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Long-term adaptation to color

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When the environment changes, the visual system adjusts to maintain accurate color perception. Such adaptations happen at different time scales, and long-term effects are of particular interest because they may engage mechanisms of long-lasting neural plasticity. Long-term adaptation to changes in the color of the environment produce strong and long-lasting changes in color perception, with the general effect of neutralizing the dominant color. Large individual differences and details of the time course are currently unexplained, and the limits of adaptation remain unexplored. Experience with an environment appears to allow observers to adapt more strongly and quickly to it. Long-term color adaptation may serve as a model system for understanding general mechanisms of neural plasticity, including those relevant for therapies for visual disorders.

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How plastic is the visual system? One approach to this question places observers in novel environments, where, to keep them seeing well, their visual systems must adapt. Research into long-term visual adaptation began in the 1890’s, with Stratton’s experiments with inverting prisms, and interest has waxed and waned over the years [1]. The topic is once again trending, as therapies based on methods of inducing long-term visual plasticity are tested on visual disorder patients. For example, playing video games and watching movies with displays intended to rebalance the eyes may improve vision in people with amblyopia (‘lazy eye’, reviewed in Ref. [2]). To improve these therapies, we need to know how to produce stronger, more permanent, and more generalizable changes in visual perception. Because its basic mechanisms are relatively well understood, color vision may serve as a model system in which to answer these questions.

This paper reviews how experience can produce long-lasting changes in adult color perception (Box 1). Investigations of adult visual plasticity can be divided between those that train observers on a specific task, known as ‘perceptual learning’, and those that manipulate the environment in which observers can perform many different tasks, ‘adaptation’. Most studies of color vision are of the latter type (though for a recent exception, see Ref. [3]). A typical experiment, for example, measures changes in color perception that occur as an observer wears deep red glasses for multiple days.

Formal measurements of color perception

Changes in perceived colors produced by environmental changes are often quantified by asking observers to adjust the color of a small patch, usually on a black background, until it appears neutral (Figure 1). In one version of the task, observers set neutral points relative to a subset of colors, for example ‘unique yellow’ that appears to contain neither red nor green, while another involves finding colors that appear fully neutral, that is, they appear gray or ‘achromatic’. As observers adapt to an environment, and their perception changes, the color coordinates (Box 1) that they set to be neutral shift. For example, wearing red lenses causes unique yellow to be set to more and more reddish coordinates over time [8,9] (Figure 1d).

Many other measures of color perception are possible, of course (e.g. other articles, this issue). Neutral settings have proven useful because they do not require memory, because observers can make them with high reliability, and because they can often be used to predict the perceived colors of many other stimuli (e.g. [10]).

Long-term adaptation to colored lenses

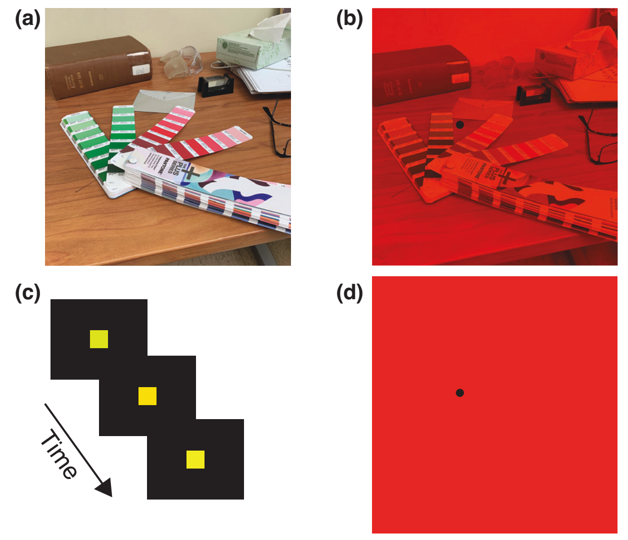
When the mean color coordinates of the environment shift suddenly away from what we are accustomed to, the color appearance of the world gradually shifts back toward what is was before the change. For example, immediately after putting on sunglasses the world appears tinged with the lenses’ color, but the tint fades over time. The first published observation of this phenomenon was in 1694 by de la Hire [11], a polymath better known for contributions to astronomy and mathematics. In many situations, particularly for smaller changes in illumination or lens color, much of the compensation happens instantly and has been studied as ‘color constancy’ (for reviews, see Refs. [12,13]). Other perceptual consequences evolve over time. Short-term effects of adaptation to changes in mean color coordinates, from seconds to minutes, have been well characterized [14,15].

Box 1 Quantifying colors

Visual environments are complex, and a great success of the field has been to develop ways to describe them quantitatively. Calculations begin with the spectra of light reaching the eye from all points in the scene, which are the relevant input for color (and all) vision. Because, under normal viewing conditions, light spectra are absorbed by just three classes of photoreceptors, complete descriptions of this input can be computed as just three numbers, such as hue, saturation and brightness, the x,y, –z, coordinates of the CIE color space, or the relative excitation of the long-wavelength, medium-wavelength, and short-wavelength sensitive cones. Accordingly, we will term the physical stimulus for color perception as **'color coordinates'**.

Given a quantification, the simplest way to characterize the physical attributes of a scene is by its mean value, which roughly corresponds to the dominant color. The next simplest is to consider its variance with respect to the mean; in vision science the term contrast is used to capture the range of the different color coordinates visible in the scene (e.g. different saturations). Combined, these statistics provide us with the gamut of colors present in a given scene, which varies in different environments (Figure 1a and b).

Figure 1



Current Opinion in Behavioral Sciences

Methods used in long-term adaptation studies. **(a)** An office scene. **(b)** An office scene photographed through a strong red lens. Natural images generally differ in both mean and contrast [4–7], and most manipulations in experiments discussed here, such as changes in the color of illumination or lenses, change both as well. The red lens causes the world to be dominated by redness but also reduces the range of colors of a particular hue that are present (a change in contrast, for example, the scene now contains very little green). **(c)** To set unique yellow, a neutral point, observers adjust the color of a small patch to appear a yellow that contains neither red nor green. **(d)** To simulate effects similar to a small amount of adaptation to red lenses, stare at the dot for 30–45 s and then shift gaze to the corresponding dot in panel b. Notice (without moving your eyes, and after a few seconds of perceptual stabilization) how the envelope's perceived color is now more neutral in appearance and the other patches may appear more colorful. These effects become stronger over hours and days of adaptation.

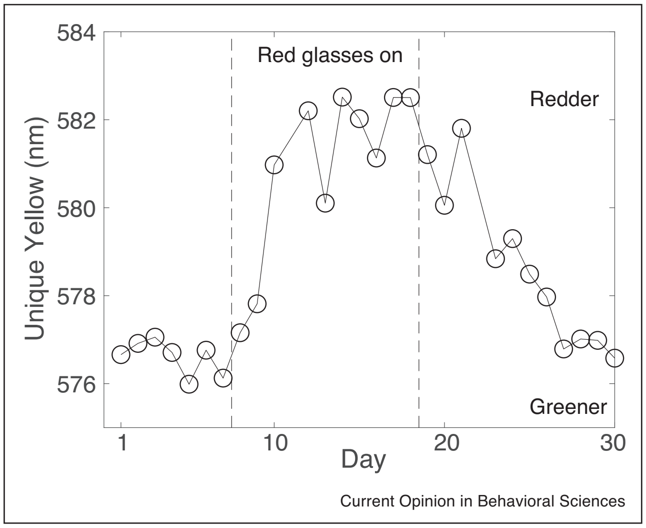
Though the manipulation required for studying longer-term changes is remarkably simple — observers can just wear colored lenses or sit in a room with filtered lighting over a number of days — surprisingly few multiple day experiments have been conducted. The first published report consisted of a single observer's qualitative observation that the world regained its normal appearance over time [16]. Since that time, fewer than 20 observers have been tested in total, with about one paper appearing every decade [9,10,16–19,20••].

What are the effects of multiple days' adaptation to colored lenses? Formal measurements agree with Kohler's initial observations that the world viewed through the lenses comes to regain its prior appearance. For example, wearing red glasses or being exposed to a red environment causes unique yellow settings to shift by greater and greater amounts across days (Figure 2; [8,9,18]). The shift is in the direction of more reddish color coordinates, indicating that what previously appeared reddish is becoming more neutral over time, canceling the effects of the lenses or lighting. Effects of multiple-day adaptation are much longer lasting than the effects of short-term adaptation [8], remaining robust when measured the morning after a day of wearing lenses, before donning them for a subsequent day [9,18,19]. Because of this endurance, observers often are adapted for only part of each day [9,18,19,20••].

The effects of long-term adaptation are likely due to neural mechanisms that are independent from mechanisms of short-term adaptation. One piece of evidence for this is the lack of an interaction: Long-term adaptation causes an equal shift in unique yellow, whether short-term adaptation is present or not [19]. A second piece of evidence for independence is that simple after-images, due to short-term adaptation, are centered around the shifted neutral point produced by long-term adaptation [20••]. For example, short-term adaptation to the color that appears neutral following long-term adaptation produces little to no afterimage.

Details of the time course of adaptation across days remain unclear, however. Strong individual differences are evident both within and across reports [9,18,20••]. Some observers showed neutral points that shifted gradually across 10 or even 20 days. However, others showed large shifts primarily during the first day or two of adaptation. Some showed only small effects in total across days, and some appeared to adapt nonmonotonically, with effects declining after initially strengthening. This individual variability also makes it difficult to determine whether adaptation asymptotes, that is, whether there is a limit to the amount that can be produced.

Figure 2



Sample long-term adaptation effects. Data are replotted from an observer in Neitz *et al.* [9]. After donning red glasses, unique yellow shifted toward redder color coordinates, and slowly returned to its prior values after the glasses were removed.

Effects may also depend upon the strength of the color changes being adapted to. In one recent study with six observers, adaptation did not grow measurably across five days, though it did strengthen over the course of each day [20••]. The yellow lenses used in this study likely produced smaller changes in the scene color coordinates than the red lenses used in prior work, which may have limited long-term adaptation.

Does the world seen through colored glasses ever appear completely normal? For weaker lenses, this may happen almost immediately, through the very rapid mechanisms that support color constancy [20••]. For stronger lenses, formal measurements are lacking. In order to isolate longer-term effects, past work intentionally attempted to foil constancy mechanisms, by testing with a small patch of light on a black field in a darkened room. How the natural world appears after long-term wear of strongly colored lenses remains unmeasured, except through introspection [16].

The neural mechanisms of long-term adaptation also remain relatively unexplored. Color perception begins with the absorption of light by the cone photoreceptors, continues in retinal neurons that combine cone outputs in opposing fashion, and in further cortical stages where responses to colors become even more complex. Short-term adaptation to changes in mean color coordinates can be well explained by gain changes in cone signals (von Kries adaptation [21]), and this may account for some of the effects observed with colored lenses. However, the bulk of such gain changes likely take place in the retina, and so cannot explain the interocular transfer of longer-term adaptation reported in one experiment [9]. Adapting to colored lenses likely also depends upon second-stage 'color-opponent' mechanisms that compute sums and differences of cone signals. Shorter-term adaptation to color contrast is known to produce gain changes in these mechanisms (see below), and such effects generally show interocular transfer [22].

Natural experiments

Natural experiments provide additional evidence of long-lasting adaptation to changes in scene color. As people age, the lens of the eye yellows, shifting the spectrum of light reaching the retina. Neutral settings in older observers do not show a corresponding shift, however, indicating that long-term adaptation occurs [23–26]. When the yellowed lens is replaced as treatment for cataract surgery, the long-term adaptation is evident as a negative aftereffect; because the more yellow scene has become neutral, the unfiltered world appears bluish. Remarkably, this aftereffect takes months to fade [27].

A related natural manipulation is the slow changes in the color of the non-equatorial environment that occur across seasons, due to green plant life in the warmer months. Unique yellow settings shift toward greenish color coordinates in the summer, indicating that observers neutralize, to some extent, the shift in the natural environment ([28•]; for a review of older attempts to address this question, see Ref. [29]).

Learning to adapt

Can observers learn to adapt more rapidly and strongly to environmental changes as they gain experience with them? This question has received attention since the earliest studies of both prism glasses and colored lenses, because it may implicate 'learning' that could differ in mechanism from adaptation [16,30]. Some evidence suggests that the answer for color vision may be 'yes'. People who were prescribed colored glasses (as a treatment for 'visual stress' [31]) provided a natural manipulation in which to examine the issue. These observers showed stronger immediate adaptation to their prescribed color than did naive observers, suggesting that they had indeed learned to adapt more efficiently [32••]. Such learning also provides an alternative account for Tregillus *et al.*'s [20••] results. The color changes produced by yellow lenses may be similar to natural changes in illumination (e.g. illumination by direct sun versus blue sky), and observers may have already learned to rapidly and strongly adapt, precluding the need for further changes in adaptation strength across days.

Recent related work has tested whether humans in fact have learned to immediately compensate for common illuminant changes; that is, whether color constancy is better for naturally occurring lights. Earlier work suggested that compensation for familiar, natural illuminants is not better than for other illuminants [33], but more recent results with different paradigms suggest that experience may have an effect [34–36]. However, because our experience with natural illuminants begin at an early age, these effects could be due to developmental plasticity. It is an open question whether adults can learn to improve color constancy for a particular illuminant.

An alternative approach is to create unusual changes to the environment, that observers have presumably never experienced before, and test whether they can learn to adjust. One early report recounted experience in a 'negative' gray-scale world, seen through a video camera and on a television monitor, where contrast was reversed [37]. A more recent report used a head-mounted video camera connected to virtual reality goggles to place observers in an environment where scene color coordinates were rotated in hue, with red mapping to blue, blue mapping to green, and green mapping to red [38•]. Interestingly, the two observers reported initial failures of color constancy: when room lights were turned on and off perceived colors of objects changed dramatically. Over the course of days, however, the constant appearance of objects returned.

Long-term adaptation to contrast

Most of the work reviewed above used manipulations that affect both the mean and contrast of the environment. Many laboratory studies isolating contrast adaptation have examined effects of short-term exposure to patterns of stripes, balanced to not disturb the mean of the adapting scene (beginning with [39,40]). Recently, a few have measured effects of longer-term adaptation to changes in contrast, for example [41]. One recent study focused on chromatic contrast; observers adapted to high contrast red-green grating patches for an hour, five days in succession [42]. However, no evidence for long-term adaptation to color contrast was found. Adaptation strength asymptoted within a few minutes and did not change in strength or speed across the five days tested.

A related line of work adapted observers to monocular long-term changes in contrast. In adults, the balance between the two eyes can be temporarily changed by patching one with a translucent occluder, reducing the contrast available to it [43]. Eye balance is measured through tasks that present different images to each eye, for example, binocular rivalry, where perception alternates between two unfusable images. Following patching, percepts are biased toward those dependent upon information from the patched eye, indicating an increase in strength of the signals originating from it (for a recent review see Ref. [2]). This increase can last for relatively long durations following return to the normal environment.

The role of color in adaptation to monocular contrast deprivation remains unclear. Conflicting results have been reported on whether changes in eye balance last longer when tested with colored versus black and white patterns; results likely depend upon the type of test administered [44,45••]. Depriving one eye of luminance contrast while leaving color contrast present in both eyes (accomplished by presenting processed videos separately to the two eyes) produced effects selective for luminance test patterns [45••]. However, depriving an eye of color contrast (by showing it black and white movies, while the other eye viewed unaltered color movies) produced little effect on eye balance, for either color or black and white tests.

Finally, probably the most well-studied long-lasting adaptation to color contrast is the McCollough effects, where alternating pairs of colored stripes produce negative after effects [46,47]. Famously, a few minutes of adaptation can produce effects that last weeks. The relationship between this and other forms of long-term color adaptation remains unclear.

Conclusions

Adult color vision adapts to long-term changes in the environment. Adaptation becomes stronger and longer lasting as the adapting duration lengthens from hours to days to weeks. Surprisingly few observers have been tested in long-term paradigms, however, and there are large unexplained individual differences in adaptability across observers. Experience with particular environments appears to allow more rapid and stronger adaptation, but this remains to be shown in controlled laboratory experiments.

The neural mechanisms of long-term adaptation to color are also largely unstudied. Better understanding of them could have a number of translational applications. For example, in color anomalous observers, signals in color opponent mechanisms that compute reddish versus greenish (long-wavelength cone signals minus medium-wavelength cone signals) may be reduced compared to normal observers, which in turn may diminish the perceived colorfulness of the natural world. Understanding how and when long-term adaptation produces gain changes in color opponent mechanisms could inform therapies designed to alter the affected mechanisms . Such therapies could involve perceptual learning approaches, the wearing of colored lenses, or other novel interventions. Similar approaches may also aid color perception in gene therapy treatments for dichromacy.

Finally, better understanding of long-term adaptation will also add to general knowledge of adult neuroplasticity. Central theoretical issues addressable with color adaptation include: What limits the maximal attainable amount of neural change in response to changes in the environment? What determines how such changes generalize to other environments? And what underlies individual differences in the amount of neuroplasticity? Better answers to these questions could eventually aid treatment for many disorders, both visual and nonvisual.

Conflict of interest statement

Nothing declared.

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