# Visual mode switching: Improved general compensation for environmental color changes requires only one exposure per day

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**When the visual environment changes, vision adapts in order to maintain accurate perception. For repeatedly encountered environmental changes, the visual system may learn to adjust immediately, a process called "visual mode switching." For example, following experience with red glasses, participants report that the glasses' redness fades instantly when they put the glasses on. Here we tested (1) whether once-daily experience suffices for learning to switch visual modes and (2) whether effects of mode switching apply to most stimuli affected by the environmental change. In Experiment 1, 12 participants wore bright red glasses for a single 5-hr period each day for 5 days, and we tested for changes in the perception of unique yellow, which contains neither red nor green. In Experiment 2, we tested how mode switching affects larger parts of the color space. Thirteen participants donned and removed the glasses multiple times a day for 5 days, and we used a dissimilarity rating task to measure and track perception of many different colors. Across days, immediately upon donning the glasses, the world appeared less and less reddish (Experiment 1), and colors across the whole color space appeared more and more normal (Experiment 2). These results indicate that mode switching can be acquired from a once-daily experience, and it applies to most stimuli in a given environment. These findings may help to predict when and how mode switching occurs outside the laboratory.**

## Introduction

When the visual environment changes, the visual system also alters its responses, optimizing its function to keep us seeing well. This adaptation happens gradually and plays a key role in maintaining accurate perception in different environments (Clifford et al., 2007; Kohn, 2007; Wark et al., 2007; Webster, 2015). For example, putting on sunglasses causes the world to appear tinted with the lens' color, but as the visual system adapts, the tint fades away and the world gradually appears normal.

For repeatedly encountered environmental changes, it would be beneficial if the visual system could learn to adjust to them more rapidly and strongly. For example, adjustment to prescription spectacle lenses may take time when first worn, but readaptation may be almost instantaneous. The more rapid adjustment could serve the many perceptual goals aided by adaptation generally, including detection and discrimination of objects and their properties (e.g., Dragoi et al., 2002; Krekelberg et al., 2006), facilitating perceptual constancy (e.g., Abrams et al., 2007), and improving neural coding efficiency (e.g., Sharpee et al., 2006; Wainwright, 1999).

We previously found evidence of stronger, more rapid adjustment with experience in color vision and termed it *visual mode switching* (Li et al., 2020). We asked participants to wear a pair of bright red glasses for five 1-hr periods per day for 5 days. We tracked color adaptation by asking participants to identify "unique yellow," a chromaticity that contains no red or green in it. When participants first put on the glasses on the first day, the world appeared very reddish, so they chose a much shorter wavelength for unique yellow, which was physically very greenish (we use the term *physical color* to refer to the coordinates of the stimulus in a standard color space, e.g., the CIE system, or the Macleod–Boynton space described below). Across days, the world appeared significantly less

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reddish immediately after putting on the glasses, with unique yellow settings shifting reliably toward longer wavelengths (i.e., being physically less greenish). This indicates that the visual system learned to adjust more rapidly, switching to "red-glasses mode" to maintain stable and accurate vision.

Mode-switching effect may involve mechanisms of classic adaptation, perceptual learning, perceptual inference, and others. Here, we use “learning” simply to indicate that participants have acquired an improved ability to switch between different visual modes, without suggesting a particular mechanism.

Other prior work has also reported evidence of mode switching in vision (Engel et al., 2016; Gislén et al., 2003, 2006; Yehezkel et al., 2010), as well as in audition (Hofman et al., 1998) and sensorimotor domains (Redding et al., 2005; Welch et al., 1998; Wolpert & Flanagan, 2016). Mode switching may be a general strategy to optimize sensory and motor processing.

Many aspects of mode switching remain unstudied both behaviorally and neurally. Here, we aim to answer two questions: (1) whether mode switching can be learned with relatively infrequent changes of the environment and (2) in color vision specifically, how mode switching affects larger parts of the color space. Answering these two questions will help determine the specific conditions under which mode switching can occur. In general, knowledge of mode switching may aid perceptual training methods for visual disorders and for coping with unusual visual environments.

In our prior work, participants put on and removed the red glasses five times each day, yielding 25 environmental changes over the 5 days. However, it remains unknown what comprises a new mode in the world (i.e., the requirements that the visual system demands in order to establish one). In addition, for potential applications of mode switching, it may be convenient to use less burdensome protocols. Thus, for both theoretical and applied reasons, it is of interest to test whether such frequent environmental changes are necessary to produce the mode-switching effect or whether less common changes, say once daily, can suffice. Past work has examined the effects of a single daily multihour exposure to a colored environment, either wearing red glasses or living under red illumination (Belmore & Shevell, 2008; Eisner & Enoch, 1982; Neitz et al., 2002). But whether adaptation became more rapid, immediately after entering the red environment, was not tested.

To investigate the effect of once-daily experience with an environmental change, we asked participants to wear the red glasses for one single 5-hr period each day for 5 days. This manipulation kept the total number of hours in the red environment the same as in our prior work but greatly reduced the frequency of environmental changes. The red glasses selectively remove most of the energy at short wavelengths (Figure 1A), compressing the gamut of colors reaching the eye and shifting it toward red (Figure 1B). For example, the greenest light from our monitor (black dot) fell in an orange part of color space through the glasses (gray dot). Participants again performed a unique yellow setting task when wearing and not wearing the red glasses, identifying the color that contains neither red nor green (Jameson & Hurvich, 1955). We hypothesized that participants might still learn to switch visual modes even with only once-a-day experience with the color change.

The second question we address here involves the effects of mode switching on a more complete measure of appearance. Our prior work just measured a single color—unique yellow. Here we measure how mode switching affects a large part of color space. We used multidimensional scaling (MDS) on data from a perceptual dissimilarity rating task to reconstruct a portion of participants’ subjective color space and examine how experience with the red glasses changes it across days. MDS is a technique that can be used to build a multidimensional perceptual space, where the distance between two points is determined by the reported dissimilarity between a stimulus pair. Many studies have used MDS to reconstruct the perceptual spaces of normal trichromats, as well as dichromats, and anomalous trichromats (e.g., Boehm et al., 2014; Cavonius & Mollon, 1984; Helm, 1964; Jordan et al., 2010; Paramei et al., 1991), using this as a perceptual measure of colorfulness.

Participants in our second experiment donned and removed the glasses multiple times a day for 5 days, as in prior work. We used a dissimilarity rating task to measure and track color appearance, as well as MDS to reconstruct the subjective color space, with and without the glasses. We hypothesized that wearing red glasses would cause the colors to appear more similar to each other, suggesting that the perceptual color space was greatly compressed. As vision adapts, colors should subjectively regain more normal appearances, producing a gradual expansion of color space. If mode switching can affect the whole color space, then following the 5 days of glasses wear, the color space should be less compressed when participants first put the glasses on, indicating a rapid adjustment of the whole color space.

## Experiment 1

### Methods

#### Participants

Twelve participants (21 to 28 years of age, four males) were recruited through the University of

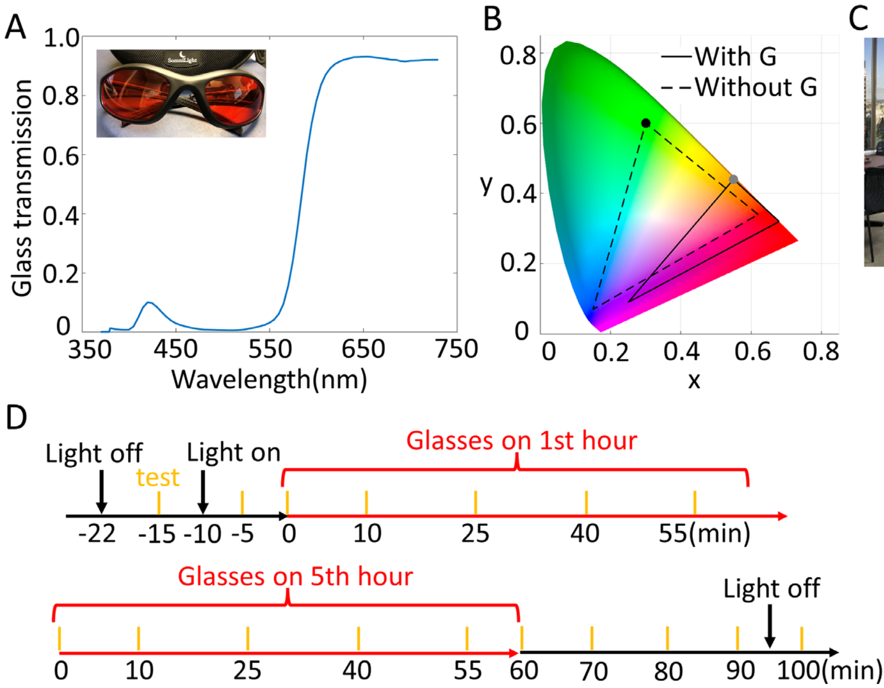


Figure 1. Glasses' transmittance and test procedures of Experiment 1. (A) The transmission spectrum of the red glasses used in Experiments 1 and 2. The glasses filter out most of the light at short wavelengths and let pass most of the light at long wavelengths. (B) The gamut of the test display without (dashed line) and through (solid line) the glasses, plotted in CIE color space. The glasses compress the gamut and shift it toward red chromaticities. For example, the greenest light from the monitor (black dot) falls in the orange region of the color space through the glasses (gray dot). (C) Test display. The test patch was a 0.5° square centered on a background image of a naturalistic office scene, separated by a 5.7° black square. Participants adjusted the color of the test patch to unique yellow. The office image was presented on the test display to give participants context information when making the adjustments. (D) Test procedures. Two 1.5-hr test sessions were conducted on each day. The upper panel illustrates the test procedure during the first session. Orange bars indicate a 5-min test. Participants were first dark-adapted for ∼7 min and tested in the darkened room without the background image. Then, participants recovered in the fully lit room for 5 min and performed the task again under natural illumination, with the background image presented in this and subsequent tests. Participants then put the red glasses on and were tested five times during the 1 hr of glasses wear. The lower panel illustrates the test procedure in the second session, which began at the start of the fifth hour of wearing glasses. First, participants repeated the identical glasses-on tests as during the first hour. Then, participants removed the glasses and were tested four times. Finally, participants were dark-adapted and tested again, with no room lighting and no background image.

Minnesota community. This number was expected to allow adequate statistical power, based on the effect size in our prior work (Li et al., 2020). All participants had normal color vision, assessed by the Ishihara Color Blindness Test, and all reported having normal or corrected-to-normal (using contact lenses) visual acuity. None had been exposed to a tinted environment for extended periods of time prior to this study. Experimental procedures were approved by the University of Minnesota Institutional Review Board. All participants provided written informed consent prior to the study.

### *Apparatus*

An NEC MultiSync FP2141 CRT monitor (NEC Corporation, Tokyo, Japan), with a screen resolution of 1,024 × 768 pixels and a refresh rate of 85 Hz, was used to present visual stimuli. The monitor was gamma-corrected and calibrated using a Photo Research PR655 spectroradiometer (PhotoResearch, Syracuse, NY). Participants viewed the display at a distance of 50 cm. Visual stimuli were programmed in MATLAB using the psychophysics toolbox (Brainard, 1997).

### *Glasses*

Adapting glasses were commercially available bright red glasses made by SomniLight (Shawnee, KS, USA). The glasses filter out most of the light at short wavelengths and let pass most of the light at long wavelengths. The glasses' transmittance was measured by placing them in front of the spectroradiometer and recording sunlight. As shown in Figure 1A, the transmittance is more than 90% at wavelengths over 620 nm and less than 10% at wavelengths below 550 nm. Figure 1B shows the gamut of the monitor with and without the glasses. The effect of the glasses on the testing display is to compress the gamut and shift it toward red chromaticities.

### Procedure

Participants wore the glasses for a single 5-hr period per day for 5 consecutive days. On each day, participants came to the lab in the morning, put on the glasses, and immediately participated in a 1-hr test session. Then, they left the lab and went about their daily activities with the glasses on for 3 hr. During the fifth hour of wear, participants came back to the lab and participated in a second 1-hr test session with the glasses on, identical to that in the morning.

Most tests were conducted in a fully lit room, which allowed participants to adapt to the glasses in the context of a natural environment. Participants viewed the testing display through a 3-foot felt-lined "tunnel," which prevented the ambient light from reaching the display. Participants sat in front of the "tunnel" and positioned their heads at its entrance with a chinrest, keeping a viewing distance of 50 cm. Participants did not adapt to the white point of the display before the start of the test session.

During the test sessions, participants adjusted the color of a target to unique yellow, a hue that contains no red or green in it. They were instructed to make adjustments based on the light reaching their eyes without thinking about what the color of the target on the display should be, for tests both with and without the glasses. The target was a 0.5° square centered on a naturalistic background (a chromatic image of an office scene). The background image had a mean luminance of 20 candela/m$^2$. A 5.7° black square separated the target from the background (Figure 1C).

To identify unique yellow, participants pressed the left arrow button to reduce the redness in the target, the right arrow button to reduce greenness, and then the right control button to indicate a unique yellow match. The up and down arrow buttons had the same effects as the left and right arrow buttons, respectively, but were for adjustments with smaller steps. The target was presented for 200 ms at 1.5-s intervals. Participants had 20 s at most to make one single unique yellow setting, so they were encouraged to make matches relatively quickly and had a reasonable number of matches in each block.

Displayed colors were defined using a modified version of the MacLeod–Boynton color space (MacLeod & Boynton, 1979). The space is scaled and shifted so that the origin corresponds to a nominal white point of Illumination C and so that sensitivity is roughly equated along the LM and S axes (Webster et al., 2000). To calculate coordinates in this space, we first computed cone responses using the stimulus spectrum and the Smith and Pokorny (1975) cone fundamentals scaled so that the sum of L- and M-cone responses was 1, and S-cone responses divided by this sum also equaled 1. We then computed initial coordinates in the MacLeod–Boynton color space as $r_{mb} = (L - M)/(L + M)$ and $b_{mb} = S/(L + M)$. Lastly, we shifted and scaled these coordinates:

$$LM = (r_{mb} - 0.6568) \times 2168$$
$$S = (b_{mb} - 0.01825) \times 6210$$

where LM is the red–green coordinate and S is the S-cone coordinate in the modified space, 0.6568 and 0.01825 are the MacLeod–Boynton coordinates of Illumination C, and 2168 and 6210 are constants to scale the LM and S axes so that a value of 1 roughly equals detection threshold (Webster & Mollon, 1995).

We constrained stimuli to fall along a nominally isoluminant plane (set at 51 candela/m$^2$, defined by the LM and S axes) when not wearing the glasses to reduce the effects of brightness on the judgments. We used the CIE Photopic V($\lambda$) luminance function, modified by Judd (1951), to define nominal isoluminance.

When making the unique yellow adjustments, participants moved the stimulus along a circle in this plane, where "hue angle" was changing and luminance and contrast (radius of the circle) were held constant. The radius of the hue circle was 80, which is a chromatic contrast of roughly 80 times the detection threshold (see above), and was held constant during the adjustment. The stimuli were not corrected for the glasses, so they were not held at strictly constant luminance and contrast for glasses-on adjustments.

Participants adjusted the hue angle of the stimulus between a green endpoint at 200° and a red endpoint at 360°, with coarser or finer steps of 5° or 1° per button press, respectively. At the beginning of each trial, the hue angle of the stimulus was set randomly from 290° ± 45° (i.e., the interval from 245° to 335°). We tracked and stored each step of participants' adjustments and confirmed that they did not use the endpoints as anchors for their settings.

At the beginning of the morning test session, participants were dark-adapted for ~7 min, and then they performed five 1-min blocks of the task in the darkened room. There was no background image on the display during this test, with only the target stimulus presented. Then, participants recovered in the fully lit room for 5 min and performed five blocks of the task again under natural illumination with the background image presented in this and subsequent tests. Participants then put the red glasses on and were immediately tested again. Participants were also tested after 10, 25, 40, and 55 min of wearing the glasses.

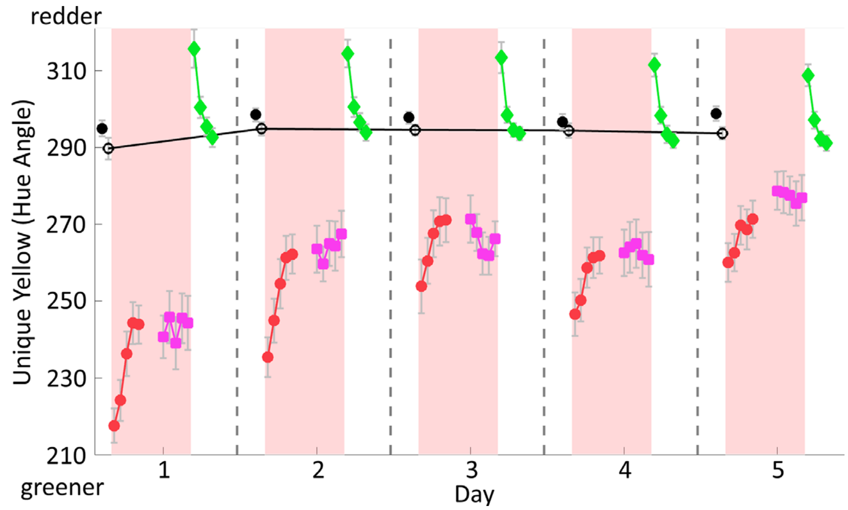


Figure 2. Results of Experiment 1 ($N = 12$). Mean unique yellow settings in hue angle are plotted as a function of time for 5 days. The white background indicates tests when not wearing the glasses, and the light red background indicates tests when wearing the glasses. The black filled circles are settings made after dark adaptation in the darkened room with no background image on the display. The black open circles are settings made under natural illumination in a fully lit room, with the background image presented. The red filled circles indicate settings made during the first hour of wearing the glasses, and the magenta squares are settings made during the last hour of glasses wear. The green diamonds represent settings made after removing the glasses. Each symbol represents the mean of unique yellow settings made during a 5-min test. The gray bars represent standard errors of the mean, computed across participants.

During each block of the test, participants made as many matches as they could, and there was a short break of a few seconds between blocks. Between tests, participants took a break and watched videos of their choice on a laptop or phone display.

After the morning test session, participants left the lab and went about their daily activities with the glasses on for 3 hr. At the end of the fourth hour of glasses wear, participants came back to the lab to participate in the second test session. They repeated the identical task blocks as during the first hour of glasses wear. Then, participants removed the glasses and were immediately tested again as well as 10, 20, and 30 min after removing the glasses. Finally, participants were dark-adapted again and performed a last test, with no room lighting and with no background image (we did not observe any reliable changes of settings in this last test over days, and it is not required for testing any of our hypotheses, and so we do not report its results further here). The full test procedure is illustrated in Figure 1D.

## Results

Figure 2 plots mean unique yellow settings, in hue angle, as a function of time, for 5 days, averaged across 12 participants. A small hue angle indicates a physically greener hue on the screen, and a larger hue angle indicates a physically redder hue. When participants first put on the glasses, the world appeared very reddish (Figure 1), so they set the stimulus to be more physically green (shorter wavelengths) to cancel the redness from the glasses and produce unique yellow (Figure 2, red filled circles). As participants adapted to the red environment over the first hour of wearing the glasses, the redness faded, so they set the stimulus to be less physically green (longer wavelengths) to produce unique yellow. This is reflected by the upward slope of the five settings within the first hour of glasses wear on a given day. We term this effect, which builds over the hourlong course of wearing the glasses, *gradual adaptation*.

### Effects of once-daily 5-hr glasses wear

*Once-daily experience suffices to produce faster and stronger adjustment.* Across days, when participants first put on the glasses, the world immediately appeared less and less reddish. This is reflected by the rising trend of the first unique yellow setting after putting on the glasses across days, indicating stronger immediate adjustment, with less and less physical green initially required to produce unique yellow. A linear fit demonstrated that this change was reliable (Figure 3, red filled circles, $t(11) = 5.13$, $p < 0.001$). The change was not due to lingering adaptation effects across days, as baseline measures, either in the dark or under light, did not change significantly over days (see below). This trend suggests that participants learned to adjust to the glasses more rapidly through once-daily multihour experience with them, effectively switching to “red-glasses mode.”

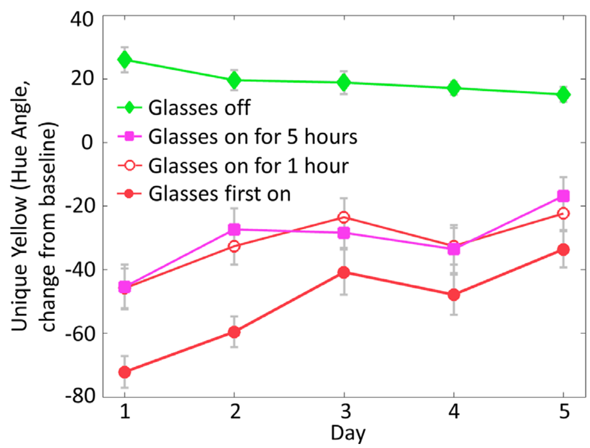


Figure 3. Unique yellow settings across 5 days. Red filled circles are settings made immediately after putting on the glasses (i.e., rapid adjustment). Red circles and magenta squares denote settings made after wearing the glasses for 1 hr and 5 hr, respectively. Green diamonds indicate settings made after removing the glasses (i.e., the aftereffect). Each symbol represents the mean setting of a 5-min test, and data have been corrected for possible baseline variations. The gray bars are standard errors of the mean across participants. The rapid adjustment grew significantly over days, and the aftereffect decreased over days. Settings made at the end of the first hour did not differ reliably from those made at the end of the fifth hour of wearing glasses on each day.

Each datapoint in Figures 2 and 3 represents the mean unique yellow setting averaged across five 1-min blocks within each test. To better evaluate the timing of the effect, we also conducted linear fits to participants' averaged settings within only the first 1-min block in each test and to participants' very first unique yellow setting in the first block. In both cases, unique yellow settings made immediately after donning the glasses shifted significantly across days ($t(11) = 5.76$, $p < 0.001$ for the first block; $t(11) = 4.22$, $p < 0.01$ for the first setting), indicating relatively quick adjustment to the red glasses. Supplementary Figure S2 shows the complete time course of the first-hour glasses-on settings as a function of 1-min blocks on all 5 days.

*Gradual adaptation during the first hour decreased over days*. There was a trend for the amount of adaptation during the first hour of glasses wear to become smaller over days, from over 25° on day 1 to about 10° on day 5. This trend was not present in our previous work. To quantify this gradual adaptation, we fit a line to the unique yellow settings within each first hour of wearing the glasses. The change in the slope of this linear fit across 5 days was marginally reliable ($t(11) = -2.25$, $p = 0.046$).

*Gradual adaptation asymptoted after the first hour of glasses wear.* Participants wore the red glasses for 5 continuous hours each day, but adaptation increased only during the first hour. We compared unique yellow settings at the end of the first hour (red open circles in Figure 3) to those at the end of the fifth hour (magenta squares in Figure 3) on each day. There was no reliable difference between the two tests on all 5 days (all $p > 0.05$). Thus, adaptation grew in strength within the first hour of glasses wear and remained relatively constant afterward, at least as measured by the unique yellow setting task.

*Baseline unique yellow did not change across days*. We measured baseline unique yellow, made before putting the glasses on each day, under two different conditions. One was after dark adaptation, tested in a darkened room with no background image on the screen (black filled circles in Figure 2); the other was under room light, tested with the background image provided (black circles in Figure 2). We found that neither of these two baseline measurements changed significantly across days (both $p > 0.1$), although both had a small trend toward redder (see Discussion). To make sure that the other effects we observed were not driven by variations in baseline settings, in separate analyses, we subtracted each of the two baseline values from all settings within the day, to correct their effects. All these baseline-corrected results showed a very similar overall pattern across days as the uncorrected results (Supplementary Figure S3).

*The color aftereffect became weaker across days*. After removing the red glasses, participants experienced a classical color aftereffect in which the world appeared slightly greenish (von Helmholtz, 1924; Krauskopf & Gegenfurtner, 1992; van Lier et al., 2009). To cancel this effect, they needed to add physical red to produce unique yellow (green diamonds in Figure 2). The settings shifted back to baseline over the 30 min of testing as the aftereffect faded. The immediate aftereffect became significantly less strong over days, as the unique yellow setting made within the first 5-min test after removing the glasses shifted significantly toward baseline (after correcting for each day's preadaptation baseline, Figure 3, green diamonds, $t(11) = -3.13$, $p < 0.01$). The uncorrected results showed a very similar but less reliable shift of the immediate aftereffect over days ($t(11) = -1.97$, $p = 0.07$), possibly due to the relatively physically greener baseline unique yellow settings made on the first day.

## Comparison with effects of five 1-hr periods of glasses wear

The one-time-a-day experience produced comparable mode-switching effects, gradual adaptation effects, and classical aftereffects as the five-times-per-day experience (Li et al., 2020). To test for differences in the mode-switching effect (immediate adjustment when putting on the glasses), we compared the following measurements between the present and our previous study: the first glasses-on unique yellow setting on the first day, the first glasses-on setting on the last day, and the slope of the linear fit to the first glasses-on settings across days. None of these measures differed reliably between the two studies (all $p > 0.5$), using either baseline-corrected or uncorrected results.

We tested for differences in gradual adaptation by computing the average amount of hue angle change toward red per hour during the first hour of glasses wear. In the present study, this quantity was 19.4°/hr. This quantity was numerically larger but did not significantly differ from the mean amount of the gradual adaptation during the 1-hr adaptation periods in our prior work (13.3°/hr, $p > 0.1$).

The size of the classical color aftereffect, characterized by the mean of the immediate aftereffect across 5 days, also did not differ significantly between the two studies ($p > 0.05$). In addition, the slope of the linear fit to the first glasses-off settings across days did not differ between the two studies ($p > 0.05$). Finally, the decay constant of the aftereffect, which has been found to be influenced by the length of adaptation duration (e.g., Bao & Engel, 2012; Hershenson, 1989; also see review Kohn, 2007), also did not differ significantly between the two studies ($p > 0.05$).

## Discussion

The present results confirmed that experience with red glasses allows participants to learn to switch visual modes, adjusting to them immediately to a greater extent each day. A single adaptation period sufficed for the acquisition of mode switching, producing equal-sized effects to past work with repeated switching between the glasses-on and glasses-off environments. Future work could profitably examine how long the red-glasses wear needs to be in order to allow participants to learn to switch modes.

Perhaps surprisingly, neither of the two baseline settings changed across days. The first setting, made with no context when participants were dark-adapted, was similar to those in the past studies, where unique yellow shifted to be more physically red (longer wavelengths) due to long-term exposure to a red environment (e.g., Belmore & Shevell, 2008, 2011; Neitz et al., 2002). We found a trend in this direction, but it did not reach statistical reliability. The second baseline measurement was taken while adapted to the office scene context (Figure 1C) and was the same as in our previous work (Li et al., 2020), where we observed a small but significant shift of unique yellow to be more physically green (shorter wavelengths) over time. Such a trend was not visible in the current data. We had hypothesized that dark adaptation and the presence of visual context might account for the differences between baseline trends in past studies, but further work will be needed to determine precisely what factors produce reliable shifts.

We observed equal-sized color aftereffects immediately after removing the glasses in the present experiment as in our prior work (Li et al., 2020). This is surprising because the aftereffect was measured after 5 hr of glasses wear in this study, whereas in the previous study, it was preceded by only 1 hr of adaptation. However, as described above, adaptation did not keep growing significantly in strength after the first hour, which may have led to a comparable aftereffect as only adapting to the glasses for 1 hr. The decay of the aftereffect within each day was also comparable after 1 hr and 5 hr of adaptation. This is surprising as longer exposure generally causes slower aftereffect decay (see review by Kohn, 2007).

However, we did observe a decrease of the size of the initial aftereffect over days, consistent with our prior work. We interpret this change as the visual system learning to switch more rapidly back to “normal mode” following removal of the red glasses. This mode switching may have prevented us from observing the expected increase in aftereffect strength and duration following 5 versus 1 hr of glasses wear. We speculate that our test setting provided the visual system rich cues to the context that it could use to identify that the “normal” environment was present and so adjust rapidly to its “normal mode.”

Adaptation within a given session reached a limit; during the last hour of adaptation, unique yellow settings did not even show a slight trend toward increasing (slope of a linear fit to settings during the last hour did not significantly differ from zero on all 5 days, all $p > 0.1$). Prior work on multiple-hour adaptation to luminance contrast reports mixed findings: in one case, adaptation reached a limit after 30 and 60 min for two participants (Magnussen & Greenlee, 1985), but in another, adaptation grew in strength for up to 8 hr of exposure (Bao & Engel, 2012). Past work on multiple-hour adaptation to color has revealed that adaptation grows stronger over days, but these studies did not measure the time course of adaptation within a day (Belmore & Shevell, 2008, 2011; Eisner & Enoch, 1982; Hill & Stevenson, 1976; Kohler, 1963; Neitz et al., 2002).

We interpret our results in terms of a processing “mode” that should apply to all or most stimuli in a given environment. While participants’ verbal reports suggested that most colors they experienced returned to a more normal appearance, both Experiment 1 and Li et al. (2020) only measured the perception of a single color—unique yellow. In Experiment 2, we aimed to examine the effects of mode switching with a more complete measure of color appearance—perceptual dissimilarities between colors in a large part of the color space.

# Experiment 2

## Methods

### Participants

Thirteen participants (21 to 32 years of age) of the University of Minnesota community were recruited. All had normal color vision, as assessed by an online version of the Ishihara Color Blindness Test, and all reported having normal or corrected-to-normal (using contact lenses) visual acuity. None had been exposed to a tinted environment for extended periods of time prior to this study. Experimental procedures were approved by the University of Minnesota Institutional Review Board. All participants provided written informed consent prior to the study.

### Apparatus

Visual stimuli were presented on a MacBook Air (Apple, Cupertino, CA, USA) laptop delivered to the participants, and all tests were conducted remotely. The display type was a built-in Retina LCD, with a screen resolution of 2,560 × 1,600. The laptop display was calibrated and gamma-corrected using a portable monitor calibration tool, SpyderX Elite (Datacolor, Lucerne, Switzerland). Testing code and visual stimuli were delivered using MATLAB (MathWorks, Natick, MA, USA). Participants were instructed to keep their eyes 30 cm away from the screen, measured by a ruler, and to maintain this viewing distance throughout the test.

### Glasses

Participants wore the same pair of red glasses as the ones used in Experiment 1. The spectral transmission of the glasses is shown in Figure 1A. Supplementary Figure S1 demonstrates the gamut of the laptop display with and without the glasses. The gamut of the display seen through the glasses was again compressed and shifted toward red chromaticity. Figures 4A and 4B also reflect the effect of the red glasses on our stimuli (see below).

### Procedure

During the main experiment, participants wore the red glasses for 5 hr per day for 5 consecutive days. On each day, participants first wore the red glasses for 1.5 hr in the morning while participating in a testing session. Then, they removed the glasses and, after an hour, wore the glasses for two 1-hr periods, separated by 1 hr without glasses. After a last 1-hr period without the glasses, participants did the second testing session with glasses on, identical to that in the morning. The experimental procedure is illustrated in Figure 4C. When not being tested, participants attended to their routine everyday activities, with glasses on or off, experiencing various illumination conditions.

Participants were tested remotely, with a research assistant meeting with them online and giving instructions. Participants did all the testing sessions in the same location and were instructed to keep the lighting condition in the testing room consistent across 5 days.

In each test session, participants viewed pairs of filled color circles, 1.5° in diameter, on a naturalistic background image (an office scene) displayed on the laptop. The two circles were 2.5° apart, each 1.25° from the center of a 6° black square (Figure 4D).

A color difference rating task was used to measure color perception, with and without wearing the glasses. Participants rated the difference between each color pair on a scale of 0 to 9, where 0 was to be used if the color pair appeared identical, and 9 indicated the biggest difference. Before the experiment started, participants were shown an image of the entire stimulus set, with patches positioned according to their location in Commission Internationale de l'Eclairage $L^*a^*b^*$ (CIELAB) space (see below, Figure 4A). They were given the following instructions: "These are the colors you will be seeing during the test and you will be presented with 2 colors at a time and your task is to rate how different a pair of colors are on a scale of 0–9. 0 is used if the pair is identical or probably identical; 9 is used for the biggest difference/largest distance (for example, this red and green on the outer circle). You can probably see that the colors on the inner circle are more similar to each other and to the gray in the middle than those on the outer circle. So your difference rating between the more intense (more saturated) green on the outer circle and gray should be greater than your difference rating between the grayish green on the inner circle and gray. In this same way, the grayish green and grayish red should be rated as less different than the intense green and intense red." To ensure that participants rated the color difference based on their perception and used the same criterion for glasses-on and glasses-off ratings, we emphasized, "Please give your ratings based on what you see and try **not** to think about what the color should be or what the color is on the display, particularly when you wear the glasses. Please try to keep your criterion the same throughout the experiment for both glasses-on and glasses-off ratings. So, a difference of 9 with glasses on should be the same as the difference of 9 when glasses are off."

Colors were defined in CIELAB space. CIELAB was intended to be more perceptually uniform than some other color spaces, with a given numerical change corresponding to a similar change in perceived color across the space. Thirteen colors were chosen from two

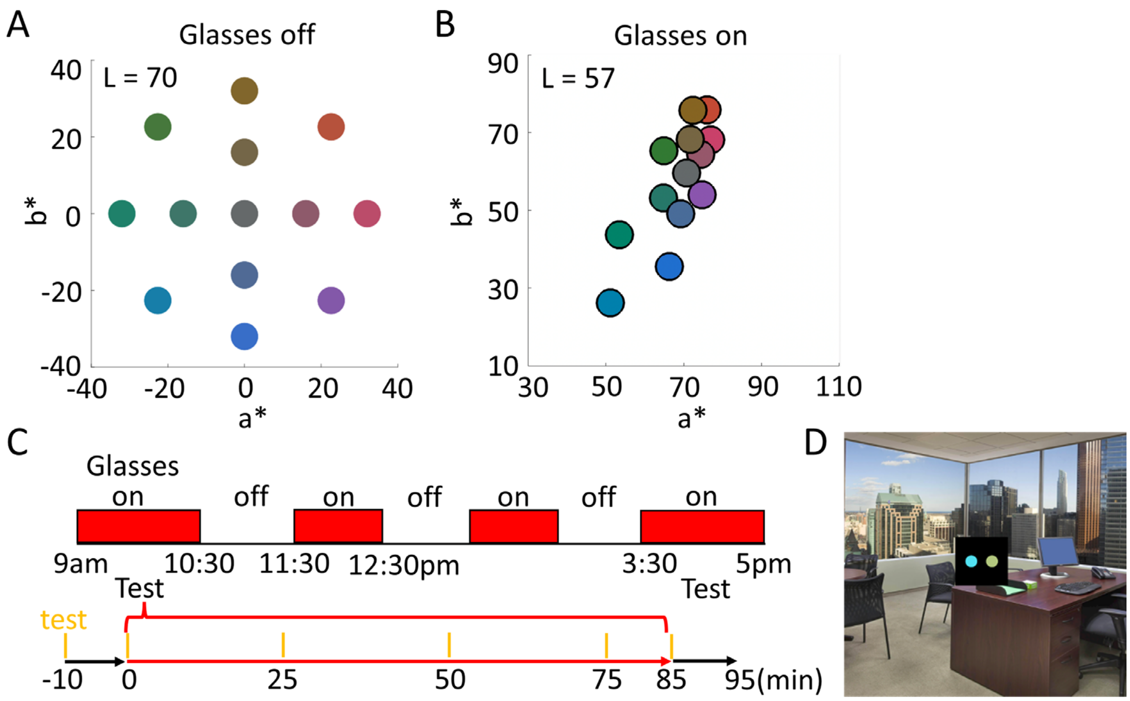


Figure 4. Experimental procedures and stimuli space of Experiment 2. (A) Stimuli used in tests. Thirteen colors of equal luminance were chosen from two concentric circles in the CIELAB color space, including eight unique and intermediate hues of high saturation, four unique hues of low saturation, and one gray. (B) CIELAB coordinates of stimuli used in glasses-on tests seen through the glasses. Glasses-on colors were set to be of equal luminance when seen through the glasses, so also fall on an isoluminant plane in CIELAB space. The stimulus space was compressed and shifted toward red chromaticities by the glasses. (C) Experimental procedures. The upper panel shows the times when participants wore the glasses on each day. The lower panel shows procedures in each of two test sessions that were conducted during the first and last 1.5 hr of wearing the glasses. Orange bars indicate the time of test: 10 min before putting on the glasses, immediately after putting on the glasses, and then following 25, 50, and 75 min of glasses wear. Participants then removed the glasses and were immediately tested again. (D) Test display. Participants viewed pairs of filled color circles centered on the same background image as in Experiment 1. The two circles were 1.5° in diameter, 2.5° apart, each 1.25° from the center of a 6° black square. Color circles were presented for 500 ms followed by a 1.5-s gap.

concentric circles in the CIELAB space, including eight unique (reddish, greenish, blueish, and yellowish) and intermediate hues of high saturation, four unique hues of low saturation, and one gray (Figure 4A). These colors formed 78 nonidentical pairs in one test run.

All color stimuli were isoluminant when tested with the red glasses off, with a luminance of 150 candela/$m^2$. To compensate for the effect of the glasses on stimuli's luminances (i.e., reddish hues appearing brighter than greenish hues when seen through the glasses), we equalized the luminances of the stimuli used for testing with the glasses on. We first computed CIE coordinates (x, y, Y, where x and y are chromaticity coordinates and Y is luminance) for our stimuli seen through the glasses. We then set the luminance (Y) of these stimuli to be equal for all and as large as possible given the gamut of our display, while not changing their chromaticities (x, y values). Finally, we calculated the RGB values that produced these equal-luminance colors with glasses on. We also computed the CIELAB coordinates of these colors as seen through the glasses (Figure 4B). Thus, the glasses-off and glasses-on stimuli had the same CIE xy coordinates on the display (i.e., the same chromaticities), and the glasses-on stimuli were also isoluminant when seen through the glasses (at a level of 30 candela/$m^2$).

Each color pair was presented for 500 ms followed by a 1.5-s gap. Before starting the test, a palette showing all 13 color stimuli was presented so that participants could judge the full range of color differences. Responses were collected using the laptop keyboard. Participants judged all 78 color pairs, presented in random order, in a block that lasted about 3 min. They performed three blocks in a "test," with no breaks between blocks. Participants indicated their perceived dissimilarity between members of the pair with a keypress (0–9).

At the beginning of each 90-min testing session, participants performed one test (three blocks) with natural vision. Then, they put the glasses on and immediately did a second test. Participants were also tested after 25, 50, and 75 min of wearing the glasses. Between tests, participants watched videos of their choice on the same laptop used for the test. At the end of the testing session, participants removed the glasses and were immediately tested again. The full test procedure is illustrated in Figure 4C.

### Data analysis

We averaged the dissimilarity ratings for each color pair across the three blocks in each test. We then divided each participant's ratings for all color pairs in all tests and sessions by their mean baseline rating to the saturated red–green pair across 5 days to eliminate the impact of individual differences in anchor points for ratings of perceptual dissimilarities and averaged the results across participants. The scaled results showed a very similar overall pattern within and across days to the unscaled data. We then applied a two-dimensional metric MDS on the normalized dissimilarity matrix containing ratings of all pairs of colors to reconstruct the subjective color space. We chose two dimensions as our stimuli fall on an isoluminant plane, both with and without the glasses, and the two dimensions roughly correspond to the "red–green" and "blue–yellow" opponent system (Cavonius & Mollon, 1984; Helm, 1964). We used metric, instead of nonmetric, MDS because the dissimilarity ratings are numerical distances and have meanings on their own. For consistent visualization, we rigidly rotated all points in the MDS solutions so that the saturated red stimulus fell on the x axis (i.e., had a 0 coordinate on the vertical axis). We also averaged the ratings across all color pairs in each test to compute the mean pairwise color differences and plotted them as a function of test time and day.

To better understand the change in perceptual color space after 5 days, we built a model that began with cone absorptions and predicted our data, dissimilarity between pairs of stimuli viewed with the glasses on. Fully modeling the relationship between cone absorptions and perceptual distance (i.e., dissimilarity or discriminability) across a large portion of color space is an important unsolved problem in color science. Here, for convenience, we simply assumed that a linear transform of a color-opponent space can approximate perceptual distance between pairs of colors for a plane through color space reasonably well (Boehm et al., 2014).

First, we calculated cone absorptions for colors seen through the glasses by multiplying the stimulus spectra by the glasses' transmission spectrum and then by cone fundamentals (Stockman & Sharpe, 2000). Then, we calculated outputs of cone opponent mechanisms as $L - M$ and $S - (L + M)$, with letters indicating the relative absorptions by the three cone classes. Next, we searched for the affine transformation that best aligned the outputs of the cone opponent mechanisms with the reconstructed perceptual color space, on day 1, immediately after putting on the glasses. This produced a model that fit the day 1 dissimilarity data reasonably well (see below).

We then tested whether changes in perception from day 1 to day 5 could be modeled by scaling the response of each cone type independently, consistent with a generalized version of von Kries scaling (e.g., Brainard et al., 1997; Wade & Wandell, 2002). We fixed the coefficient of the L cones at 1 and searched for coefficients for M and S cones that produced the best fit to the perceptual dissimilarity data on day 5 (using the same color-opponent mechanisms and affine transformation). To do so, we minimized the mean squared error between predicted and actual pairwise color distances.

## Results

### Effects within 1-hr testing sessions

*Gradual color adaptation within a session expanded perceptual color space.* Colors seen through the glasses again all appeared very reddish, causing all pairs to be rated as relatively similar. As participants adapted while wearing the glasses during the 90-min testing session, colors subjectively regained more normal appearances, and the dissimilarity between colors gradually increased. As above, we term adaptation effects that arise during the interval of wearing the glasses *gradual adaptation*. To quantify this trend, we computed the mean pairwise difference rating in each test (i.e., the average rating across all pairs within a test) for all tests and test sessions on the 5 days (shown in Figure 5). The upward slope of the connected red filled circles in each testing session indicates that color pairs on average appeared more dissimilar over time.

To better characterize the effect of the glasses on the whole color space and how it changed over time, we used MDS to reconstruct perceptual color spaces from the mean dissimilarity ratings in each test. Figure 6 plots MDS solutions for tests before, after ~90 min of wearing the glasses, and after removing the glasses, over 5 days. The reconstructed space in the baseline tests (leftmost column in Figure 6) had a very similar configuration to the stimuli plotted in CIELAB space (Figure 4A), meaning that distances between colors in CIELAB space are relatively closely matched to perceived dissimilarities. Wearing red glasses compressed the reconstructed color space, as all colors became much closer compared to the baseline space. After the ~90-min adaptation, the color space expanded, and this can be seen on all 5 days. The figure plots the results from morning testing sessions; afternoon test sessions showed a very similar pattern within and across sessions (see Supplementary Figure S4).

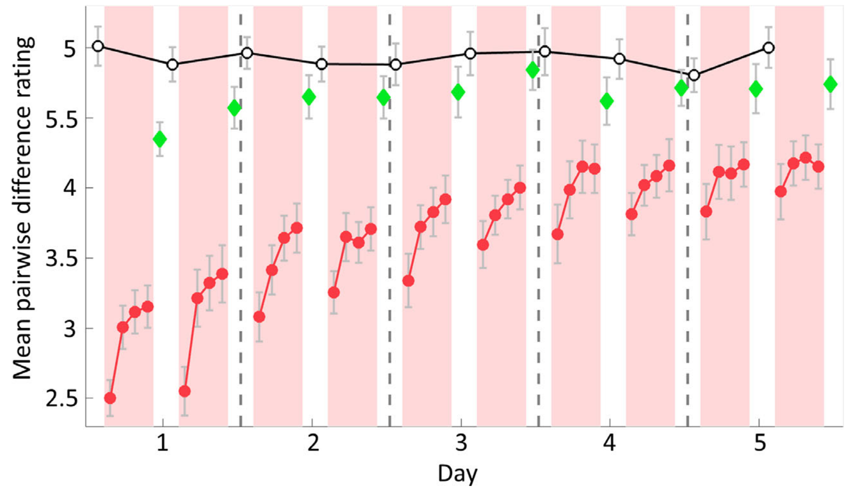


Figure 5. Results of Experiment 2 ($N = 13$). Mean pairwise difference ratings, computed as the average rating across all color pairs within a test, are plotted as a function of test time and day. The white background indicates tests when not wearing the glasses, and the light red background indicates tests when wearing the glasses. The black circles are baseline mean pairwise difference ratings, measured at the beginning of each session with glasses off. The red filled circles represent ratings with the glasses on, and the green diamonds are ratings after removing the glasses. The gray bars plot standard errors of the mean across participants.

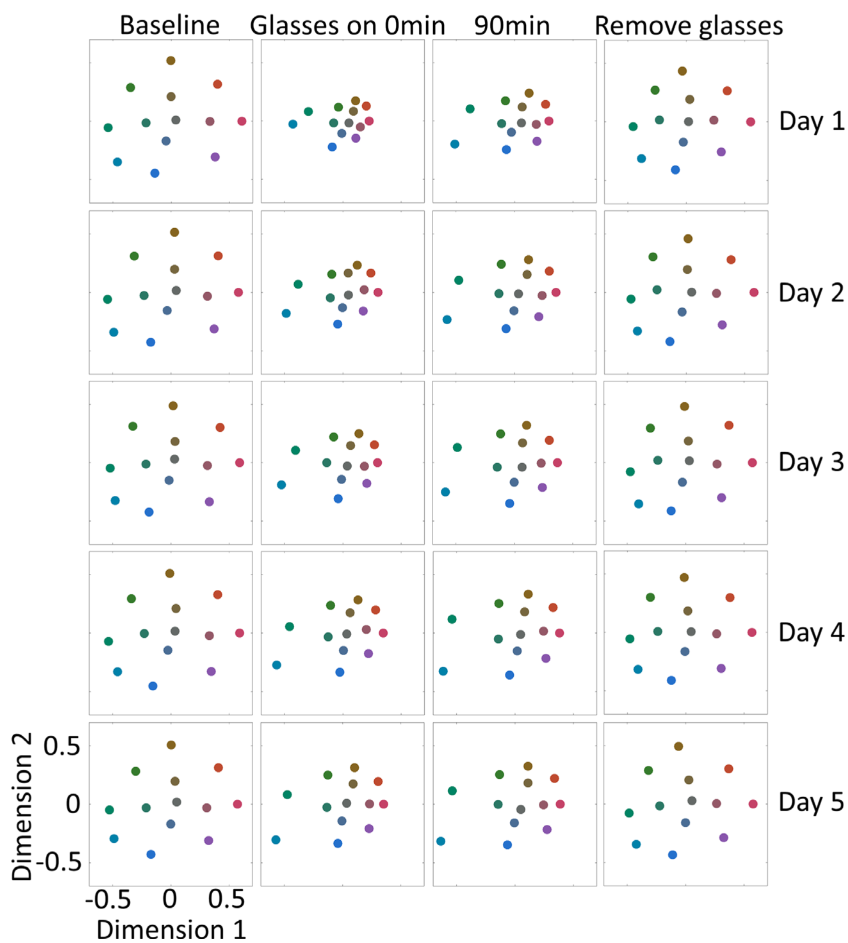


Figure 6. Perceptual color spaces reconstructed using MDS from normalized difference ratings. Results are shown for tests performed before wearing the glasses, immediately after putting on the glasses, 90 min after putting on the glasses, and immediately after removing the glasses. Results in the first test sessions on 5 days are shown here, and the results in the second test sessions can be found in Supplementary Figure S4 and are very similar. Perceptual color spaces were rotated to best coincide with the glasses-off stimuli in CIELAB color space.

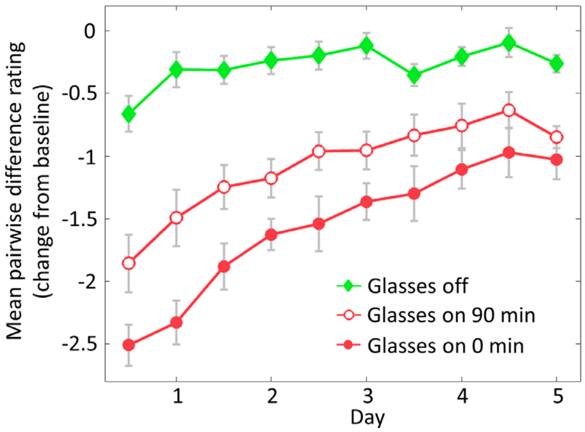


Figure 7. Immediate adjustment, gradual adaptation, and aftereffect characterized by mean pairwise difference ratings on 5 days. The red filled circles represent the mean pairwise difference ratings in the first test with the glasses on in all sessions (i.e., immediate adjustment). The red open circles are ratings in the last test with the glasses on in each session (i.e., the gradual adaptation). The green diamonds are ratings after removing the glasses (i.e., aftereffect). The gray bars represent standard errors of the mean across participants. Data have been corrected for baseline shifts by subtracting the baseline rating in each session, immediately before putting on the glasses. The immediate adjustment grew significantly over days. The ratings after removing the glasses also increased significantly, indicating that the aftereffect decreased significantly over days.

*Why is the reconstructed color space that shape with glasses on?* Green and blue-green were relatively further away from other test colors in the perceptual spaces estimated using MDS when the glasses were on. To understand why we observed this shape, we plotted the physical stimuli that reached the participants through the glasses also in CIELAB space (Figure 4B). The glasses caused colors to shift toward red chromaticity and move closer to each other in CIELAB space, but the green and blue-green stimuli remained further away from other colors. These larger distances between green, blue-green, and other physical colors were reflected in participants' dissimilarity ratings and perceived color spaces when glasses were on. (The rotation of points is a free parameter in the MDS solution, which explains the different orientations of the compressed set of colors in the two spaces.)

## Effects across days

*Stronger, faster adjustment across whole perceptual color space.* Over days, color pairs appeared more dissimilar immediately after putting on the glasses. This is reflected in Figure 5 by the rising trend of the mean pairwise difference rating in the first test with the glasses on in each session. Figure 7 plots the baseline-corrected results after subtracting the baseline rating in all tests in each session (red filled circles for the first test with the glasses on). Linear trend analysis showed that this increase was significant ($t(12) = 9.41$, $p < 1e\text{-}6$, Figure 7, red filled circles).

The perceptual color spaces estimated from ratings in the first test with the glasses on expanded across days (the 0-min color spaces; Figure 6 and Supplementary Figure S4, column 2 from left). By the fourth and fifth days, the 0-min perceptual color space was even more expanded than that after 90-min adaptation on the first day. These results indicate that participants can learn to immediately adjust their perception of colors throughout color space when first putting the glasses on.

*Expansion of perceptual color space was relatively uniform.* Figure 8A plots the trajectories of all colors in the glasses-on 0-min perceptual color space from day 1 (filled circles) to day 5 (arrow end). It can be seen that the expansion happened across the whole color space relatively uniformly, with all colors shifting by an amount proportional to their distances from the center, except the blue-green stimulus. As a test of this uniformity, we plotted dissimilarity ratings between each pair of colors for day 1 versus day 5 (Figure 8B). The fact that the points fall along a line indicates that a single scale factor (the slope of the line) can account for the change in dissimilarity across the 5 days. We fit a line to the data to estimate the scale factor (which equaled 1.42), and scaling day 1 dissimilarities by this factor produced a good fit to the day 5 data, as shown in Figure 8C, where points fall along the identity line.

*Expansion of perceptual color space can be modeled by changes in cone sensitivities.* We tested whether this expansion could be accounted for by a common model of chromatic adaptation, generalized von Kries adaptation (e.g., Brainard et al., 1997; Wade & Wandell, 2002), that is, scaling of cone responses. We first fit a simple model to the day 1 data, in which cone outputs fed into red–green and blue–yellow opponent mechanisms, and the outputs of these mechanisms were linearly transformed (via a full affine transformation) so that the Euclidean distance between the transformed outputs for each color pair matched as closely as possible the distance in the reconstructed color space for that pair (see Methods). Figure 9A shows that the model fit the day 1 data well. Figure 9B plots the day 5 data against the model fit to the day 1 data. The fact that this plot too is roughly a straight line indicates that a uniform scaling of model outputs should also account for the change from day 1 to day 5.

To test whether scaling of cone responses could produce such a change across days, we searched for coefficients of the M and S cones, relative to the L cones (see Methods), that minimized the mean squared error between the adjusted model and the data. This minimum was reached when both M- and S-cone

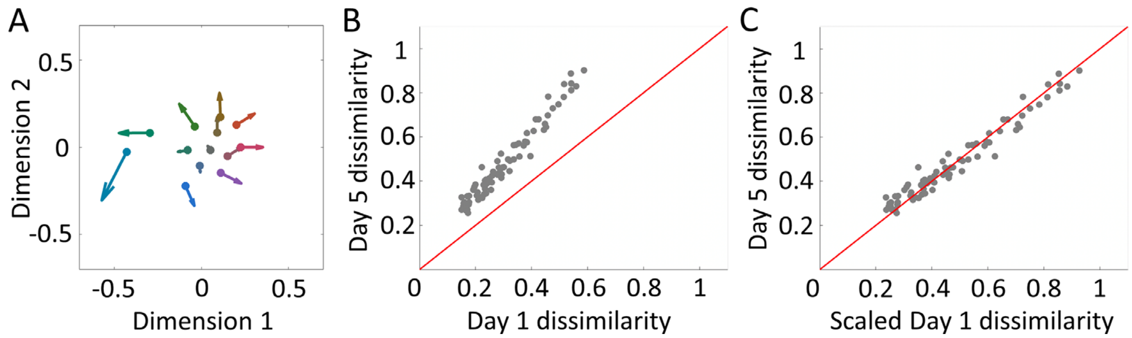


Figure 8. Uniform expansion of the perceptual color space over days. (A) Trajectories of all colors in the glasses-on 0-min perceptual color space from Session 1 (filled circles) to Session 10 (arrow end). (B) Normalized dissimilarity ratings immediately after putting on the glasses on day 1 and day 5. The red line is the identity line. (C) Day 1 and day 5 dissimilarity ratings after scaling day 1 ratings by a single factor.

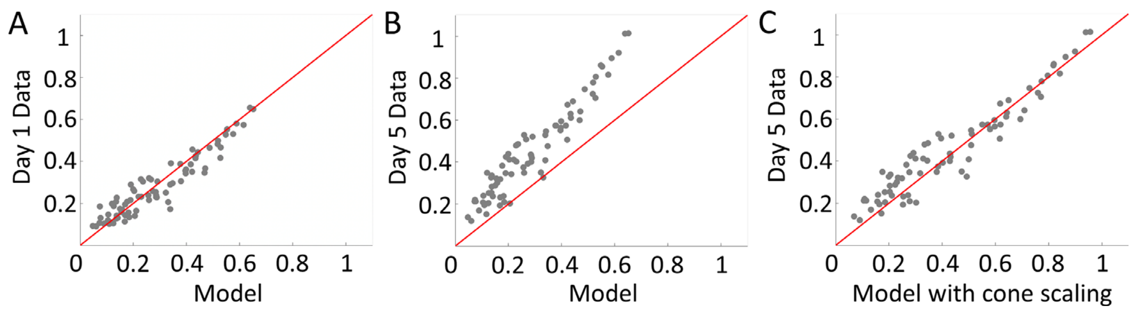


Figure 9. Cone scaling model of the expansion of the perceptual color space. (A) Model predictions of pairwise distances versus distance data from day 1. (B) Model predictions versus day 5 data, before scaling M- and S-cone sensitivities. (C) Model predictions after cone scaling versus the data from day 5.

coefficients were approximately 1.5. After applying this M- and S-cone scaling, the model fitted the day 5 data reasonably well, and the pairwise color distances in the two spaces fell along the identity line (Figure 9C).

A coefficient of 1.5 indicates that in order to expand the perceptual color space immediately after putting on the glasses, the relative strengths of M- and S-cone responses needed to be greater than before experience with the red environment, or alternatively, the L-cone strength needed to be relatively reduced. This makes intuitive sense since the red glasses' main effect was to reduce the relative response of M and S cones. The model confirms that scaling these responses back up provides a possible account of the effects of mode switching.

*Color aftereffect became weaker over days.* As in Experiment 1, participants experienced a color aftereffect that made the world appear slightly greenish after removing the glasses. The common greenish tint made all color pairs appear slightly more similar, compared to before wearing the glasses. This is reflected by smaller pairwise difference ratings after removing the glasses (Figure 5, green diamonds) than before putting on the glasses (Figure 5, black circles). The perceptual color spaces reconstructed from ratings after removing the glasses (Figure 6 and Supplementary Figure S4, rightmost column) were also slightly compressed compared to the baseline spaces (Figure 6 and Supplementary Figure S4, leftmost column) within the same session. Importantly, the rising trend of the green diamonds in Figure 5 indicates that the aftereffect became weaker, and colors appeared less similar immediately after removing the glasses over days. This change was reliable (linear fit $t(12) = 2.28$ , $p < 0.05$, Figure 7, green diamonds).

*Baseline ratings did not change significantly over days.* We did not find a change in baseline pairwise difference ratings over days (Figure 5, black circles, $p > 0.5$). The perceptual color space reconstructed from baseline ratings also did not change across days (Figure 6 and Supplementary Figure S4, leftmost column). To ensure that the effects we observed above were not affected by daily fluctuations in the baseline, we corrected its effect by subtracting the baseline mean pairwise rating in each session from mean pairwise ratings in all tests within the same session. These baseline-corrected results showed a similar pattern to the uncorrected results (Supplementary Figure S5).

*The amount of gradual adaptation decreased over days.* We quantified the amount of gradual adaptation as the difference in mean pairwise dissimilarity ratings between the first (Figure 7, red filled circles) and last (Figure 7, red open circles) tests made with glasses on in each session. This index decreased from 0.65 on day 1 to 0.18 on day 5. Linear trend analysis demonstrated that the decrease was reliable ($t(12) = -3.02$, $p = 0.01$).

# Discussion

The results of Experiment 2 indicate that participants' ability to learn to compensate for the red glasses applies to many colors. The red glasses compressed perceptual color space, and switching to "red-glasses mode" expanded the perceptual color space closer to its original form, to a greater extent each day, and colors appeared more and more dissimilar to each other. This finding suggests that besides calibrating the perceptual neutral point (measured in Experiment 1 and our past work), mode switching also helps to maintain an accurate perception of color appearance generally.

Our MDS results replicated previous findings that perceptual color space reconstructed using MDS is at least two-dimensional, with dimensions roughly corresponding to the "red–green" and "blue–yellow" opponent systems (e.g., Cavonius & Mollon, 1984; Helm, 1964). Past work has also used MDS to reconstruct the perceptual space of dichromats and anomalous trichromats (e.g., Boehm et al., 2014; Jordan et al., 2010; Paramei et al., 1991). Interestingly, anomalous trichromats show an expanded perceptual color space compared to what models of their receptoral differences predict (Boehm et al., 2014). Postreceptoral compensation has been hypothesized to underlie this expansion in anomalous trichromats and may also be one of the mechanisms that underlie the mode-switching effect we observed here.

In our data, the perceptual color space expanded uniformly over days, with all colors shifting away from the center by an amount roughly proportional to their distances from the center, except for blue-green (Figure 8A). The larger perceptual shift is likely due to the larger physical shift produced by the glasses for that color. As described earlier, wearing the red glasses shifted and compressed the physical color space generally (Figure 4B) but left the blue-green stimulus as an outlier, farthest away from the other stimuli. Perception initially resembled this pattern (Figure 6, Day 1, 0 min). While most colors moved away from the center, blue-green also moved away from green and toward blue, regaining the appearance midway between green and blue that it had with the glasses off. Future work can adapt participants to different color changes to test if nonuniformities of expansion generally aid recovery of perceptual appearance.

Scaling cone sensitivities modeled the uniform expansion of perceptual color space over days reasonably well, which suggests that mode switching may share some mechanisms with classical adaptation; for example, it may be that color adaptation speeds up through experience with the red glasses over days. The fact that the model could not fit the data perfectly indicates that mode switching likely involves other mechanisms beyond classical adaptation.

# General discussion

In both experiments, experience with an environmental change allowed the visual system to adjust to that change more rapidly and strongly across days. Experiment 1 demonstrated that a once-daily experience is sufficient for such an effect, with no need for multiple switches between different environments (see McLean et al. [2022] for a similar investigation into 5-hr vs. five 1-hr periods for a single day of adaptation to monocular magnification). Experiment 2 showed that the effect of mode switching applies to many stimuli in a given environment, causing them to appear more and more normal over time, at roughly equal speed. Together, these findings indicate that visual mode switching can occur under a relatively wide range of conditions and can affect a wide range of stimuli. This general applicability of mode switching may allow it to aid the many functional goals served by visual adaptation and other forms of plasticity.

## Prior work on mode switching

The first report of visual mode switching in color perception dates to the 1950s. Ivo Kohler (Kohler, 1951; English translation published in Kohler, 1963) first qualitatively documented the effect of wearing and removing colored lenses for many days (~20) and reported that over days, the color of the lenses faded more and more strongly as soon as they were put on. Since then, studies of multiple days of exposure to a colored environment have been relatively few (Belmore & Shevell, 2008, 2011; Hill & Stevenson, 1976; Neitz et al., 2002; Tregillus et al., 2016), despite the fact that the manipulation can be very simple, including wearing colored lenses or staying in room with colored lighting. These later studies did not investigate possible effects of mode switching, however, instead focusing on effects that remain when the glasses were no longer worn (what we term changes in baseline, discussed below).

Learning to switch perceptual processing modes has been reported in some other visual and nonvisual domains. For example, participants readapted faster to cylindrical lenses that created a sort of astigmatism in a second testing session, compared to the first time they wore the lenses (Yehezkel et al., 2010). Long-term habitual wearers of colored lenses adapted more rapidly to the color change their lenses produced than naive observers (Engel et al., 2016). There is also strong evidence for visual mode switching from underwater vision. Thai Sea Nomad children, who have a lot of experience seeing underwater without visual aids, were found to have much better underwater vision than European cohorts (Gislén et al., 2003), and European children were able to improve their underwater vision after repeated diving training (Gislén et al., 2006). In both cases, the stronger and more rapid adjustment was likely due to improved pupil constriction underwater. Fast readaptation to experienced environments has also been found in other sensorimotor domains, where observers adapted to visual-vestibular conflicts (Welch et al., 1998), prisms that displace the visual field (Redding et al., 2005), and force fields that disturb motor outcomes (Wolpert & Flanagan, 2016). Mode switching may also take place in audition (Hofman et al., 1998).

## Effects on baseline measures of color perception

Long-term exposure to a red environment causes unique yellow settings to become more and more physically reddish, as perceived reddishness fades and what used to appear reddish becomes more and more normal, and these effects are measurable even in a neutral environment (e.g., Belmore & Shevell, 2008; Eisner & Enoch, 1982; Neitz et al., 2002). We replicated this trend in Experiment 1 here, but it was small and not statistically reliable. In our past work with repeated 1-hr exposures, we found a small but significant shift of baseline in the opposite, greenish direction over days (Li et al., 2020). A similar opposite trend in baseline shift was also found in some previous studies (Engel et al., 2016; Tregillus et al., 2016). We had hypothesized that the presence or absence of visual context during viewing (lacking in many past studies, where observers were dark-adapted) may have affected which trend was seen, but Experiment 1 did not find differences between baseline measured with and without visual context.

The different trends across studies could simply be due to differences between observers: Past work on the time course of color adaptation across days found large individual differences (Belmore & Shevell, 2011; Li et al., 2020; Neitz et al., 2002; Tregillus et al., 2016; also see review by Tregillus & Engel, 2019). Some participants showed strong adaptation primarily during the first day or two, some showed gradual increases in adaptation across 10 or even 20 days, some only demonstrated small effects across days, and some others had effects that declined after initial growth. Exploring how individuals differ in their rate and amount of adaptation and identifying potential factors that contribute to these differences would be a valuable direction for future research.

## Other effects in the present work

The color aftereffect, measured immediately after removing the glasses, decreased across days in both Experiments 1 and 2, consistent with Li et al. (2020). These results may imply that participants also learned to more rapidly readjust to the familiar, natural environment over time. Future work could explore if and how mode switching to a familiar environment is different from adjusting to a newly experienced unfamiliar environment.

In both Experiments 1 and 2, the amount of gradual adaptation that happened within the hour after putting on the glasses decreased over days, a trend not present in our past work (Li et al., 2020). This difference may be affected by small changes in methodology across studies, such as the different glasses-wearing protocols and small differences in tasks. Nevertheless, it suggests that the input to the mechanisms controlling gradual adaptation may be first affected by mode switching (i.e., gradual adaptation may slow down as the residual reddishness following mode switching becomes smaller across days).

## Neural mechanisms of visual mode switching

Mode switching is an example of neural processing in perception that depends not only on the stimulus but also on the temporal context, which in this case is past experience with red glasses. In the domain of color vision, other well-known context effects include color contrast (i.e., color appearance shifts depending on the immediate spatial surrounding region) and color adaptation (i.e., appearance shifts depending on prior exposure to a color). The mode-switching effects we observed may arise from changes in these previously studied mechanisms that produce color contrast, color adaptation, and, more generally, color constancy. This possibility is bolstered by the fact that the cone scaling model could account for effects of mode switching reasonably well. Similar models also account for effects of color adaptation (e.g., Brainard et al., 1997; Wade & Wandell, 2002).

A number of neural loci have been identified as potentially responsible for color context effects, including retinal sources (Boynton & Whitten, 1970; Lee et al., 1999; Rieke & Rudd, 2009), early visual cortex (Engel, 2005; Engel & Furmanski, 2001; Wade & Wandell, 2002), and higher-level ventral areas along the color processing pathway (Bannert & Bartels, 2017; Engel, 2005; Goddard et al., 2019; Mullen et al., 2015). Plasticity is generally believed to increase as one ascends the visual pathways (e.g., Haak & Beckmann, 2019; Solomon & Lennie, 2007). So, while experience with an environment could in principle affect any stage, mode switching may most likely involve changes in the regions further along the processing stream.

## Conclusions

In sum, our results demonstrate that the visual system can learn to adapt to an experienced environment more rapidly and strongly. This mode switching can be induced by a once-daily experience and applies to many stimuli in the environment. These findings may help to predict when and how mode switching can occur outside the laboratory, including possibly in the presence of visual disorders or following interventions to aid them.

*Keywords: visual mode switching, visual plasticity, color adaptation*

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# References

Abrams, A. B., Hillis, J. M., & Brainard, D. H. (2007). The relation between color discrimination and color constancy: When is optimal adaptation task dependent? *Neural Computation, 19*(10), 2610–2637, https://doi.org/10.1162/neco.2007.19.10.2610.

Bannert, M. M., & Bartels, A. (2017). Invariance of surface color representations across illuminant changes in the human cortex. *NeuroImage, 158*, 356–370, https://doi.org/10.1016/j.neuroimage.2017.06.079.

Bao, M., & Engel, S. A. (2012). Distinct mechanism for long-term contrast adaptation. *Proceedings of the National Academy of Sciences, 109*(15), 5898–5903, https://doi.org/10.1073/pnas.1113503109.

Belmore, S. C., & Shevell, S. K. (2008). Very-long-term chromatic adaptation: Test of gain theory and a new method. *Visual Neuroscience, 25*(3), 411–414, https://doi.org/10.1017/S0952523808080450.

Belmore, S. C., & Shevell, S. K. (2011). Very-long-term and short-term chromatic adaptation: Are their influences cumulative? *Vision Research, 51*(3), 362–366, https://doi.org/10.1016/j.visres.2010.11.011.

Boehm, A. E., MacLeod, D. I. A., & Bosten, J. M. (2014). Compensation for red-green contrast loss in anomalous trichromats. *Journal of Vision, 14*(13), 19, https://doi.org/10.1167/14.13.19.

Boynton, R. M., & Whitten, D. N. (1970). Visual adaptation in monkey cones: Recordings of late receptor potentials. *Science, 170*(3965), 1423–1426, https://doi.org/10.1126/science.170.3965.1423.

Brainard, D. H. (1997). *The Psychophysics Toolbox. Spatial Vision, 10*(4), 433–436, https://doi.org/10.1163/156856897x00357.

Brainard, D. H., Brunt, W. A., & Speigle, J. M. (1997). Color constancy in the nearly natural image. 1. Asymmetric matches. *Journal of the Optical Society of America A, 14*(9), 2091–2110, https://doi.org/10.1364/JOSAA.14.002091.

Cavonius, C. R., & Mollon, J. D. (1984). Reaction time as a measure of the discriminability of large colour differences. In C. P. Gibson (Ed.), *Colour coded vs. monochrome electronic displays* (pp. 17.1–17.10). London, UK: HMSO.

Clifford, C. W. G., Webster, M. A., Stanley, G. B., Stocker, A. A., Kohn, A., Sharpee, T. O., . . . Schwartz, O. (2007). Visual adaptation: Neural, psychological and computational aspects. *Vision Research, 47*(25), 3125–3131, https://doi.org/10.1016/j.visres.2007.08.023.

Dragoi, V., Sharma, J., Miller, E. K., & Sur, M. (2002). Dynamics of neuronal sensitivity in visual cortex and local feature discrimination. *Nature Neuroscience, 5*(9), 883–891, https://doi.org/10.1038/nn900.

Eisner, A., & Enoch, J. M. (1982). Some effects of 1 week's monocular exposure to long-wavelength stimuli. *Perception & Psychophysics, 31*(2), 169–174, https://doi.org/10.3758/BF03206217.

Engel, S. A. (2005). Adaptation of oriented and unoriented color-selective neurons in human visual areas. *Neuron, 45*(4), 613–623, https://doi.org/10.1016/j.neuron.2005.01.014.

Engel, S. A., & Furmanski, C. S. (2001). Selective adaptation to color contrast in human primary visual cortex. *The Journal of Neuroscience, 21*(11), 3949–3954, https://doi.org/10.1523/JNEUROSCI.21-11-03949.2001.

Engel, S. A., Wilkins, A. J., Mand, S., Helwig, N. E., & Allen, P. M. (2016). Habitual wearers of colored lenses adapt more rapidly to the color changes the lenses produce. *Vision Research, 125*, 41–48, https://doi.org/10.1016/j.visres.2016.05.003.

Gislén, A., Dacke, M., Kröger, R. H. H., Abrahamsson, M., Nilsson, D. E., & Warrant, E. J. (2003). Superior underwater vision in a human population of sea gypsies. *Current Biology, 13*(10), 833–836, https://doi.org/10.1016/s0960-9822(03)00290-2.

Gislén, A., Warrant, E. J., Dacke, M., & Kröger, R. H. H. (2006). Visual training improves underwater vision in children. *Vision Research, 46*(20), 3443–3450, https://doi.org/10.1016/j.visres.2006.05.004.

Goddard, E., Chang, D. H. F., Hess, R. F., & Mullen, K. T. (2019). Color contrast adaptation: FMRI fails to predict behavioral adaptation. *NeuroImage, 201*, 116032, https://doi.org/10.1016/j.neuroimage.2019.116032.

Haak, K. V, & Beckmann, C. F. (2019). Plasticity versus stability across the human cortical visual connectome. *Nature Communications, 10*(1), 3174, https://doi.org/10.1038/s41467-019-11113-z.

Helm, C. E. (1964). Multidimensional ratio scaling analysis of perceived color relations. *Journal of the Optical Society of America, 54*(2), 256–262, https://doi.org/10.1364/JOSA.54.000256.

Hershenson, M. (1989). Duration, time constant, and decay of the linear motion aftereffect as a function of inspection duration. *Perception & Psychophysics, 45*(3), 251–257, https://doi.org/10.3758/BF03210704.

Hill, A. R., & Stevenson, R. W. (1976). Long-term adaptation to ophthalmic tinted lenses. *Modern Problems in Ophthalmology, 17*, 264–272.

Hofman, P. M., Van Riswick, J. G. A., & Van Opstal, A. J. (1998). Relearning sound localization with new ears. *Nature Neuroscience, 1*(5), 417–421, https://doi.org/10.1038/1633.

Jameson, D., & Hurvich, L. M. (1955). Some quantitative aspects of an opponent-colors theory. I. Chromatic responses and spectral saturation. *Journal of the Optical Society of America, 45*(7), 546–552, https://doi.org/10.1364/JOSA.45.000546.

Jordan, G., Deeb, S. S., Bosten, J. M., & Mollon, J. D. (2010). The dimensionality of color vision in carriers of anomalous trichromacy. *Journal of Vision, 10*(8), 12, https://doi.org/10.1167/10.8.12.

Judd, D. B. (1951). Report of U.S. Secretariat Committee on Colorimetry and Artificial Daylight. In *Proceedings of the Twelfth Session of the CIE, Stockholm* (vol. *1*, p. 11). Paris, Freance: Bureau Central de la CIE.

Kohler, I. (1951). *Über Aufbau und Wandlungen der Wahrnehmungswelt. Insbesondere über 'bedingte Empfindungen'*. Wien, Germany: Rohrer: Osterreichische Akademie der Wissenschaften, Philosophisch-historische Klasse. Sitzungsberichte 227, Band 1.

Kohler, I. (1963). The formation and transformation of the perceptual world. *Psychological Issues, 3*(4, Monogr. No. 12), 1–173.

Kohn, A. (2007). Visual adaptation: Physiology, mechanisms, and functional benefits. *Journal of Neurophysiology, 97*(5), 3155–3164, https://doi.org/10.1152/jn.00086.2007.

Krauskopf, J., & Gegenfurtner, K. (1992). Color discrimination and adaptation. *Vision Research, 32*(11), 2165–2175, https://doi.org/10.1016/0042-6989(92)90077-V.

Krekelberg, B., van Wezel, R. J. A., & Albright, T. D. (2006). Adaptation in macaque MT reduces perceived speed and improves speed discrimination. *Journal of Neurophysiology, 95*(1), 255–270, https://doi.org/10.1152/jn.00750.2005.

Lee, B. B., Dacey, D. M., Smith, V. C., & Pokorny, J. (1999). Horizontal cells reveal cone type-specific adaptation in primate retina. *Proceedings of the National Academy of Sciences, 96*(25), 14611–14616, https://doi.org/10.1073/pnas.96.25.14611.

Li, Y., Tregillus, K. E. M., Luo, Q., & Engel, S. A. (2020). Visual mode switching learned through repeated adaptation to color. *ELife, 9*, e61179, https://doi.org/10.7554/eLife.61179.

MacLeod, D. I. A., & Boynton, R. M. (1979). Chromaticity diagram showing cone excitation by stimuli of equal luminance. *Journal of the Optical Society of America, 69*(8), 1183, https://doi.org/10.1364/JOSA.69.001183.

Magnussen, S., & Greenlee, M. W. (1985). Marathon adaptation to spatial contrast: Saturation in sight. *Vision Research, 25*(10), 1409–1411, https://doi.org/10.1016/0042-6989(85)90218-4.

McLean, I. R., Manning, T. S., & Cooper, E. A. (2022). Perceptual adaptation to continuous versus intermittent exposure to spatial distortions. *Investigative Ophthalmology & Visual Science, 63*(5), 29, https://doi.org/10.1167/iovs.63.5.29.

Mullen, K. T., Chang, D. H. F., & Hess, R. F. (2015). The selectivity of responses to red-green colour and achromatic contrast in the human visual cortex: An fMRI adaptation study. *European Journal of Neuroscience, 42*(11), 2923–2933, https://doi.org/10.1111/ejn.13090.

Neitz, J., Carroll, J., Yamauchi, Y., Neitz, M., & Williams, D. R. (2002). Color perception is mediated by a plastic neural mechanism that is adjustable in adults. *Neuron, 35*(4), 783–792, https://doi.org/10.1016/S0896-6273(02)00818-8.

Paramei, G. V., Izmailov, Ch. A., & Sokolov, E. N. (1991). Multidimensional scaling of large chromatic differences by normal and color-deficient subjects. *Psychological Science, 2*(4), 244–249, https://doi.org/10.1111/j.1467-9280.1991.tb00142.x.

Redding, G. M., Rossetti, Y., & Wallace, B. (2005). Applications of prism adaptation: A tutorial in theory and method. *Neuroscience & Biobehavioral Reviews, 29*(3), 431–444, https://doi.org/10.1016/j.neubiorev.2004.12.004.

Rieke, F., & Rudd, M. E. (2009). The challenges natural images pose for visual adaptation. *Neuron, 64*(5), 605–616, https://doi.org/10.1016/j.neuron.2009.11.028.

Sharpee, T. O., Sugihara, H., Kurgansky, A. V., Rebrik, S. P., Stryker, M. P., & Miller, K. D. (2006). Adaptive filtering enhances information transmission in visual cortex. *Nature, 439*(7079), 936–942, https://doi.org/10.1038/nature04519.

Smith, V. C., & Pokorny, J. (1975). Spectral sensitivity of the foveal cone photopigments between 400 and 500 nm. *Vision Research, 15*(2), 161–171, https://doi.org/10.1016/0042-6989(75)90203-5.

Solomon, S. G., & Lennie, P. (2007). The machinery of colour vision. *Nature Reviews Neuroscience, 8*(4), 276–286, https://doi.org/10.1038/nrn2094.

Stockman, A., & Sharpe, L. T. (2000). The spectral sensitivities of the middle- and long-wavelength-sensitive cones derived from measurements in observers of known genotype. *Vision Research, 40*(13), 1711–1737, https://doi. org/10.1016/S0042-6989(00)00021-3.

Tregillus, K. E. M., & Engel, S. A. (2019). Long-term adaptation to color. *Current Opinion in Behavioral Sciences, 30*, 116–121, https://doi.org/10.1016/j.cobeha.2019.07.005.

Tregillus, K. E. M., Werner, J. S., & Webster, M. A. (2016). Adjusting to a sudden "aging" of the lens. *Journal of the Optical Society of America A, 33*(3), A129–A136, https://doi.org/10.1364/JOSAA.33.00A129.

van Lier, R., Vergeer, M., & Anstis, S. (2009). Filling-in afterimage colors between the lines. *Current Biology, 19*(8), R323–R324, https://doi.org/10.1016/j.cub.2009.03.010.

von Helmholtz, H. (1924). *Helmholtz's treatise on physiological optics* (Trans. from the 3rd German ed.; J. P. C. Southall, Ed.). Rochester, NY: Optical Society of America, https://doi.org/10.1037/13536-000.

Wade, A. R., & Wandell, B. A. (2002). Chromatic light adaptation measured using functional magnetic resonance imaging. *The Journal of Neuroscience, 22*(18), 8148–8157, https://doi.org/10.1523/JNEUROSCI.22-18-08148.2002.

Wainwright, M. J. (1999). Visual adaptation as optimal information transmission. *Vision Research, 39*(23), 3960–3974, https://doi.org/10.1016/S0042-6989(99)00101-7.

Wark, B., Lundstrom, B. N., & Fairhall, A. (2007). Sensory adaptation. *Current Opinion in Neurobiology, 17*(4), 423–429, https://doi.org/10.1016/j.conb.2007.07.001.

Webster, M. A. (2015). Visual adaptation. *Annual Review of Vision Science, 1*, 547–567, https://doi.org/10.1146/annurev-vision-082114-035509.

Webster, M. A., Miyahara, E., Malkoc, G., & Raker, V. E. (2000). Variations in normal color vision II unique hues. *Journal of the Optical Society of America A, 17*(9), 1545, https://doi.org/10.1364/JOSAA.17.001545.

Webster, M. A., & Mollon, J. D. (1995). Colour constancy influenced by contrast adaptation. *Nature, 373*(6516), 694–698, https://doi.org/10.1038/373694a0.

Welch, R. B., Bridgeman, B., Williams, J. A., & Semmler, R. (1998). Dual adaptation and adaptive generalization of the human vestibulo-ocular reflex. *Perception & Psychophysics, 60*(8), 1415–1425, https://doi.org/10.3758/BF03208002.

Wolpert, D. M., & Flanagan, J. R. (2016). Computations underlying sensorimotor learning. *Current Opinion in Neurobiology, 37*, 7–11, https://doi.org/10.1016/j.conb.2015.12.003.

Yehezkel, O., Sagi, D., Sterkin, A., Belkin, M., & Polat, U. (2010). Learning to adapt: Dynamics of readaptation to geometrical distortions. *Vision Research, 50*(16), 1550–1558, https://doi.org/10.1016/j.visres.2010.05.014.