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Color Contrast Adaptation

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Synonyms

Colorfulness adaptation; Habituation; Variance adaptation

Definition

Changes in sensitivity or appearance in response to spatial or temporal variations in color

Concepts

All sensory systems continuously adjust sensitivity or adapt to match their responses to the current stimulus context. In vision, these adjustments occur at many levels along the visual pathway and adjust to most if not all of the properties encoded by the visual system, from simple image features to high-level representations like the attributes of a face [1]. Thus adaptation to color is a specific example of a very general and ubiquitous process affecting everything we see.

Most studies of color or "chromatic adaptation" have focused on the changes in sensitivity and perception resulting from exposure to a change in the average color of the stimulus [2]. Chromatic adaptation begins as early as the photoreceptors, which like a camera must adjust their limited response range so that it is centered on the current light level. Since the different cone classes are each light adapting independently, a light that differentially stimulates the cones will lead to a change in the relative sensitivity to different spectra. For example, a longwave (reddish) spectrum is a strong stimulus for the L cones while a weak stimulus for the S cones. Thus in the presence of this light the L-cone sensitivity will be reduced while the S-cone sensitivity will be increased. Sensitivity changes that occur independently in the cones and vary inversely with the light level are known as von Kries adaptation. Adjustments of this kind tend to renormalize color percepts so that the cone signals are equated for the current spectrum. Thus after adapting to the longwave spectrum the responses in the L and S cones will become more similar and the initially red light will appear more gray. In turn, a light that appeared gray before the adaptation will appear bluish after adapting, as a negative afterimage of the red adapting color. This chromatic adaptation is thought to play an important role in color constancy, by adjusting sensitivity to discount

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changes in the color of objects resulting from changes in the illumination [3].

However, in addition to the mean, color vision also adapts to the range or variance of the color distribution. These adjustments are known as contrast adaptation [2]. Contrast adaptation is again a very general process and has been very widely studied in the case of spatial vision, where it is the range of luminance levels that is typically varied [4]. For example, exposure to a high contrast grating (alternate light and dark bars) results in a loss in contrast sensitivity. The threshold contrast difference for detecting the grating increases, while the apparent contrast of visible gratings decreases. These effects are selective for the spatial properties of the grating. That is, sensitivity is reduced for patterns that have a similar size (spatial frequency) or orientation as the adapting grating, while little affected for spatially distinct patterns. This also again leads to negative aftereffects in the appearance of other patterns. After adapting to a tilted grating, a vertical grating appears tilted in the opposite direction (the tilt aftereffect) and the perceived size or spatial frequency of gratings appears biased away from the adapting grating. Like the example above of the cones, these results are again consistent with gain changes in different mechanisms or visual "channels" sensitive to different spatial properties of the stimulus, each adjusting according to the level at which they are stimulated. Indeed, measurements of the selectivity of the aftereffects of contrast adaptation were a primary tool in the study of spatial and temporal vision and in the development of channel models of visual coding [4]. For this reason, adaptation has often been described as "the psychologist's electrode." However, it should be noted that the aftereffects also depend on the network properties and interactions within the system and thus not simply on how each mechanism adapts in isolation [5].

History

Contrast adaptation in the context of color vision has received much less attention, and there are far fewer studies compared to chromatic (mean) adaptation. It is nevertheless an important and robust phenomenon with important functional implications. While some earlier studies examined adaptation to temporal color contrast (flicker), a study by Krauskopf, Williams, and Heeley [6] was seminal in exploiting color contrast adaptation to examine the color selectivity of the aftereffects. Their stimulus was a sinusoidal modulation of the color or luminance of a uniform field along different directions in color space. All had the same mean and thus produced the same state of chromatic adaptation. However the flicker reduced sensitivity to detecting a color change (an effect they called habituation), and these effects were again selective for the color of the adapting stimulus. For example, adapting to reddish-greenish flicker made it harder to detect these colors than other colors. These aftereffects could not be accounted for by response changes in the receptors, and instead pointed to desensitization in postreceptoral mechanisms that drew on different combinations of the cone signals. For instance, adapting to achromatic flicker strongly modulates the signals in all of the cones. This reduced sensitivity to luminance variations (in mechanisms that sum the cone inputs), but had little effect on chromatic variations (which are instead detected by mechanisms sensitive to the differences between the cone signals). The pattern of selectivity revealed three primary adaptable mechanisms tuned to achromatic stimuli or to chromatic stimuli that varied the excitation of the L vs. M cones or the S cones versus the L and M cones. These were thus identified as the "cardinal directions" of color space and were subsequently shown to correspond to the color tuning of the primary pathways carrying information from the retina to the cortex [7]. The cardinal axes have since become a standard metric for designing and interpreting experiments in color vision, impacting thousands of studies. It is therefore noteworthy that it was through color contrast adaptation that they were first firmly established, though again surprisingly few studies have followed up on the properties and consequences of this adaptation.

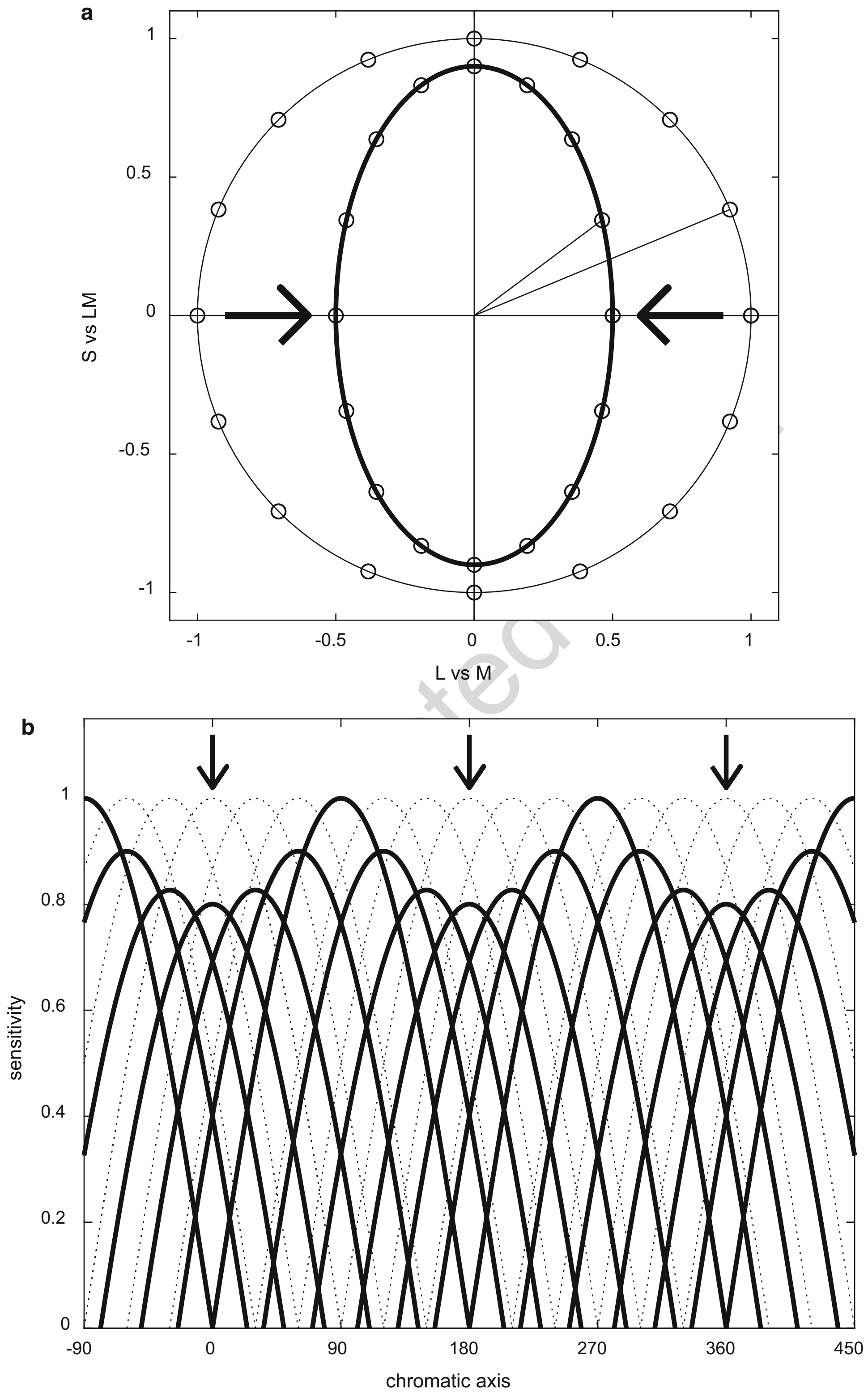
Further analyses by Krauskopf and colleagues showed that there was also some selectivity of the adaptation for chromatic directions intermediate to the cardinal axes [8]. This finding established the presence of additional "higher order color mechanisms," which have also strongly influenced modern approaches and theories about human color vision. Subsequently Webster and Mollon [9] explored how the adaptation to temporal color contrast affected color appearance. The adaptation produced large and selective changes in both saturation and hue. Specifically, adapting to a given axis in color space (e.g., a modulation along the LvsM cardinal axis) reduced perceived contrast (saturation) the most along the adapting axis, and biased the perceived hue of other chromatic directions away from the adapting axis and toward an orthogonal direction in color space (Fig. 1a). For example, the LvsM adaptation caused a previously pure blue or yellow hue to appear less like the LvsM (reddish-cyan) axis and more like the hues (purple or lime) of the S cardinal axis. Both the saturation and hue changes are consistent with a loss of sensitivity in the mechanisms tuned to the adapting mechanisms, though there is also evidence for a dissociation, since at high test contrasts, colors can exhibit a large hue bias despite small changes in their perceived contrast.

Key Principles

The adaptation-induced biases in hue are similar to spatial orientation aftereffects, but reflect tilt aftereffects in the perceived direction (hue) within color space. As with spatial orientation, the changes in color appearance from contrast adaptation can be selective for any arbitrary color direction, again implicating multiple mechanisms tuned to different directions in color space. However, unlike the tilt aftereffect, which at best produces a subtle bias in perceived orientation (about 2 deg), the biases in hue can be dramatic and up to 30 deg. or more. This difference is consistent with a broader tuning for hue mechanisms compared to orientation channels, at least at the level at which the adaptation is occurring. The common effects of adaptation across different stimulus dimensions point to common coding principles underlying the representations for different visual attributes [1, 4]. In particular, they suggest that the kinds of multiple-channel population codes that are widely assumed for form and motion perception also underlie the representation of color appearance (Fig. 1b). The representation implied by contrast adaptation is thus very different from the traditional two-channel (red vs. green and blue vs. yellow) model of opponent color theory, but is consistent with a wealth of behavioral and physiological evidence for multiple higher order color mechanisms.

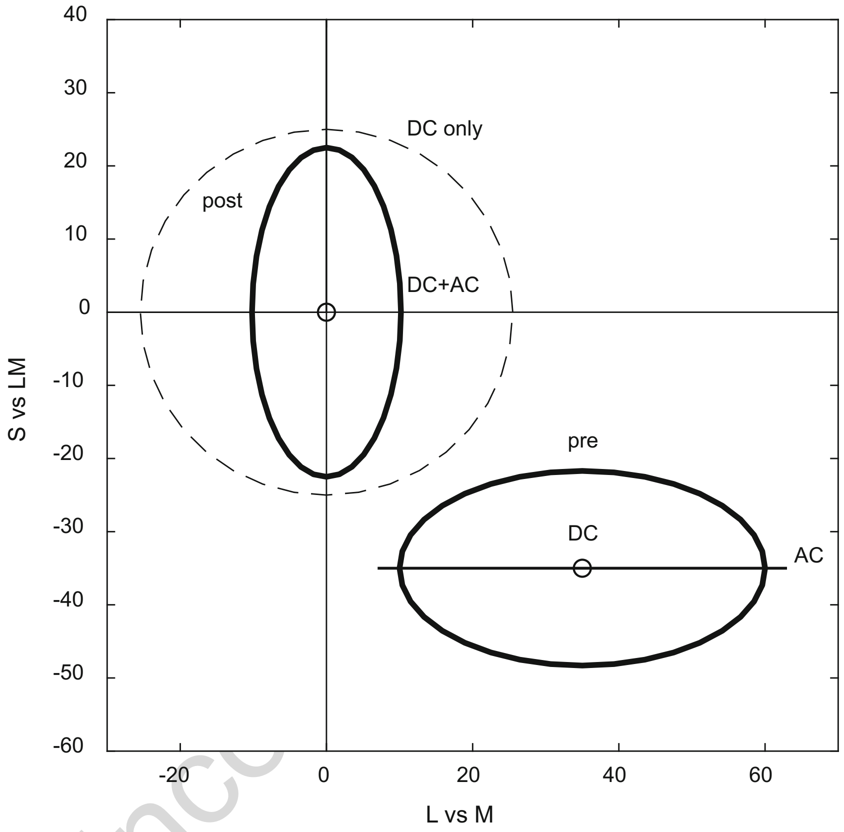
In contrast to chromatic adaptation, the primary sites of the sensitivity changes in color and spatial contrast adaptation are thought to be cortical. This is suggested by the fact that the color aftereffects are also selective for spatial properties of the stimulus like orientation and that the adaptation shows some interocular transfer, properties that the neurons first become selective for in primary visual cortex. Cells earlier in the visual pathway show weak adaptation to chromatic contrast, though the degree of adaptation observed depends on the approach to measure it. Neural correlates of contrast adaptation have also been found in the response changes in single cells or in the brain activity (BOLD responses) measured by fMRI. However, the actual relationships between different neural and perceptual measurements of contrast adaptation are complex and uncertain.

Thus in terms of their properties, chromatic adaptation and contrast adaptation reflect adjustments to two different statistics of the stimulus (the mean and the variance) arising at two different stages of the visual system (retinal and cortical) [2]. Consistent with this, the two types of adaptation produce separable effects on sensitivity and appearance (Fig. 2). Both types of adaptation also have a spatial analog. Just as a uniform color surround alters the hue of a central field (simultaneous color contrast), surrounding a field with a high-contrast background alters the perceived contrast, an effect which once more reflects very general processes of contrast normalization in sensory systems [10].



Color Contrast Adaptation, Fig. 1 (**a**) Effects of contrast adaptation on color appearance. The outer circle depicts a set of test stimuli with equal contrast but spanning different angles within the LvsM and SvsLM plane.

Color Contrast Adaptation, Fig. 1 (continued) Adaptation to the LvsM axis (arrows) selectively reduces sensitivity to the LvsM component of each test stimulus. This reduces perceived contrast (saturation) and also rotates the perceived hue angle away from the adapting axis. (**b**) Both the contrast and hue changes are consistent with response changes in multiple mechanisms tuned to different axes in the chromatic plane. Adaptation to the LvsM axis (arrows) reduces the responses in mechanisms sensitive to this axis, thus biasing the distribution of responses across the cannels



Color Contrast Adaptation, Fig. 2 Combined effects of chromatic adaptation and color contrast adaptation. "Pre" shows a set of colors centered on a yellowish mean (DC) chromaticity, while "post" plot the perceived colors after adaptation. Chromatic adaptation adjusts to the DC color so that it appears gray and shifts the set of colors so that they appear centered on the origin (DC only). If observers are adapted to the same mean DC chromaticity but contrast is varied along the LvsM axis (AC,) then in addition to the mean color change there is a loss in perceived contrast along the LvsM axis (DC + AC)

Phenomena

Both types of adaptation are important in natural viewing [1]. For example, the perceived contrast or colorfulness of natural or artificial images depends on the contrasts of the images that observers are adapted to. Color contrast in natural scenes is not random and instead tends to have a strong blue-yellow bias in part because of the dominant colors of earth and sky. The visual system is thus naturally exposed to stronger blue–yellow contrasts. Adaptation to this predicts the consistent finding that observers tend to be less sensitive to blue–yellow stimuli compared to other chromatic directions. These sensitivity differences are also evident in most uniform color spaces, which attempt to scale stimuli so that equal perceptual differences correspond to equal distances within the space. In these spaces the differences in cone signals are larger along the blue–yellow quadrant, implying weaker visual sensitivity. Ecosystems also vary systematically in their color contrasts and this suggests that individuals exposed to different environments (e.g., a forest or desert) may be held in different states of contrast adaptation. Moreover, contrast adaptation is also likely to be a factor in how the visual system adapts to the unnatural environments than humans increasingly occupy. An important case is the new generation of wide gamut lighting and displays. These increase the chromatic contrasts that observers are exposed to, and this predicts that adaptation to this increase will consequently reduce their contrast sensitivity.

It is less well appreciated that both chromatic and contrast adaptation also adjust to variations within or between observers [1]. For example, it is in part because of these adjustments that color perception remains relatively stable as we age or as the world falls on different retinal locations [11]. The stability arises because in this case the visual system is recalibrating to match a world that itself remains stable. In the case of contrast an intriguing example is how the world might appear to a color deficient observer. Anomalous trichromats retain three kinds of cones but with only small differences in the spectral peaks of their two longer-wave pigments. This reduces the reddish-green contrasts signaled by these cones, yet the visual system could potentially adapt to the weakened contrast and thereby increase sensitivity so that these colors appear stronger. To mediate this stability, the mechanisms of adaptation must themselves remain stable with aging, and importantly, color contrast adaptation appears to remain robust across the adult lifespan, with potentially even larger adaptation effects in older populations.

The timescales of color contrast adaptation are not well characterized, and there is conflicting evidence as to whether or not the effect can build up with longer periods of adaptation. Strong aftereffects of spatial contrast adaptation can occur with brief exposures, and at least some adjustments can occur within a few milliseconds, recalibrating perception with each eye movement. For other adjustments it is advantageous to average over longer times (e.g., to adjust to the average color or contrast of a scene rather than to each individual surface as it is fixated). There is also growing evidence for adaptation effects that unfold over hours, days or even months [12]. A classic example is the McCollough Effect, in which the color aftereffects are contingent on the spatial orientation of the adapting pattern [13]. These aftereffects may persist permanently until they are actively extinguished by adapting to the complementary stimulus. However, it is not known how the McCollough Effect – or for that matter other types of long-term adaptation – are related to the short-term response changes measured in conventional studies of contrast adaptation.

Because the general ways that chromatic and contrast adaptation alter color perception are known in principle, it is possible to simulate how the world might look to observers adapted to different environments or different observers adapted to the same environment [14] (Fig. 3). This process of adapting the images rather than the observer also has the advantage that adaptation can be simulated for very long timescales that are impractical to study by changing the observer. Measuring visual performance for these adapted images can then reveal some of the perceptual consequences and advantages of contrast adaptation, by assessing what observers can see and do with images that have been adapted to better match their current sensitivity [15].

Function

The fact that adaptation is a hallmark property of all sensory processes suggests it confers essential advantages, and a wide variety of interrelated functions have been proposed [1]. One set derives from information theory and emphasizes the role of adaptation in optimizing coding efficiency by matching the limited response range of neurons to the current range of stimuli. This also predicts the role of adaptation in normalizing or equating the

Color Contrast Adaptation, Fig. 3 Monet's Sunrise (Marine). The palette of the original left image was adapted to equate the mean and contrast to a color distribution characteristic of natural outdoor scenes (after [14]). Digital image courtesy of Getty's Open Content Program

responses across different mechanisms. This normalization is also closely related to ideas about how adaptation contributes to perceptual constancy. If the world or the observer changes, then adaptation implements a compensatory adjustment to discount the change and thus stabilize perception. A further related advantage is predictive coding, in which the sensory system adapts to remove the response to the absolute or expected stimulus level in order to preserve resources for signaling the relative differences or unexpected properties. In turn, this principle has been associated with the hypothesized effects of adaptation on heightening the perceptual salience of novel colors or spatial stimuli in the environment.

Cross-References

- ▶ Adaptation; Afterimage
- ▶ Chromatic Scene Statistics
- ▶ Color Processing
- ▶ Color Scene Statistics
- ▶ Color Vision
- ▶ Cortical
- ▶ Opponent Theory

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