus may converge because these differences are partially discounted by adaptation to the common spatial structure of scenes. Notably, in both cases, it is the similarities or differences in the environment—and not the intrinsic differences between observers—that determine how the visual system is normalized. Thus, at least some aspects of our private internal experience are controlled by public external variables that can be objectively measured.

The effects of adaptation also have important implications for the actual contents of visual awareness. The decorrelation model proposed by Barlow was built around the idea that adaptation serves to discount ambient information in order to enhance sensitivity to novel patterns. These novel patterns, or *suspicious coincidences*, may be the most important information to the observer, and thus processes that highlight them may be highly beneficial (Barlow, 1990). The role of adaptation in regulating visual salience remains largely unexplored, because most studies have focused on understanding how adaptation influences the encoding of the adapting pattern itself. However, the negative aftereffects characteristic of adaptation support this view, since they “draw attention” to the ways in which the test differs from

the adapter. In this regard, it is interesting to note that the consequences of adaptation are often much more striking in the test stimulus than in the stimulus to which we are adapted. Thus, the perceptual aftereffects of color and form are vivid imprints of sensitivity changes that often pass unnoticed during adaptation. If adaptation is part of our everyday visual experience, then perhaps most of what we notice about the world is a perceptual aftereffect.

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