Visual mode switching: Behavior & Neuroimaging

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Abstract

"Color context effects" describe empirical results or phenomena where a surround, either in space or time, changes perception of the color of a target. The strength of color context effects may be influenced by our familiarity with the specific context. We term stronger and faster context-dependent processing under familiar contexts “visual mode switching”. Mode switching could help to stabilize vision in the changing visual environment and aid many perceptual goals, including improving the detection or discrimination of objects and their properties, and making neural codes more efficient. This dissertation presents three behavioral studies investigating whether visual mode switching can be learned through experience with a context, and whether it affects many stimuli in a given environment. Study 1 explored whether mode switching can occur after wearing strongly tinted glasses for five 1-hr periods per day for five days. We found that over days the tint faded more and more rapidly upon donning the glasses, indicating that the visual system learned to rapidly adjust to the tinted environment, switching modes to stabilize color vision. Study 2 tested whether wearing tinted glasses for a single 5-hr period each day for five days suffices for learning to switch visual modes. We found that mode switching can be acquired from a once-daily experience. In study 1 and 2, we tested for changes in the perception of unique yellow, which contains neither red nor green. Study 3 explored whether effects of mode switching can apply to many stimuli affected by the environmental change. We used a dissimilarity rating task to measure and track perception of many different colors, and found that colors across the color space appeared more and more normal immediately after putting on the glasses. These findings may help to predict when and how mode switching occurs outside the laboratory. Lastly, in study 4 we conducted a pilot functional MRI (fMRI) experiment to investigate the neural mechanisms of visual mode switching. We adopted a similar paradigm as in the behavioral studies. The fMRI design worked well and allowed us to identify brain regions that had changes in their responses to colors seen while wearing the red glasses before and after five days of experience with them. We found that both the primary and extrastriate visual cortex may be involved in mode switching. Taken together, these findings help us better understand how experience alters both visual perception and cortical processing of color.

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1 Review: Color context effects

1.1 Introduction to color context effects

The apparent color of an object depends not only on the spectral content of the light that reaches the eye but also on its spatial and temporal characteristics. I will refer to the spatial and/or temporal surround that is near a target for which we measure perception as “context”. Often, the perception of a target depends on this context, and such “context effects” represent an important part of color perception.

In the domain of color vision, there are various aspects of the context that can influence the appearance of a target. Changes in the color appearance of a target induced by its immediate spatial surrounding region are called *color contrast* (illustrated in Figure 1.1). Target appearance shifts caused by prior exposure to a color (at the same location) are called *color adaptation*. These effects are distinct from each other, but they may share neural and computational mechanisms, and may serve common goals (e.g., Hurlbert & Wolf, 2004). One important goal of color vision is *color constancy*, the robustness of perceived surface color despite changes in the spectrum of the light reaching the eye from the surface, caused, for example by changes in the scene's illumination.

Figure 1.1. **Illustration of a color contrast effect.** The two squares in the middle are physically identical and reflect the same light to our eyes. Yet, they appear different because they are embedded in different surroundings.

1.1.1 Spatial context

One simple but powerful context effect is simultaneous color contrast, which occurs when the color of a surface induces its complementary color in an adjacent surface (Figure 1.1). For example, a small gray patch can appear pinkish when surrounded by a large green background.

The inducing surface is typically a single uniform surround (e.g., Chichilnisky & Wandell, 1995; Shepherd, 1999; Walraven, 1973; Ware & Cowan, 1982). More complex, chromatic patterned background also can induce larger color appearance shifts (Monnier & Shevell, 2004). Color contrast happens almost instantaneously (e.g., Rinner & Gegenfurtner, 2000) and can produce large effects in perceived surface color.

Perceptual evidence suggests that effects of color contrast may arise very early in visual processing. In many cases, for example, the changes in color appearance of a target can be predicted by assuming that the presence of the surround scales cone responses in proportion to the amount that it stimulates each cone type, a computation known as Von Kries adaptation (e.g., Chichilnisky & Wandell, 1995). The scaling factor for each cone type may, however, depend on the activities of all cone types (Delahunt & Brainard, 2000). Fully explaining perceptual results may also require subtracting a portion of the cone responses from the surround from the responses to the center, in addition to the divisive process of scaling (e.g., Walraven, 1976).

Other color appearance phenomena that are directly related to the spatial structure of the target includes crispening and spreading. Crispening refers to the increase in the perceived magnitude of color differences when the background on which the two stimuli are compared is similar in color to the stimuli themselves (Takasaki, 1966, 1967; Whittle, 1992). Spreading is the apparent mixture of a color stimulus with its background, when the stimuli increase in spatial frequency or become smaller (Broerse et al., 1999). Another phenomenon, similar to spreading, is the watercolor effect (WCE), where color filling-in (i.e., an empty region appears to be filled with color of its surround) happens within white areas bordered by colored lines (Pinna et al., 2001). Finally, color appearance may also depend on the amount of variation of colors within the background (Barnes et al., 1999; Brown & MacLeod, 1997).

1.1.2 Color adaptation

Color adaptation is another phenomenon that highlights contextual processing in the visual system. In color vision, adaptation has two forms: adaptation to the overall mean color (e.g., adaptation to the chromaticity of lighting); and to variations in color relative to the mean, known as contrast.

When the mean color coordinates of the environment change, the visual system adjusts, so that the color appearance of the world gradually shifts back toward “normal”. The effect was first documented by de La Hire in 1694 and has been widely studied since then. An illusory perception of complementary color, called an "afterimage", may be observed when a stimulus is first adapted to, and then removed (e.g., von Helmholtz, 1924; Krauskopf & Gegenfurtner, 1992).

Adaptation to the dominant color can occur at different time scales. It may happen instantaneously when the color changes are moderate or small, which has been studied as color constancy (see below), and adaptation may evolve over timescales from seconds to minutes (Rinner & Gegenfurtner, 2000; Shevell, 2001), or even progress over hours when the color shift is strong and/or long-lasting (Belmore & Shevell, 2008; Li et al., 2020; Neitz et al., 2002).

Vision also adapts to color contrast. Color contrast adaptation can change color appearances both by reducing their saturation and by changing their hue. The perceived contrast (saturation) of colors that are similar to the adapting color are reduced the most. The perceived hues of other colors are generally biased away from the adapting color (e.g., Webster & Mollon, 1994, 1995).

Neurally, adaptation can occur in multiple stages along the visual pathway. Adaptation to changes in the dominant color includes sensitivity changes in cones (Boynton & Whitten, 1970; Lee et al., 1999; Rieke & Rudd, 2009), calibrations in post-receptoral pathways (Walraven et al., 1990; Zaidi, 2012), and adjustments in cortical stages of color processing (Rinner & Gegenfurtner, 2000). Perceptual, physiological, and neuroimaging evidence suggests that contrast adaptation arises primarily from sensitivity changes of cortical neurons (Derrington et al., 1984; Engel & Furmanski, 2001; Gilinsky, 1968; Krauskopf et al., 1982; Webster, 1996).

1.1.3 Color constancy

Color constancy is a way to describe empirical results in which we perceive the color of a target consistently despite changes in illumination conditions (reviews by Foster, 2011; Witzel & Gegenfurtner, 2018). Such stability in perceived color is important in identification and communication of objects and materials through color.

How constant are we? Constancy can vary from nearly zero to almost perfect, depending on experimental conditions and tasks, as well as the instructions the observers receive (e.g., reviews by Foster, 2011; Witzel & Gegenfurtner, 2018). Perfect compensation might be disadvantageous because it might prevent information about the illumination from reaching perception, but a lack of constancy could simply be due to the insufficient or incorrect information available from the context. Very high constancy can be achieved when testing in naturalistic scenes with many contextual cues (Allred & Olkkonen, 2013; Brainard, 1998).

How is color constancy achieved? Computationally, color constancy results from an inference about reflectance that takes into account illumination. Because illumination also affects the context, context effects are key mechanisms that allow the inference process to happen accurately. Strategies for estimating the illumination chromaticity from context information includes space-average chromaticity (Buchsbaum, 1980), assumption that “brightest is white” (Hurlbert, 1998), specular highlights (Lee, 1986), mutual reflections (Funt et al., 1991), and higher-order image statistics (Golz & MacLeod, 2002).

Perceptually, some amount of color constancy is computed immediately and may be due to color contrast type effects; some happens slowly and may be due to color (and color contrast) adaptation (Hurlbert & Wolf, 2004; Smithson & Zaidi, 2004; Valberg & Lange-Malecki, 1990; Webster & Mollon, 1995). High-level processes including recognition of objects with known color also contribute to color constancy (Hansen et al., 2006).

Neurally, color constancy is the result of a multitude of processes at different stages of the chromatic pathways: cone adaptation, spatial comparisons taking place on retina, LGN, primary visual cortex (V1), and higher cortical areas (see reviews by Foster, 2011; Smithson, 2005).

1.1.4 Context effects in lightness perception

Similar to color vision, lightness perception is also context dependent. For example, in "luminance simultaneous contrast" (lightness induction) a gray target appears lighter on a black background than on a white background (e.g., Hering, 1964; Horeman, 1963). Another related compelling example of a context effect in lightness perception is the Craik-O'Brien-Cornsweet illusion (or Cornsweet illusion), where two surfaces of equal luminance appear to have different lightness if the border between them has oppositely signed luminance gradients (Cornsweet, 1970; O’Brien, 1958).

1.2 Introduction on visual mode switching and overview of this dissertation

The strength of color context effects could also be influenced by familiarity with the specific context. When a contextual change is common, the visual system might remember past context-dependent processing to produce particularly strong and rapid effects, making instantaneous adjustments to the particulars of that setting.

For example, wearing sunglasses makes the world appear tinted when we first put them on. The visual system adapts to the global color changes produced by wearing the glasses, and the tint fades over time, as illustrated in Figure 1.2. However, after much experience donning and removing the glasses, the world may appear almost normal immediately after putting them on. We term the context-dependent processing under a specific contextual setting a "mode", and the stronger and faster adjustments under familiar contexts "visual mode switching".

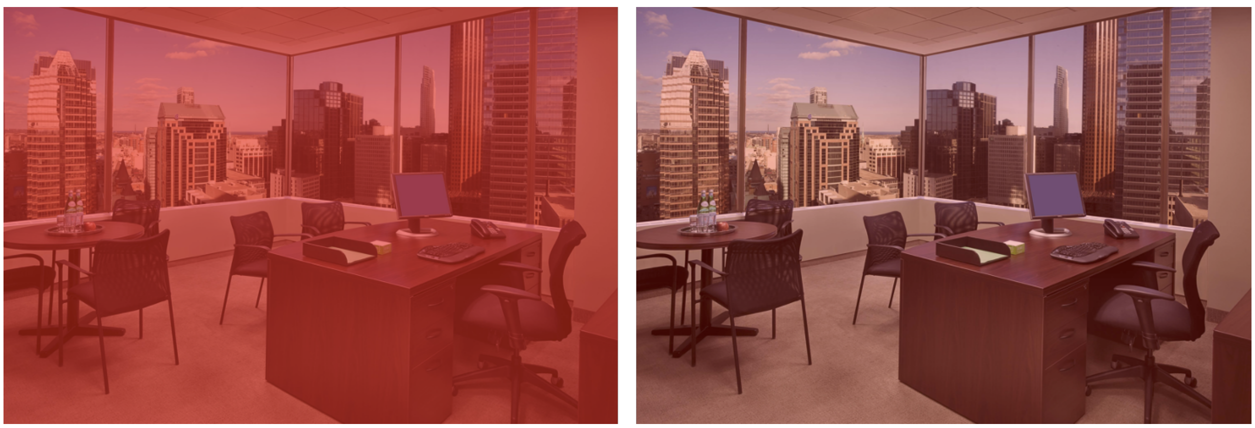


Figure 1.2. **Simulated effects of adaptation to a pair of reddish sunglasses.** The image on the left simulates the appearance of a natural scene seen through the glasses when first put on. The scene is dominated by redness, and there is a very small range of colors in it. The image on the right simulates the appearance of the scene after adapting to the glasses for a while. The reddishness fades away, and the scene appears much more colorful than before, though with some redness remaining.

Preliminary evidence for mode switching has been reported in different domains of vision. Observers can readapt faster to cylindrical lenses that create a sort of astigmatism in a second testing session, compared to the first time they wear the lenses (Yehezkel et al., 2010). In addition, long-term habitual wearers of red and green lenses adapt more rapidly to the color changes the lenses produce than naive observers do (Engel et al., 2016). Perhaps the strongest evidence for visual mode switching comes 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). European children were able to improve their underwater vision after repeated diving training (Gislén et al., 2006).

Learning to switch processing modes has also been found in audition (Hofman et al., 1998) and in the sensorimotor domain, where observers adapt to, for example, visual-vestibular conflicts; the conflicts were induced by subjects rotating their head from side to side while fixating a dot of light on a screen that moves in the same direction as the head but by only half as much as it would normally (Welch et al., 1998). Other sensorimotor conflicts can also lead to mode switching, including prisms that displace the visual field (Redding et al., 2005), and force fields that disturb motor outcomes (Wolpert & Flanagan, 2016).

Negative findings have also appeared in the literature, however. For example, clinically astigmatic observers showed little change in adaptation to their corrective lenses during 6 months following their initial prescription (Vinas et al., 2012). In another study, repeatedly adapting to yellow lenses produced little change in adaptation across 5 days (Tregillus et al., 2016). Thus, it remains unclear whether, when, and how visual mode switching can be learned for a familiar context.

Mode switching is a powerful example of perception and neural response depending not only on the object of interest, but also on the context in which we are operating. Classical models of both the brain and perception assume a stimulus produces a fixed perception and neural response, ignoring the context. Context effects have received intense interest because they demonstrate that neurons change their responses to the exact same stimulus, depending upon prior neural activity and the activity of nearby neurons. Because mode switching is a novel and particularly strong perceptual context effect, understanding how it is implemented could lead to large revisions to existing models of perception. In addition, since mode switching is relatively unstudied, work on it should lead to investigation in other visual domains (e.g., motion) and for other senses. Knowledge of mode switching may aid perceptual training for clinically important domains, such as radiographic or microscopic imagery. Understanding when and how this novel form of learning occurs may also help behavioral interventions for visual disorders, such as amblyopia or macular degeneration. It could allow interventions to be tailored to how visual cortex implements mode switching, helping people adjust to the new mode corresponding to their disordered vision.

This dissertation includes three behavioral studies that investigated learning to switch visual modes. In these studies, observers wore bright red glasses for many hours a day, for five days. On the first day the world appeared very reddish when the glasses were first put on, but across days colors appeared significantly less reddish immediately, and almost normal on the last day. This work provided strong behavioral evidence that visual mode switching 1) can be learned through repeated adaptation to a color change (Chapter 2); 2) can be learned through once-daily experience (Chapter 3 Experiment 1); and 3) can be generalized to many colors in a given visual environment (Chapter 3 Experiment 2).

In our studies, observers adapted to the red glasses in a setting with rich cues to context (e.g., lightened testing room, natural scene on the testing screen and spending time outside the lab when not being tested), which allowed the visual system to determine the viewing conditions, and hence the appropriate visual modes, and to perform context-dependent processing accordingly. These context cues may be necessary for mode switching to occur, since in studies where observers were tested with little context present, effects of long-term color adaptation were highly variable and inconsistent, with little to no effect of visual mode switching (Belmore & Shevell, 2008, 2011; Eskew & Richters, 2008; Neitz et al., 2002; Tregillus et al., 2016).

Chapter 4 contains a pilot fMRI study that explores the neural bases of visual mode switching. I used a similar behavioral paradigm as in previous studies, and measured brain responses to many colors before and after 5 days of experience with the red glasses. The paradigm allowed us to observe brain regions that had changed responses to color stimuli viewed through the red glasses before and after learning. These regions included primary visual cortex and extrastriate areas, suggesting that they may be involved in visual mode switching.

2 Visual mode switching learned through repeated adaptation to color

(Adapted from Li, Y., Tregillus, K. E., 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)

2.1 Introduction

When the visual system encounters different environments – for example a change in overall brightness, focus, or color – sensory processing also changes, in order to maintain accuracy and efficiency. Some of the processes producing such adjustments, called visual adaptation, unfold gradually (Clifford et al., 2007; Kohn, 2007; Wark et al., 2007; Webster, 2015). For example, wearing sunglasses can alter the color of an apple, making it difficult to determine if it is ripe. But as our visual system adapts, the apple's apparent color gradually returns to normal. For common environmental changes, it would be beneficial if the visual system could remember past adaptation, and rapidly switch to the appropriate state (Engel et al., 2016; Yehezkel et al., 2010). Such visual mode switching would aid the many functions that adaptation serves, including improving the detection or discrimination of objects and their properties (Dragoi et al., 2002; Krekelberg et al., 2006; McDermott et al., 2010; Müller et al., 1999; Wissig et al., 2013) and making neural codes more efficient (Seriès et al., 2009; Sharpee et al., 2006; Wainwright, 1999).

Empirical evidence for learning to switch visual modes is sparse and inconclusive, however. A few studies have found preliminary support for learning effects on visual adaptation (Engel et al., 2016; Yehezkel et al., 2010), but others have found little to no effect of experience (Tregillus et al., 2016; Vinas et al., 2012). Notably, previous work has not measured the effects of moving in and out of an environment multiple times per day over many days, and none has tested for changes in the time course of adaptation with experience. Thus, it remains unclear whether people can learn to rapidly switch visual modes with experience.

Here, we used color adaptation to test for such learning: Observers wore a pair of tinted glasses, which made the world appear very reddish (the spectral transmission of the glasses as well as the monitor gamut with and without the glasses are shown in Figure 2.1). Color adaptation in such situations is relatively well-understood, and one of its main effects is that the dominant color of the environment fades over time e.g. (Belmore & Shevell, 2008; de La Hire, 1694; Eisner & Enoch, 1982; Neitz et al., 2002; von Kries, 1902), restoring the world to its prior, "normal" appearance.

Observers in the present experiment donned and removed the glasses multiple times a day for 5 consecutive days. We hypothesized that color adaptation would speed up and/or get a head start over days, such that observers would experience a much smaller perceptual change in the color of the world when they put on the red glasses, providing evidence that they had learned to switch modes. Because it may involve mechanisms beyond classical adaptation, we will use the term "rapid adjustment" to refer to this possible empirical evidence for mode switching -- that as soon as observers put the glasses on, their effects were less prominent. Different potential mechanisms behind the shift will be considered in the Discussion.

Observers wore the red glasses for five one-hour periods, each separated by one hour without glasses (Figure 2.1). To track adaptation, we asked observers to make unique yellow settings, identifying the wavelength of light that appears neither reddish nor greenish (Jameson & Hurvich, 1955). Unique yellow is a commonly used measure in color perception, in part because observers are highly consistent in their judgments (e.g., Brainard et al., 2000; Jameson & Hurvich, 1955; Neitz et al., 2002).

On each day, observers were tested in two sessions, once in the morning and once in the afternoon, for 5 days in a row. In each session they performed: one test before putting on the glasses; 5 tests with the glasses on; and 4 tests after removing the glasses. During each test, observers made unique yellow settings for 5 one-minute blocks. Within each block, observers set as many matches as they could. Each datapoint in Figures 2.2 - 2.5 represents the average settings across a 5-minute test. The tests were all conducted in a fully lit lab room in order to provide information about the visual environment present. In a follow-up, conducted about one month after the main experiment, observers participated in one additional and identical testing session.

2.2 Materials and Methods

2.2.1 Observers

Observers included author YL and 11 members (21 to 37 years of age) of the University of Minnesota community. All had normal color vision, as assessed by the Ishihara Color Blindness Test, and normal or corrected-to-normal (using contact lenses) visual acuity. None had worn red glasses for extended periods of time prior to this study. One of the observers recruited reported that she changed her criterion for unique yellow during the study, and her data showed very large variance in baseline across days. Her data were excluded from further analysis. Experimental procedures were approved by the University of Minnesota Institutional Review Board. All observers provided written, informed consent before the start of the study.

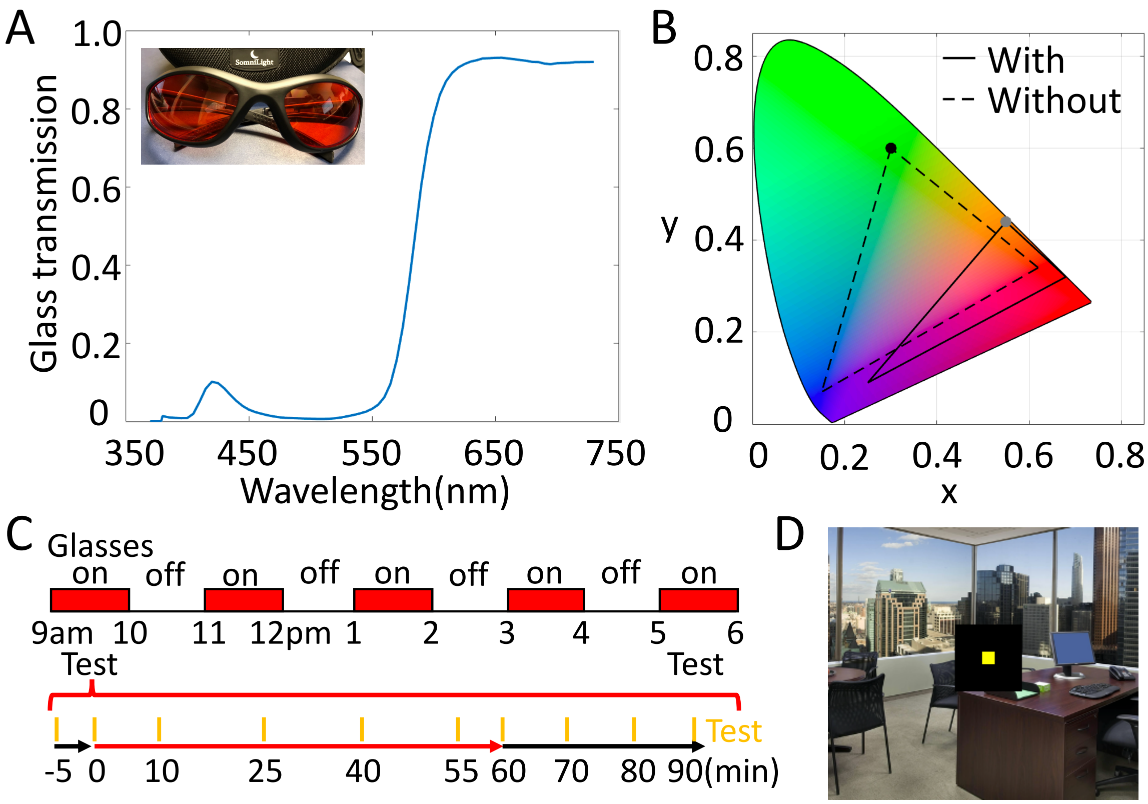


Figure 2.1. **Glasses transmission and experimental procedure.** (A) The red glasses used in this study and their transmission spectrum. The glasses filter out most of the energy at short wavelengths and maintain most of the energy at long wavelengths. (B) Monitor gamut with (solid line) and without (dashed line) the glasses plotted in CIE color space. The glasses compress the gamut and shift it towards red chromaticity. For example, the greenest light produced by the monitor (black dot) falls in an orange part of color space through the red glasses (gray dot). (C) Experimental procedures. The upper panel indicates the times when the observers wore the glasses within one day. Two test sessions were conducted, during the first and last 1hr of wearing the glasses. The lower panel illustrates the test procedure in each session. Orange bars indicate the time of test: 5 min before putting on the glasses, right after putting on the glasses, then following 10 min, 25 min, 40 min, and 55 min of wearing the glasses. Observers then removed the glasses and were tested immediately, and 10 min, 20 min, and 30 min after removing the glasses. (D) Test display. Observers adjusted the color of a square centered on a background image of a naturalistic office environment, presented on a monitor in a fully lit room. The fixed image of the office and skyline was presented on the test display to give observers context information when making the adjustments. A black square of 5.7 degrees separated the 0.5 deg square test patch from the background image. The test patch was presented for 200 ms at 1.5 sec intervals, and the observer's goal was to set it to appear unique yellow. Observers viewed the test display through a 3-foot felt-lined tunnel, on a calibrated monitor, in a fully lit lab room.

2.2.2 Apparatus

Visual stimuli were presented on a NEC MultiSync FP2141 cathode ray tube monitor, with screen resolution of 1024*768 pixels, and a refresh rate of 85 Hz. The monitor was calibrated using a Photo Research PR655 spectroradiometer, with gun outputs linearized through look-up tables. All visual stimuli were delivered in Matlab using the psychophysical toolbox (Brainard, 1997). Viewing distance was maintained at 50 cm with a chinrest.

2.2.3 Glasses

Observers wore a commercial pair of bright red glasses made by *SomniLight (Shawnee, KS)*. Black baffling was added on the top of the frame to prevent light from bypassing the glasses from above. The glasses filter out most of the light at short wavelengths and let pass most of the light at long wavelengths. We measured the glasses transmittance by placing the glasses in front of the spectroradiometer and recording the light from sunlight. The spectral transmission of the glasses (Figure 2.1A) shows that the transmittance is above 90% at wavelengths over 620 nm, and less than 10% at wavelengths below 550 nm.

To characterize the effect of the glasses on our testing display, we measured the gamut of the monitor with and without the glasses. Figure 2.1B demonstrates that the gamut of the monitor seen through the glasses becomes compressed and shifts towards red chromaticity.

2.2.4 Procedure

In the main experiment, observers wore the glasses for 5 one-hour periods per day, for 5 consecutive days. On each day, observers came to the lab in the morning and wore the red glasses for 1 hour, while participating in a testing session. Then, they left the lab and attended to their routine everyday activities, experiencing a variety of illumination conditions. They were asked to put on the glasses again one hour after they took off the glasses in the lab. During the day, they wore the glasses for three one-hour periods, each separated by one hour without glasses. At the end of the fourth one-hour period without glasses, they came back to the lab for a second testing session, identical to that in the morning. Figure 2.1C, upper panel, illustrates the procedure of the experiment. In a follow-up test session conducted about one month after the main experiment, observers came back and performed one additional and identical testing session.

Observers completed all tests in a fully lit room (with no window), with the aim of measuring perceptual experience in a context like their natural environment while adapting to the glasses. The screen was viewed through a 3-foot felt-lined ‘tunnel’, so that ambient light reaching our test display was not a significant factor. Observers sat in front of the ‘tunnel’ with their heads positioned on a chinrest located at its entrance.

During the test sessions, observers adjusted the color of a 0.5-degree square centered on a background image of a naturalistic environment (an office scene). The mean luminance of the background office image was 20 candela/m^2. A black square of 5.7 degrees separated the test patch from the background image (Figure 2.1D). The goal was to set the small square to unique yellow. We gave instructions *“Your task is to adjust the small patch to yellow, which contains no red nor green in it, based on the light reaching your eye. Try not to think about what the color of the patch on the screen should be”* to observers for both tests with and without the red glasses.

The small patch was presented for 200 ms at 1.5 sec intervals. To make adjustments observers pressed the left and down arrow buttons to reduce redness in the patch, right and up arrow buttons to reduce greenness in the patch, and then pressed the space bar when they had set the patch to appear neither reddish nor greenish. The left and right arrow buttons were for coarse adjustments, and the up and down arrow buttons were for finer adjustments. Observers had 20 sec at the most to make one single adjustment so that they didn’t get stuck in making one single setting and didn’t adapt to the test patch.

Stimuli were created using a modified version of the MacLeod-Boynton color space (MacLeod & Boynton, 1979), scaled and shifted so that the origin corresponds to a nominal white point of Illuminant C and so that sensitivity is roughly equated along the two axes (Webster et al., 2000).

We began by computing cone responses from the stimulus spectrum using the Smith & Pokorny (1975) cone fundamentals scaled so that the sum of L cone and M cone responses equaled 1 and the 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 $b_{mb} = S/(L+M)$. Finally, we scaled and shifted these coordinates:

$$LM = (r_{mb} - 0.6568) \times 2168$$

$$S = (b_{mb} - 0.01825) \times 6210$$

Where LM is the scaled red-green coordinate, and S is the scaled S-cone coordinate, 0.6568 and 0.01825 are the MacLeod-Boynton coordinates of Illuminant C, and 2168 and 6210 are constants that scale the LM and S axes so that a value of 1 is roughly equal to detection threshold (Webster & Mollon, 1995).

All settings fell along the nominally iso-luminant plane (defined by the LM and S axes, with luminance set to 51 candela/m^2) when not wearing the glasses in order to reduce brightness effects on the judgments. The photopic luminosity function we used to define nominal isoluminance was the CIE Photopic $V(\lambda)$ modified by Judd (1951).

In performing the unique yellow task, observers moved the stimulus along a circle in this plane. Thus, results are shown in "Hue Angle," where luminance and contrast (i.e., distance from the origin in the plane) were held constant. The stimuli were not adjusted for the glasses, and thus were likely not held at strictly constant luminance or contrast for judgments made while the glasses were on. The radius of the hue circle used was 80, which is a chromatic contrast of roughly 80 times detection threshold (see above) and was kept constant during the adjustment procedure.

Observers could adjust the angle of the stimulus with coarser or finer steps of 5 or 1 degree of hue angle respectively per button press. Button presses had no effect once observers reached a green endpoint at 200 degrees in hue angle and a red endpoint at 360 degrees of hue angle. At the beginning of each trial, the hue angle of the stimuli was set randomly from 290±45 degrees. We tracked observers' responses and stored each step of their adjustments. Examination of these data confirmed that they were not using the red or green endpoint as an anchor for their settings (e.g. always moving to the endpoint and then moving a fixed number of steps back).

At the beginning of each test session, observers performed five one-minute blocks of this task with natural vision. Then, they put the glasses on and immediately did five blocks of the task again. During each block, observers made as many matches as they could and between blocks, there was a break of a few seconds. Observers were also tested after 10 min, 25 min, 40 min, and 55 min of wearing the glasses. Between tests observers took a short walk and/or watched videos of their choice, or texted, on a computer or their phone.

After 1 hour, observers removed the glasses and were immediately tested again. Further tests were performed 10 min, 20 min, and 30 min after removing the glasses. The full test procedure is illustrated in the lower panel of Figure 2.1C.

2.2.5 Data Analysis

Initial analyses averaged hue angle across tests and observers, and plotted them as a function of test time and day. In order to compare unique yellow settings with and without the glasses, we also characterized the results in terms of relative gain of the cone photoreceptors (Neitz et al., 2002). The analysis assumes that unique yellow settings correspond to a balancing point between the L and M cone responses, where a scale factor (gain) is applied to responses of one of the cone classes: $L = k*M$. Effects of adaptation can be quantified by solving for k using estimates of the cone responses to the stimulus for each unique yellow setting.

We computed relative gains of cones as follows: First, we calculated the spectra of the unique yellow settings by multiplying the RGB values of the observers' settings by the gun spectra of the monitor and summing the outputs of the three guns. For the settings made with the glasses on, we further multiplied the monitor spectra by the transmission spectrum of the glasses. The spectra of the settings were then multiplied by the cone fundamentals to compute cone absorptions, using Stockman & Sharpe (2000) fundamentals, with peaks scaled to 1. Lastly, the absorptions were converted into relative gain by the ratio of L/M (which solves for k in the equation above). This same quantity was computed for settings made both with and without the glasses.

2.3 Results

The world appeared very reddish when observers first put on the glasses, and the redness faded over time as vision adapted. Figure 2.2 plots unique yellow settings (quantified as hue angle, see Methods) as a function of time, averaging across 11 observers, for the 5 days. The relatively small number (around 220) on the very first test with glasses on (red dots) indicates that observers' unique yellow was physically relatively green, which was required to cancel the redness produced by the glasses. The upward slope of each session's 5 settings shows that observers added less green to unique yellow over time, adapting to the red environment during the 1hr of wearing the glasses, with the world looking less and less red. This pattern can be seen both in the morning (with white background in Figure 2.2) and the afternoon (with light gray background) session on all 5 days.

2.3.1 Adjusting to the glasses became faster and stronger

Across days, observers learned to rapidly adjust to the red glasses. That is, when they first put the glasses on, the world appeared less and less reddish. This is visible in the graph by the rising trend of the first unique yellow setting in each session across days. A linear trend analysis (Figure 2.3 red dots) showed that this increase was reliable ($t = 6.87$, $p < 0.0001$). A number of different mechanisms could account for this empirical observation (see Discussion), but the changes were not due to lingering overall adaptation across days, as baseline measurements made before putting the glasses on showed a very different trend (see below).

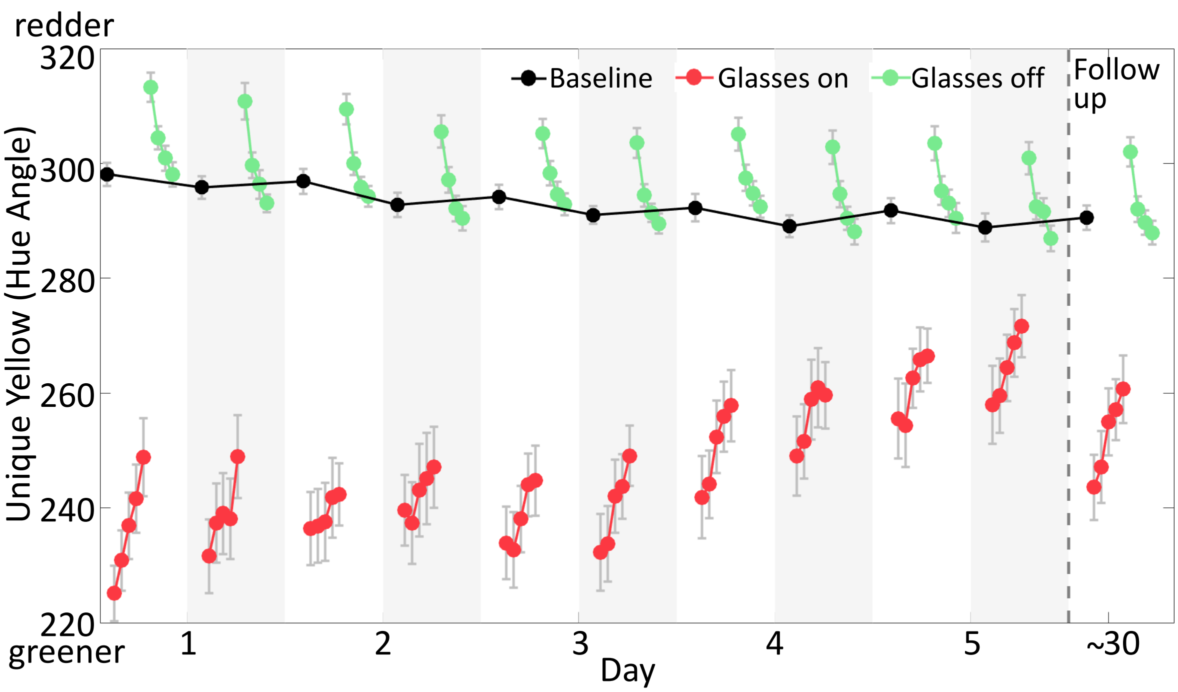


Figure 2.2. **Results of the main experiment and the follow-up tests.** Mean unique yellow settings represented in hue angle are plotted as a function of time for 5 days and the follow-up test. The black dots are baseline settings, made at the beginning of each test session with glasses off. The white background indicates morning sessions, and the light gray background indicates afternoon. The red dots plot settings with glasses on and the green dots are settings after removing the glasses. Successive symbols are plotted for each 5 min test (see Figure 2.1C). The gray bars represent standard errors of the mean, computed across participants (N = 11).

How rapidly did this effect arise? Each data point in Figures 2.2 and 2.3 represents mean unique yellow settings averaged across the five one-minute blocks that comprised each test. To better judge the timing of effects, we repeated our analysis using observers' averaged settings within only the first one-minute block. We also repeated the analysis using observers' very first unique yellow setting in the first block. In both cases, unique yellow after donning the glasses again shifted significantly across days ($t = 6.72$, $p < 0.001$ for the first block; $t = 4.11$, $p < 0.01$ for the first setting), suggesting observers adjusted to the red glasses relatively quickly (Figure A2.1; Figure A2.2 shows the complete time course of our results as a function of one-minute blocks. We did not have priori expectations about the subtle trends from block to block, and so leave their examination to future work).

The amount of gradual adaptation to the red glasses during the 1 hour of testing, on the other hand, did not change across days. To estimate this quantity, we calculated the slope of the unique yellow settings within each 1-hour session. The grand average slope was 13.30 degrees of hue angle towards red per hour, and there were no significant changes in slopes across test sessions (ANOVA, $F_{9,100} = 1.06$, $p = 0.40$). Given the increasing rapid and constant gradual effects, it is not surprising that total adaptation, i.e., the sum of the rapid and the gradual effects, quantified by the last setting with glasses on in each session, also increased across days ($t = 3.68$, $p < 0.01$, Figure 2.3 pink dots).

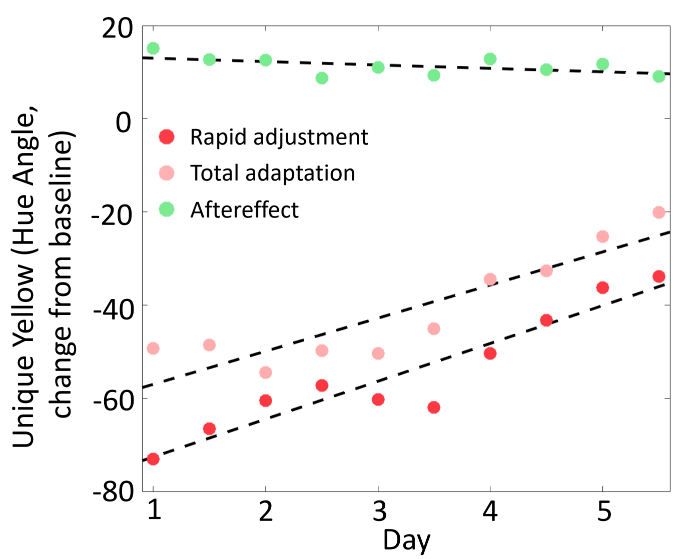


Figure 2.3. **Rapid adjustment, total adaptation effect, and color aftereffect across 5 days.** Red dots show rapid adjustments, which are mean settings from the first 5 min test of each session with the glasses on. Total adaptation effects, denoted by the pink dots, are mean settings from the test taken after 1hr of wearing the glasses. Green dots are mean settings of the first 5 min test after removing the glasses. Data have been corrected for possible baseline shifts by subtracting the baseline value for each morning session, taken immediately before putting the glasses on. The black dashed lines are linear fits to the rapid

adjustment, total adaptation, and the aftereffect. Both rapid adjustment and total adaptation effect grew significantly over days, and there was a trend for aftereffects to decrease across day.

Learned mode switching was long-lasting. About one month (36±7 days) after the main experiment, observers returned for a follow-up test. (Figure 2.2, right). Rapid adjustment to the glasses remained strong; the first block of unique yellow settings was redder than the settings from the first day of the main experiment ($t = -4.83$, $p < 0.001$). However, the effect was somewhat diminished, as the follow-up settings were greener than those made on day 5 of the main experiment ($t = 3.28$, $p < 0.01$). About 66% of the change across the 5 days was maintained in the follow-up test.

A trend for color aftereffect to change across days. When observers removed the red glasses, they experienced a classical color aftereffect (Helmholtz, 1924; Krauskopf & Karl, 1992; van Lier et al., 2009), and reported the world looked slightly greenish, thus they added red to cancel out this aftereffect when making their unique yellow settings (Figure 2.2, green dots). There was a trend for the immediate aftereffect to become less strong across days, evident in the analyses of the first 5-minute test, the first one-minute block, and the first individual match setting (all $p < 0.1$ and $p > 0.05$; Figure 2.3 green dots show the means of the first 5-min tests). We tracked the further decay of the aftereffect for half an hour after removing the glasses, as observers' settings shifted back towards baseline. The decay followed a roughly exponential shape, as previously reported for color aftereffects (Fairchild & Lennie, 1992; Fairchild & Reniff, 1995; Wright & Parsons, 1934). The decay constant, as measured by an exponential fit, did not change over days ($F_{9,96} = 0.01$, $p = 1$).

Baseline unique yellow became slightly greener across days. Baseline values of unique yellow on each day were measured as the mean setting from the first 5-minute test of the morning session, made before putting the glasses on; these settings were preceded by many hours (averaging approximately 15) since the glasses were last worn and were made without the glasses on. We observed a small but significant shift in baseline unique yellow settings over time, visible in Figure 2.2 (black dots) as the hue angle of baseline shifted towards green ($t = -3.33$, $p < 0.01$). This is surprising because adapting to the red glasses makes redness more neutral over time, thus resulting in redder unique yellow (see Discussion).

To make sure our main finding of greater rapid adaptation did not depend upon this shift in baseline, we corrected its effect by subtracting the baseline setting in the morning test session on each day from all settings within the day. These baseline-corrected results showed a very similar overall pattern across days as the uncorrected data, though some effects became slightly larger (Figure A2.3).

2.3.2 Color constancy increased across days

Color constancy, an important benefit of adaptation, is the extent to which objects appear the same color despite changes in viewing conditions (e.g. Brainard & Radonjić, 2014; Foster, 2011; Witzel & Gegenfurtner, 2018). Such stability against transient features of the environment allows color appearance to provide reliable information about object identity and state (e.g. the ripeness of an apple).

One definition of perfect color constancy is when the same physical entity, a surface or light source, is perceived as identical under different viewing conditions. In experiments on monitors, where experimenters only have direct access to pixel intensities, perceived surfaces are usually estimated using modeling of likely lights and surfaces. However, the use of colored glasses in our study affords us a more direct approach.

Specifically, if observers in our experiment had perfect color constancy, then the same physical pixels on the monitor, regardless of whether they were seen as surfaces or light sources (our experiment was ambiguous in this regard), should appear unique yellow both with and without the glasses, despite the glasses' dramatic effect on the spectrum of light reaching the eye. If these conditions hold, then the only difference between the two unique yellow settings would be the difference in viewing conditions: That is, the same physical world (monitor pixels) would be perceived identically (i.e. unique yellow) across the two situations, a reasonable definition of perfect color constancy.

To estimate the *amount* of constancy, we characterized the physical color reaching the eye using the relative gain of the long-wavelength (L) and medium-wavelength (M) photoreceptors. This measure assumes that unique yellow settings correspond to a balancing point between the L and M cone responses, where a scale factor (gain) may be applied to responses of one of the cone classes: $L = k*M$. Effects of adaptation, or other plasticity, on unique yellow can be quantified by solving for k, which is equal to L/M (Neitz et al., 2002).

Figure 2.4 plots our results using this metric and shows that color constancy improved across days. The black dots are baseline unique yellow settings before putting on the glasses; as expected, they fell around 1, where the gain of the L and M cones was equal. The red dashed line at the top of the plot reflects perfect color constancy with glasses on, calculated by assuming that the physical color corresponding to unique yellow did not change from baseline on the first day. This identical spectrum of light would of course result in very different cone absorptions with the glasses on than off, because of the glasses' effect on the light reaching the photoreceptors. On the other hand, if observers completely lacked color constancy, unique yellow settings with glasses on would simply remain at baseline values.

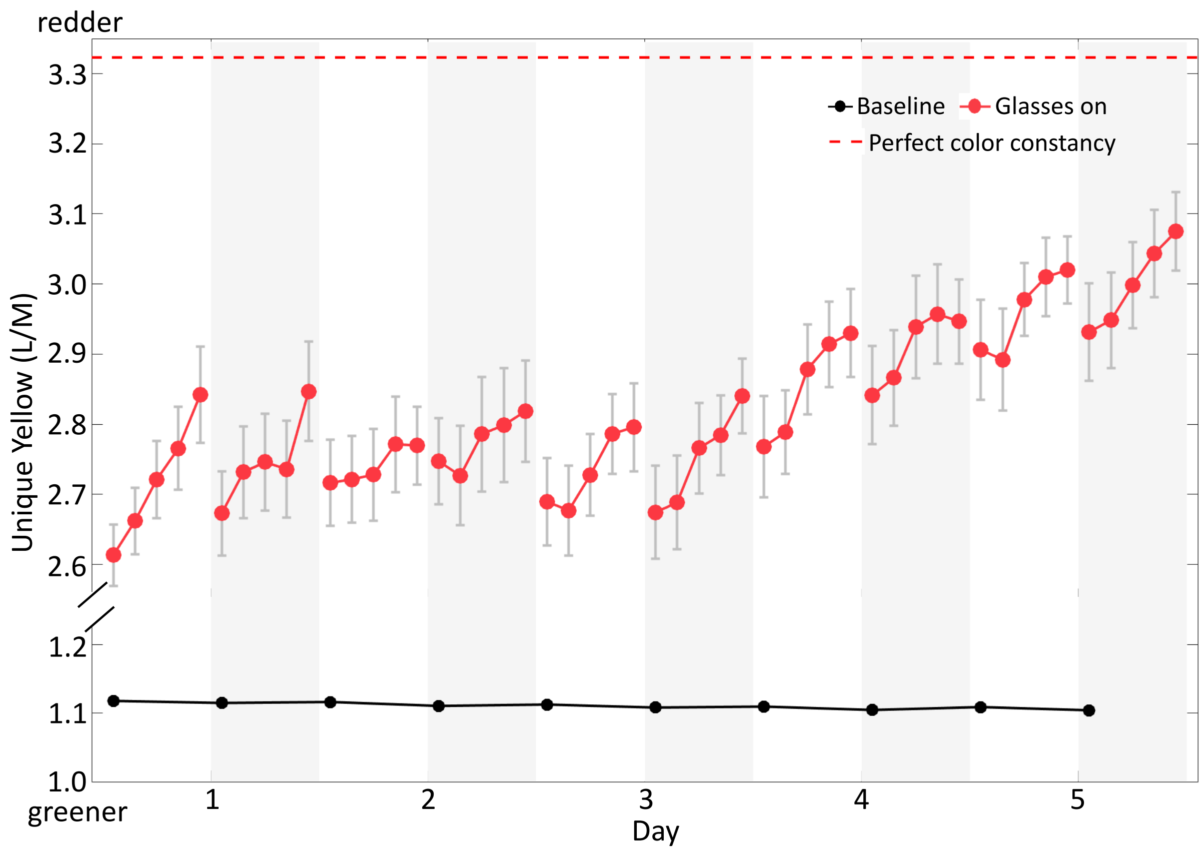


Figure 2.4. **Mean unique yellow settings across 5 days, plotted as relative gain of cones, L/M.** The red symbols show the relative gain of L and M cones (k = L/M, see text) for settings with glasses on, corrected for the red glasses transmittance. The black dots are baseline settings taken at the beginning of each test session with glasses off. If the observers showed complete absence of color constancy, the unique yellow settings with glasses on should have been at the same level as this baseline. The red dashed line above corresponds to the baseline unique yellow corrected for the red glasses' transmittance. If observers had perfect color constancy, their settings would produce identical physical colors on the monitor with and without glasses, and so should fall here when glasses were worn.

Across days, observers' unique yellow settings (red dots) steadily rose towards the perfect color constancy line, indicating that color constancy improved. The very first time they put on the glasses, observers showed about 68% of perfect constancy, as calculated by the ratio between 1) the Euclidean distance between baseline and the first unique yellow setting with glasses on and 2) the distance between baseline and perfect constancy. This pre-existing constancy was presumably due to the rapid adaptation that produces the color constancy we experience in most situations (e.g. Rinner & Gegenfurtner, 2000; Smithson & Zaidi, 2004; Webster & Mollon, 1995). The amount of constancy grew significantly as observers learned to immediately adjust to the red glasses ($t = 4.60$, $p < 0.001$), and exceeded 80% on the 5th day.

2.3.3 Individual differences in learning

Figure 2.5 plots individual differences in changes in adaptation across observers. Some observers showed a large increase in the amount of rapid adjustment over five days (sample single observer shown in upper panel in Figure 2.5A, gray circle in Figure 2.5B), while others demonstrated a flatter pattern (lower panel in Figure 2.5A, black circle in Figure 2.5B). To test if the individual differences were statistically reliable, we computed the Pearson correlation between the changes in rapid adjustment from the first day to the fifth day, and from the first day to the follow-up test. This correlation was significant ($r = 0.81$, $p = 0.003$, Figure 2.5B), indicating that observers who had a larger learning effect over 5 days also retained larger amounts a month later, a form of test-retest reliability. Thus, individuals appear to differ in their ability to learn to rapidly switch visual modes.

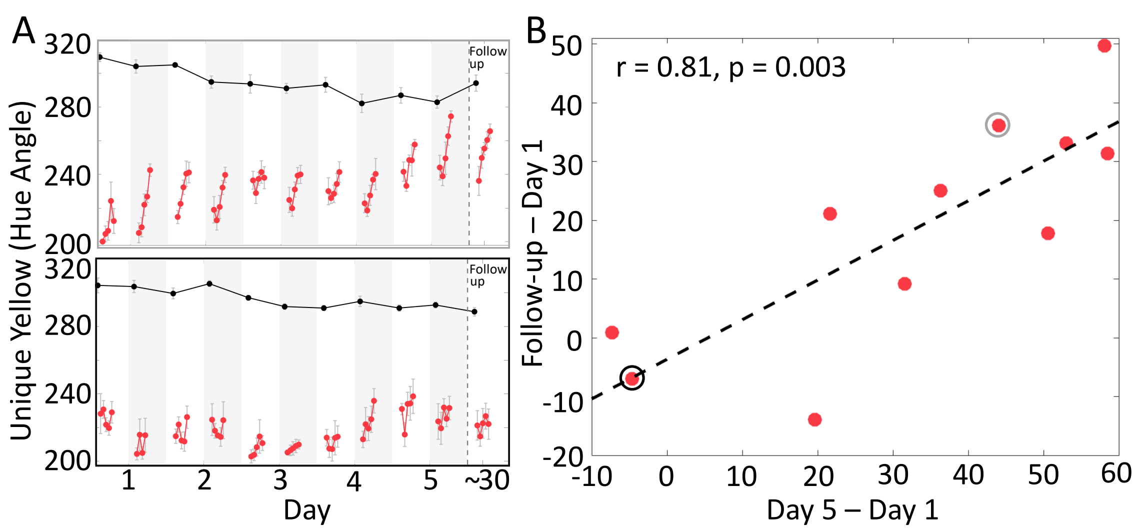


Figure 2.5. **Individual differences in learning effect.** (A) Some of individual data. Results are from 2 observers in the study. One observer (upper panel) showed a gradual increase of rapid adjustment during the five days. This observer also retained the strong rapid adjustment in the follow-up test. Another observer (lower panel) showed a flatter pattern across days and little effect of learning in the follow-up test. (B) Test-retest reliability of individual differences. The change in rapid adjustment to the glasses from the 1st day measured on the 5th day significantly correlated with the change measured in follow-up test, across observers. This indicates observers differed in their ability to learn to rapidly switch visual modes. Red dots represent observers, and the dashed line is the least-square fit. The light gray and black circles denote the individuals plotted in the upper and lower portion of panel A, respectively.

2.4 Discussion

Through experience, observers learned to rapidly adjust to the red glasses, with the world appearing less and less reddish as soon as they put them on. In general, such rapid adjustment allows us to compensate for changes in the visual environment (e.g. Dragoi et al., 2002; Krekelberg et al., 2006; McDermott et al., 2010; Müller et al., 1999; Wissig et al., 2013) while also improving neural coding efficiency (e.g. Seriès et al., 2009; Sharpee et al., 2006; Wainwright, 1999).

In situations where different visual environments alternate frequently, like wearing and removing glasses, the visual system repeatedly readjusts itself. Our results suggest that observers can learn to make the adjustments more efficiently over time, to the point where they can adjust almost immediately upon entering the new environment. Such visual mode switching should enable people to better handle the demands of the complex and changing visual world.

2.4.1 Relation to prior work

It is well accepted that color adaptation has a 'fast' and a 'slow' mechanism and involves both receptoral and postreceptoral visual processes (e.g. Augenstein & Pugh, 1977; Fairchild & Reniff, 1995; Rinner & Gegenfurtner, 2000). One plausible interpretation of our results depends on these well-studied mechanisms; it is possible that through practice a fast adaptation mechanism became able to produce stronger and more rapid effects. In the motor-learning literature this possibility has been termed 'meta-learning' because it affects parameters that govern the rate of adaptation, itself a kind of learning (Zarahn et al., 2008). Other alternative mechanisms are possible, however, including storage, and retrieval of adapted states (Lee & Schweighofer, 2009). Future work will explore these and other possibilities (see also below).

Past work examining visual mode switching has produced mixed results. For example, observers who adapted to cylindrical lenses, creating a sort of astigmatism, showed fast re-adaptation in a second testing session (Yehezkel et al., 2010). However, clinically astigmatic observers showed little change in adaptation during 6 months following their initial prescription of corrective lenses (Vinas et al., 2012). Conflicting results also appeared in color perception, where in one study adapting to yellow filters produced little change in adaptation across 5 days (Tregillus et al., 2016), while another report showed that long-term habitual wearers of red and green lenses can adapt more rapidly than naïve observers to the color changes the lenses produce (Engel et al., 2016). Variability in observer populations and experimental procedures may account for these mixed findings. A final bit of evidence for mode switching comes from a quite different paradigm, in which learning of a visual discrimination task was specific to the visual system's adaptive state, as manipulated by inducing a motion aftereffect (McGovern et al., 2012).

Our paradigm differed from past work in that observers adapted to very strong perceptual changes multiple times a day, and we tracked the detailed time course of adaptation in a test setting with rich cues to context (see below). Together, these factors likely produced larger changes and more reliable measurements of adaptation than observed previously. Testing whether factors such as the frequency of environmental change have an influence on the learning effect that we observed here is an important direction for future research.

Past work on long-term adaptation to colored environments, e.g. wearing red glasses or living under red lights continuously for part of the day, has found that adaptation grows stronger over days (Belmore & Shevell, 2008, 2011; Eisner & Enoch, 1982; Hill & Stevenson, 1976; Kohler, 1963; Neitz et al., 2002). However, these studies did not measure the time course of adaptation, or if observers could learn to rapidly switch between the different viewing conditions.

These past results were also highly variable, both within and between studies (Belmore & Shevell, 2008, 2011; Eisner & Enoch, 1982; Eskew & Richters, 2008; Hill & Stevenson, 1976; Kohler, 1963; Neitz et al., 2002; Tregillus et al., 2016), similar to the inconsistency in prior results on mode switching. One reason for this variability may be that observers were tested with little context present. For example, most tests were made in a completely darkened room, presenting only a single small test patch, making it difficult for the visual system to determine viewing conditions, and hence the appropriate adaptive state. The test setting in our experiment provided many cues that the visual system could use to tell which environment was present, i.e. whether the red glasses were on or off. These context cues may be necessary for mode switching to occur, though precisely which cues are important for which environments remains to be determined.

2.4.2 Other results from present work

Unexpectedly, we found that the baseline unique yellow setting immediately prior to the introduction of the red glasses shifted towards physically more greenish across days. The shift was in the opposite direction from the color that the glasses produced and from the shift of the adaptation effect within 1hr. A similar trend in baseline settings was also found in two previous studies (Engel et al., 2016; Tregillus et al., 2016). While we can only speculate as to the cause of this pattern, it could be due to the aftereffect following the glasses' removal. At that point, observers' judgments indicated that the world looked greenish to them, consistent with classical color aftereffects (Helmholtz, 1924; Krauskopf & Karl, 1992; van Lier et al., 2009). Adaptation across days to this greenish tint could have produced a shift in unique yellow towards green when not wearing the glasses. Long-term adaptation to aftereffects appears to be possible in other domains (Murch & Hirsch, 1972; Sheth & Shimojo, 2008).

The strengthened rapid adaptation we observed substantially improved observers' color constancy, i.e. the stability of perceived color despite the changes in viewing conditions (Brainard & Radonjić, 2014; Foster, 2011; Witzel & Gegenfurtner, 2018). Rapid adaptation, and even faster processes including 'simultaneous' local contrast, are likely major mechanisms that serve this constancy, (e.g. Rinner & Gegenfurtner, 2000; Smithson & Zaidi, 2004). A current debate in the field is whether constancy is improved for familiar, natural illuminant changes, which our visual systems may have encountered most often (Rüttiger et al., 1999; Delahunt & Brainard, 2004; Pearce et al., 2014; Radonjić & Brainard, 2016; Weiss et al., 2017). Our results suggest that training with repeated exposure can improve color constancy, at least for a very strong and unfamiliar illumination change. Observers show some amount of color constancy, and a variety of other perceptual constancies, in most natural settings, without any training. The extent to which these forms of visual mode switching are inborn, determined during development, or learned as an adult remains under investigation (Jameson & Hurvich, 1989; Sugita, 2004; Yang et al., 2015).

Relatedly, the aftereffect measured immediately upon removing the red glasses shifted toward the baseline across days, implying a faster readjustment to familiar, natural conditions over time. However, this trend was relatively small, of only modest statistical reliability, and could be specific to switches from the unnatural red-glasses conditions. The small effect, if real, could be because observers have already partly learned to rapidly adjust to the natural environment, which remains an unresolved debate, as mentioned above.

2.4.3 Mechanisms producing more rapid adjustment

Neurally, adaptation to changes in the dominant color has effects on several sites within the retina (Boynton & Whitten, 1970; Lee et al., 1999; Rieke & Rudd, 2009) as well as cortical stages of color processing (Engel & Furmanski, 2001; Rinner & Gegenfurtner, 2000). One hint toward the neural locus of change in our experiment is that changes were not observed in adaptation within the hour of glasses wearing. This independence from classical adaptation, which partly arises early in the visual system, suggests that mode switching may arise relatively late in processing (Rinner & Gegenfurtner, 2000). Identifying more precisely the extent to which learning can affect these different stages of processing could be profitably addressed in the future.

Computationally, one can view adaptation as the result of an inference process, in which the visual system must determine whether the visual environment has changed (Grzywacz & de Juan, 2003; Kording et al., 2007; Wark et al., 2009). Through exposure to the alternating colored and uncolored environment, observers in our experiment may have learned: 1) that the red environment was more likely (i.e., it had higher prior probability); 2) to more efficiently extract evidence of the red environment (giving it a higher likelihood); 3) that the red environment was likely to persist for a long time (making it costly to not adapt); 4) to speed inference by remembering, rather than re-inferring, the past adaptive state for the red environment. All these possibilities could produce stronger immediate adaptation, and they are not mutually exclusive. Future work could determine which factors are responsible for the changes of adaptation effects over time.

2.4.4 Individual differences

What are the sources of individual differences in the ability to learn to rapidly switch between the two states? Past work has shown that observers may display very different amounts of experimentally measured color constancy, depending upon whether they were asked to make judgments of surface reflectance or of reflected light (Arend & Reeves, 1986; Arend & Goldstein, 1987; Radonjić and Brainard, 2016). In a given task, observers could potentially use either of these strategies. We gave specific instructions in order to limit the impact of strategy selection (see

Methods), however, it is still possible that some observers could be "thinking" more or less in making their unique yellow judgments. This could be one source of the individual differences we found here. Compliance in wearing the glasses could also theoretically account for them, but we closely monitored compliance, and failures were very few. Future work can examine whether individual differences in other aspects of color perception, or vision more generally, can account for individual differences in mode-switching.

In sum, our results demonstrate that the visual system can learn to rapidly adjust to an experienced environment. This mode switching lessens the perceptual changes produced by changing viewing conditions, which could aid a number of perceptual tasks, for example recognition of objects or materials, discrimination between similar objects or materials, as well as improved communication with other observers. Mode switching is not limited to color vision. Similar rapid re-adaptation has been reported in audition (Hofman et al., 1998) and sensorimotor paradigms, in which observers adapt to prisms that rotate or displace their visual field (e.g. Redding et al., 2005), or force fields that disturb their motor outcomes (e.g. Wolpert & Flanagan, 2016). Visual mode switching also resembles context dependent learning that arises in conditioning and other memory paradigms. Mode switching may be a general solution to the problem of maintaining consistent behavior in a changing world.

3 Visual Mode Switching: Improved general compensation for environmental color changes requires only one exposure per day

(Adapted from Li, Y., Tregillus, K. E., & Engel, S. A. (2022). Visual mode switching: Improved general compensation for environmental color changes requires only one exposure per day. *Journal of Vision*, *22*(10), 12. https://doi.org/10.1167/jov.22.10.12)

3.1 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 re-adaptation 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-hour periods per day, for 5 days. We tracked color adaptation by asking participants to identify "unique yellow", a chromaticity that contains no red nor 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 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; 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 5 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 multi-hour 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-hour 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 3.1A), compressing the gamut of colors reaching the eye and shifting it towards red (Figure 3.1B). 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, and used 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.

3.2 Experiment 1

3.2.1 Methods

3.2.1.1 Participants

12 participants (21 to 28 years of age, 4 males) were recruited through the University of 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.

3.2.1.2 Apparatus

An NEC MultiSync FP2141 CRT monitor, with a screen resolution of 1024x768 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. Participants viewed the display at a distance of 50 cm. Visual stimuli were programmed in MATLAB using the psychophysics toolbox (Brainard, 1997).

3.2.1.3 Glasses

Adapting glasses were commercially available bright red glasses made by SomniLight (Shawnee, KS). 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 3.1A, the transmittance is more than 90% at wavelengths over 620 nm and less than 10% at wavelengths below 550 nm. Figure 3.1B 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.

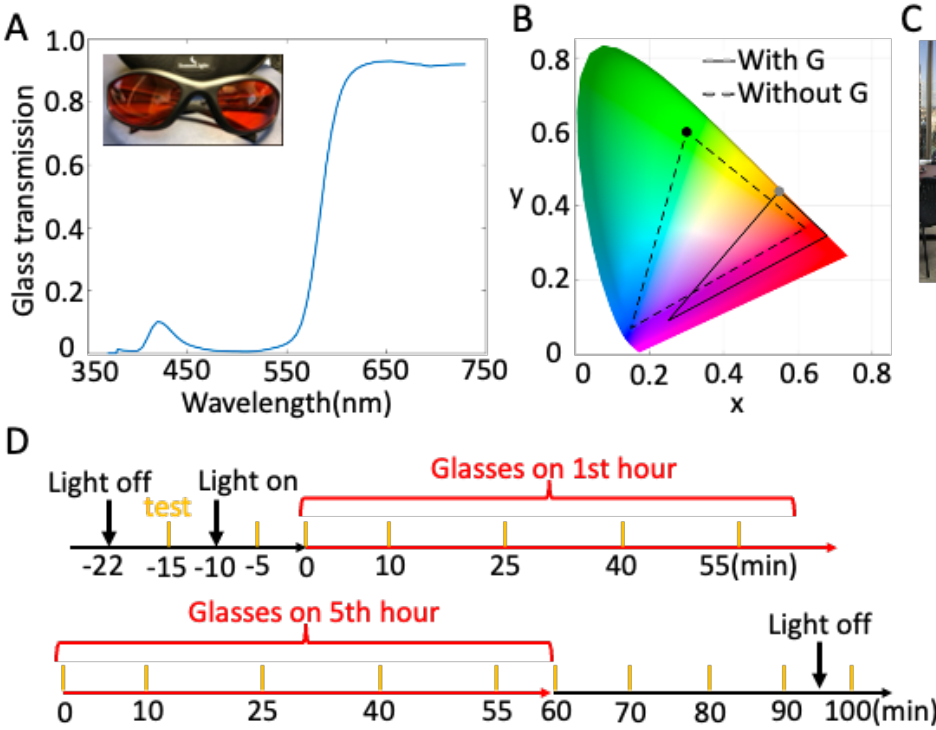


Figure 3.1. **Glasses' transmittance and test procedures of Experiment 1.** (A) The transmission spectrum of the red glasses used in Experiments 1 and 2. The glasses filter out most of the light at short wavelengths and let pass most of the light at long wavelengths. (B) The gamut of the test display 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 deg square centered on a background image of a naturalistic office scene, separated by a 5.7 deg 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-hour 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 were 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 5 times during the 1hour of glasses wear. The lower panel illustrates the test procedure in the second session, which began at the start of the 5th 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 4 times. Finally, participants were dark-adapted and tested again, with no room lighting and no background image.

3.2.1.4 Procedure

Participants wore the glasses for a single 5-hour 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-hour test session. Then, they left the lab and went about their daily activities with the glasses on for 3 hours. During the 5th hour of wear, participants came back to the lab and participated in a second 1-hour 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’, that 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 nor 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-degree 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-degree black square separated the target from the background (Figure 3.1C).

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 pressed 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 the most to make one single unique yellow setting so that 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 & 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 iso-luminant 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 iso-luminance.

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, 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 5 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. 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 hours. At the end of the 4th 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 1st 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 do not report its results further here). The full test procedure is illustrated in Figure 3.1D.

3.2.2 Results

Figure 3.2 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 3.1), so they set the stimulus to be more physically green (shorter wavelengths) to cancel the redness from the glasses and produce unique yellow (Figure 3.2, 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 5 settings within the first hour of glasses wear on a given day. We term this effect, which builds over the hour-long course of wearing the glasses, “gradual adaptation”.

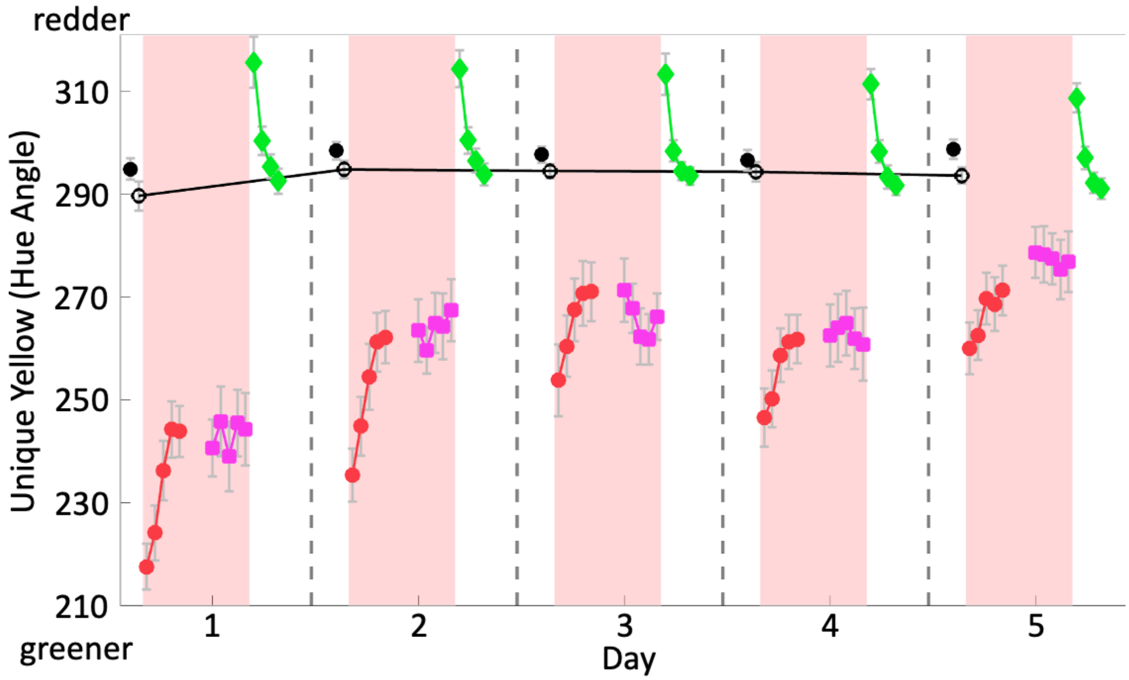


Figure 3.2. **Results of Experiment 1 (N=12).** Mean unique yellow settings in hue angle are plotted as a function of time for 5 days. The white background indicates tests when not wearing the glasses, and the light red background indicates tests when wearing the glasses. The black filled circles are 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.

3.2.2.1 Effects of once-daily 5-hour 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 3.3 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 multi-hour experience with them, effectively switching to "red-glasses mode".

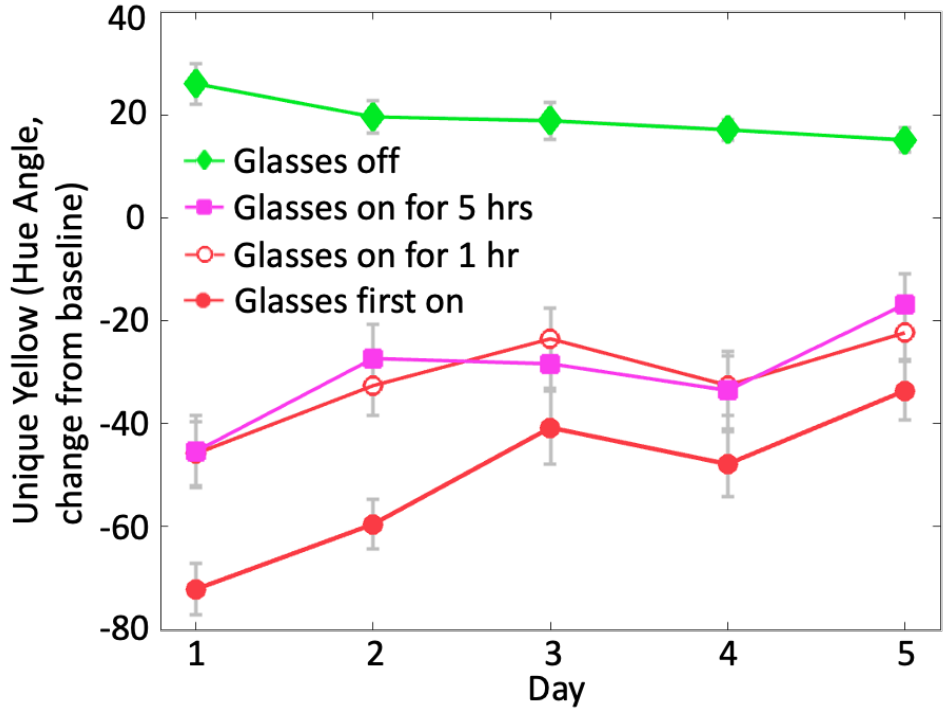


Figure 3.3. **Unique yellow settings across 5 days.** Red filled circles are settings made immediately after putting on the glasses, i.e., rapid adjustment. Red circles and magenta squares denote settings made after wearing the glasses for 1 hour and 5 hours, respectively. Green diamonds indicate settings 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 3.2 and 3.3 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. Figure A3.2 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 degrees on day 1 to about 10 degrees 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, however, adaptation only increased during the first hour. We compared unique yellow settings at the end of the first hour (red open circles in Figure 3.3) to those at the end of the fifth hour (magenta squares in Figure 3.3) 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 3.2); the other was under room light, tested with the background image provided (black circles in Figure 3.2). We found that neither of these two baseline measurements changed significantly across days (both $p > 0.1$), though both had a small trend towards 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 (Figure A3.3).

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 (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 3.2). 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 pre-adaptation baseline, Figure 3.3, 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.

3.2.2.2 Comparison with effects of 5 one-hour 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-hour 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 ($p > 0.05$).

3.2.3 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 3.1C), 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 hours of glasses wear in this study, whereas in the previous study, it was preceded by only 1 hour 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 hour. The decay of the aftereffect within each day was also comparable after 1 hour and 5 hours of adaptation. This is surprising as longer exposure generally causes slower aftereffect decay (see review 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 vs 1 hour 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 towards 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 hours’ 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.

3.3 Experiment 2

3.3.1 Methods

3.3.1.1 Participants

13 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 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.

3.3.1.2 Apparatus

Visual stimuli were presented on a MacBook Air 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 2560*1600. The laptop display was calibrated and gamma-corrected using a portable monitor calibration tool, *SpyderX Elite Datacolor*. Testing code and visual stimuli were delivered using MATLAB. 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.

3.3.1.3 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 3.1A. Figure A3.1 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 3.4 A and B also reflect the effect of the red glasses on our stimuli, see below.

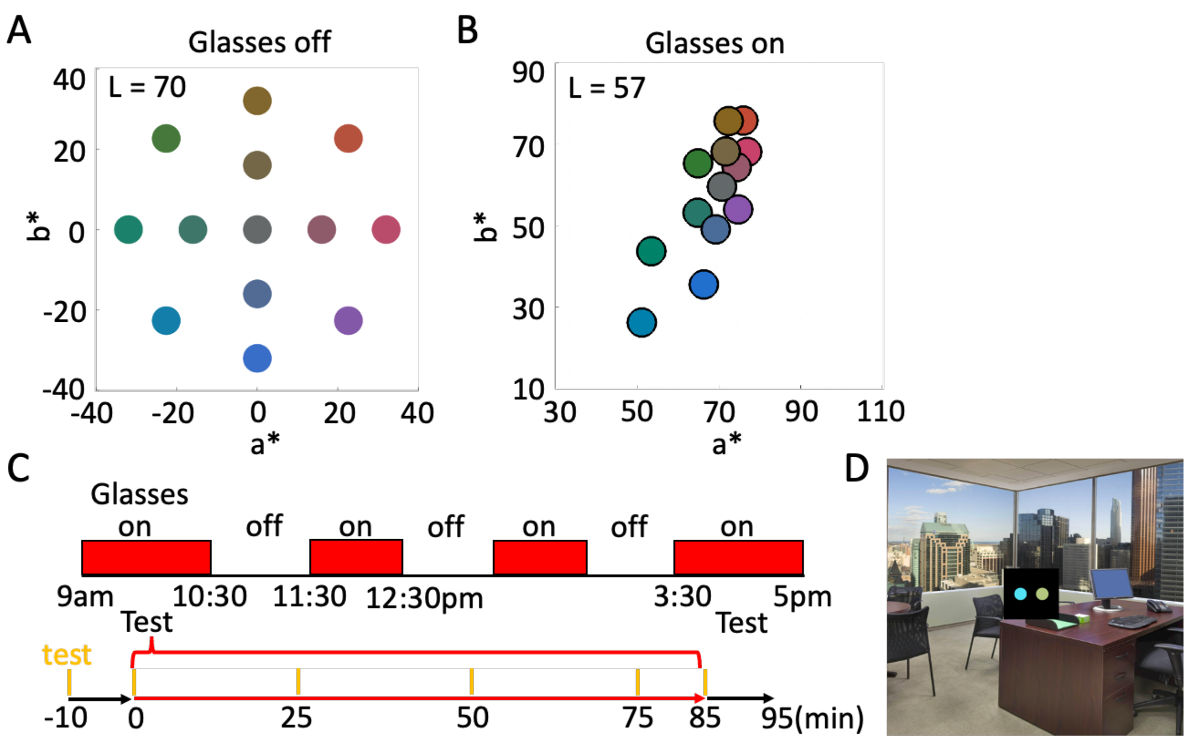


Figure 3.4. **Experimental procedures and stimuli space of Experiment 2.** (A) Stimuli used in tests. Thirteen colors of equal luminance were chosen from two concentric circles in the CIELAB color space, including 8 unique and intermediate hues of high saturation, 4 unique hues of low saturation, and 1 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 iso-luminant 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 hours of wearing the glasses. Orange bars indicate the time of test: 10 min before putting on the glasses, immediately after putting on the glasses, 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 degrees in diameter, 2.5 degrees apart, each 1.25 degrees from the center of a 6-degree black square. Color circles were presented for 500 ms followed by a 1.5 s gap.

3.3.1.4 Procedure

During the main experiment, participants wore the red glasses for 5 hours per day, for 5 consecutive days. On each day, participants first wore the red glasses for 1.5 hours in the morning, while participating in a testing session. Then, they removed the glasses and after an hour, wore the glasses for two 1-hour periods, separated by 1 hour without glasses. After a last 1-hour 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 3.4C. 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 degrees in diameter, on a naturalistic background image (an office scene) displayed on the laptop. The two circles were 2.5 degrees apart, each 1.25 degrees from the center of a 6-degree black square (Figure 3.4D).

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 CIELAB space (see below, Figure 3.4A). They were instructed "*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 Commission Internationale de l'Eclairage $L^*a^*b^*$ space (CIELAB). 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 concentric circles in the CIELAB space, including 8 unique (reddish, greenish, blueish, and yellowish) and intermediate hues of high saturation, 4 unique hues of low saturation, and 1 gray (Figure 3.4A). These colors formed 78 non-identical pairs in one test run.

All color stimuli were iso-luminant 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 to display that produced these equal-luminance colors with glasses on. We also computed the CIELAB coordinates of these colors as seen through the glasses (Figure 3.4B). 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 iso-luminant 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 3 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, 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 3.4C.

3.3.1.5 Data Analysis

We averaged the dissimilarity ratings for each color pair across the 3 blocks in each test. We then divided each participants' 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 as 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 2 dimensions as our stimuli fall on an isoluminant plane, both with and without the glasses, and the 2 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 (Figure 3.9A).

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.

3.3.2 Results

3.3.2.1 Effects within one-hour 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 3.5). The upward slope of the connected red filled circles in each testing session indicates that color pairs on average appeared more dissimilar over time.

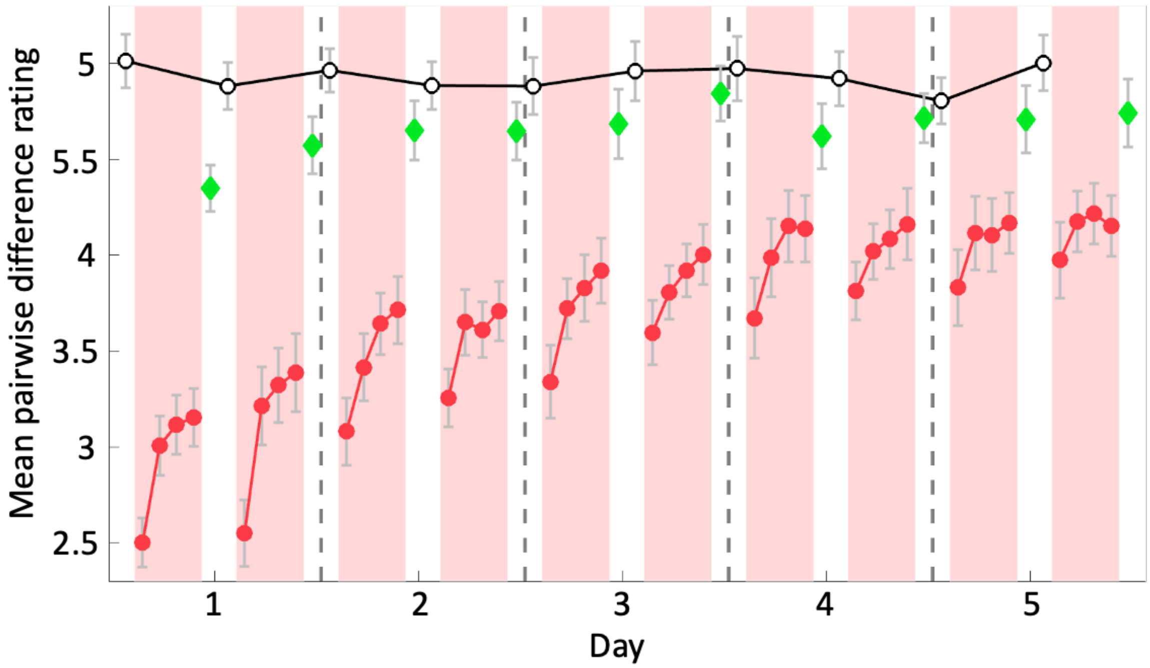


Figure 3.5. **Results of Experiment 2 (N = 13).** Mean pairwise difference ratings, computed as the average rating across all color pairs within a test, are plotted as a function of test time and day. The white background indicates tests when not wearing the glasses, and the light red background indicates 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.

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 3.6 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 3.6) had a very similar configuration to the stimuli plotted in CIELAB space (Figure 3.4A), 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 ~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 Figure A3.4).

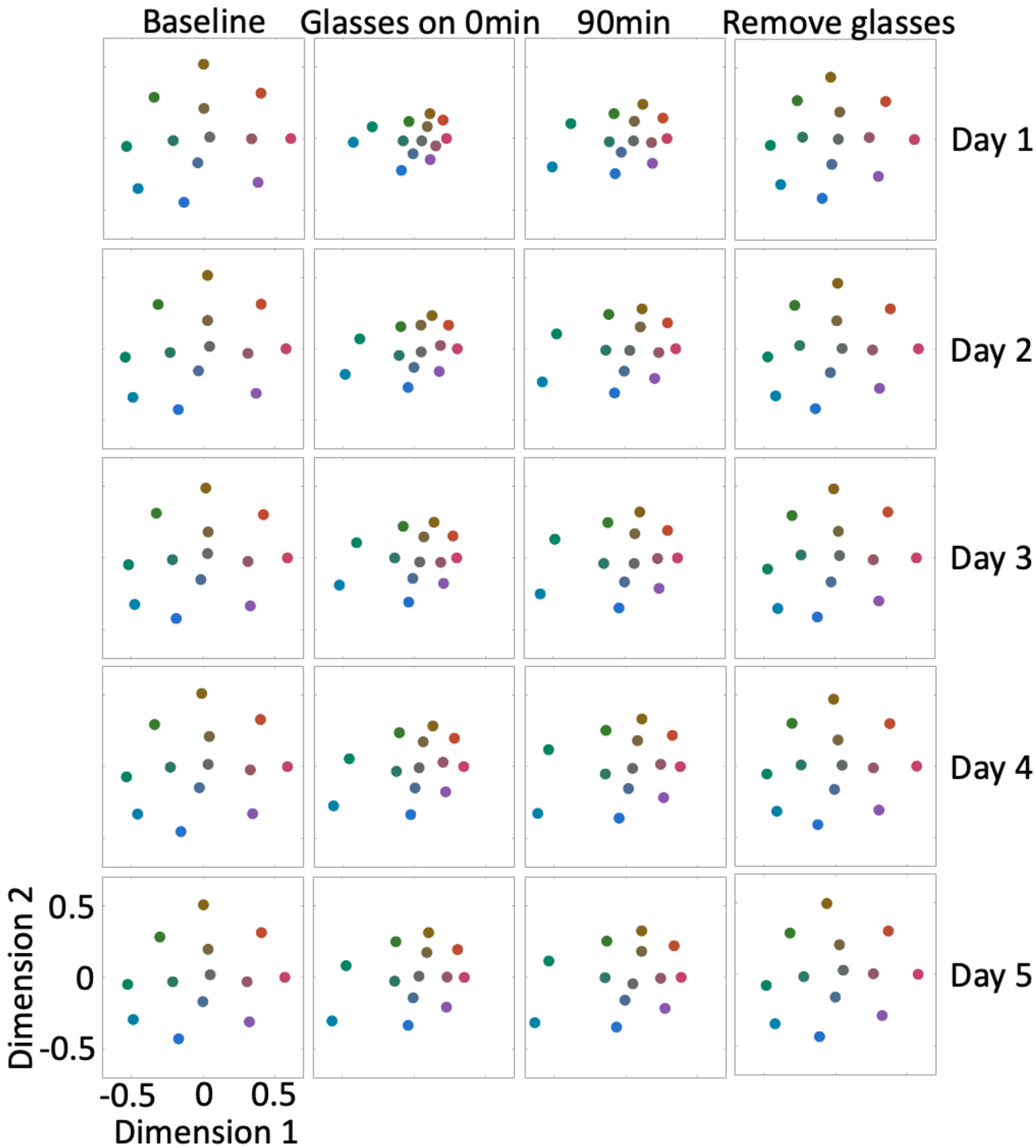


Figure 3.6. **Perceptual color spaces reconstructed using MDS from normalized difference ratings.** Results are shown for tests performed before wearing the glasses, immediately after putting on the glasses, 90 min after putting on the glasses, and immediately after removing the glasses. Results in the first test sessions on 5 days are shown here and the results in the second test sessions can be found in Figure A3.4, and are very similar. Perceptual color spaces were rotated to best coincide with the glasses-off stimuli in CIELAB color space.

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 3.4B). 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.)

3.3.2.2 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 3.5 by the rising trend of the mean pairwise difference rating in the first test with the glasses on in each session. Figure 3.7 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 ($t(12) = 9.41$, $p < 1e-6$, Figure 3.7 red filled circles).

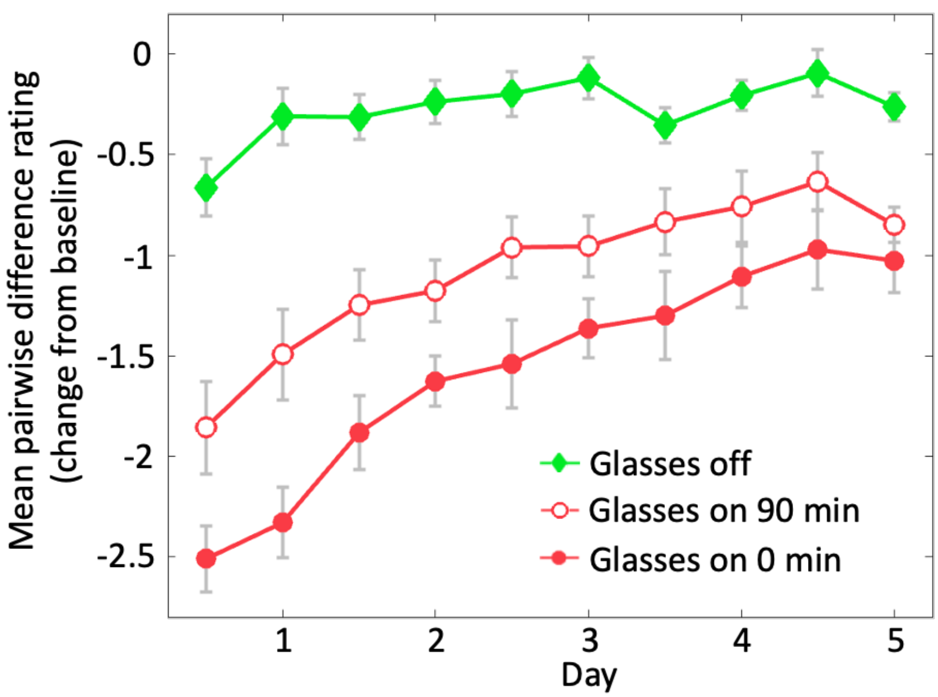


Figure 3.7. **Immediate adjustment, gradual adaptation, and aftereffect characterized by mean pairwise difference ratings on 5 days.** The red filled circles represent the mean pairwise difference ratings

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.

The perceptual color spaces estimated from ratings in the first test with the glasses on expanded across days (the 0-min color spaces; Figure 3.6 and Figure A3.4, column 2 from left). By the 4th and 5th day, the 0-min perceptual color space was even more expanded than that after 90-min adaptation on the 1st 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 3.8A 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 vs day 5 (Figure 3.8B). 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 3.8C, where points fall along the identity line.

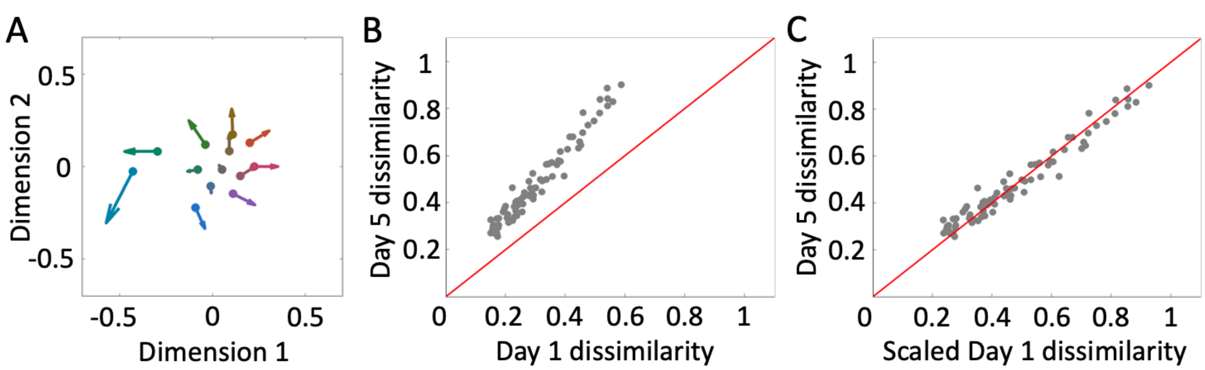


Figure 3.8. **Uniform expansion of the perceptual color space over days.** (A) Trajectories of all colors in the glasses-on 0 min perceptual color space from session 1 (filled circles) to session 10 (arrow end). (B) Normalized dissimilarity ratings immediately after putting on the glasses on day 1 and 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.

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), i.e., 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 3.9A shows that the model fit the day 1 data well. Figure 3.9B 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 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 3.9C).

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.

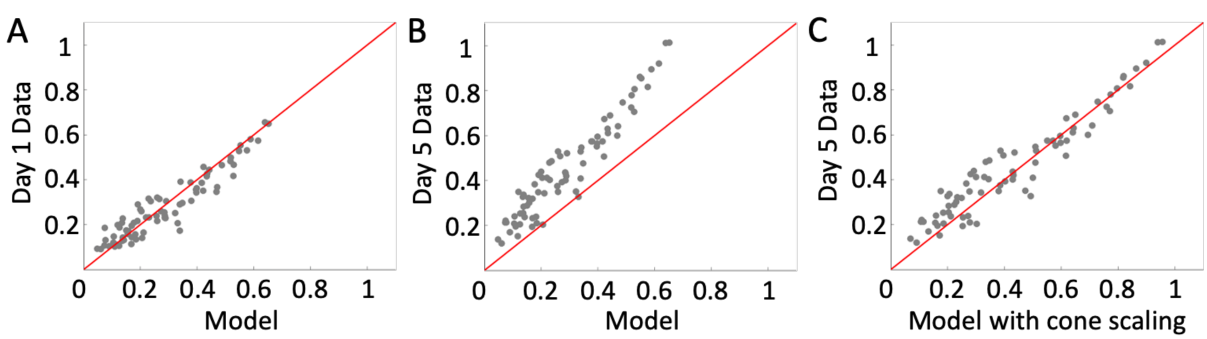


Figure 3.9. **Cone scaling model of the expansion of the perceptual color space.** (A) Model predictions

of pairwise distances vs distance data from day 1. (B) Model predictions vs day 5 data, before scaling M and S cone sensitivities. (C) Model predictions after cone scaling vs the data from day 5.

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 3.5 green diamonds) than before putting on the glasses (Figure 3.5 black circles). The perceptual color spaces reconstructed from ratings after removing the glasses (Figure 3.6 and Figure A3.4, rightmost column) were also slightly compressed compared to the baseline spaces (Figure 3.6 and Figure A3.4, leftmost column) within the same session. Importantly, the rising trend of the green diamonds in Figure 3.5 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 3.7 green diamonds).

Baseline ratings did not change significantly over days. We did not find a change in baseline pairwise difference ratings over days (Figure 3.5 black circles, $p > 0.5$). The perceptual color space reconstructed from baseline ratings also did not change across days (Figure 3.6 and Figure A3.4, 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 (Figure A3.5).

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 3.7 red filled circles) and last (Figure 3.7 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 ($t(12) = -3.02$, $p = 0.01$).

3.3.3 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). Post-receptoral 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 3.8A). 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 3.4B) but left the blue-green stimulus as an outlier, farthest away from the other stimuli. Perception initially resembled this pattern (Figure 3.6, Day 1, 0-min). While most colors moved away from the center, blue-green also moved away from green and towards 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 non-uniformities 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.

3.4 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 hours vs 5 one-hour 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.

3.4.1 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 non-visual 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 produce 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 re-adaptation 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).

3.4.2 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-hour 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.

3.4.3 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 Experiment 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.

3.4.4 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.

3.5 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.

4 Visual mode switching may involve both primary and extrastriate visual cortices: A pilot fMRI study

4.1 Introduction

In previous chapters, I provided behavioral evidence that the visual system can learn to switch perceptual modes, improving performance with experience. Such an effect can occur under a relatively wide range of conditions and can affect a wide range of stimuli. Mode switching may be a general strategy to maintain consistent perception in a continuously changing environment.

However, it remains unknown when and how the visual system switches modes. Taking color vision as an example, mode switching may be due to changes in existing mechanisms that produce color context effects including color contrast and color adaptation, and may serve the goal of color constancy. Below I review cortical color processing assessed with fMRI, and what is known about the neural mechanisms of color context effects.

4.1.1 fMRI studies of cortical color processing

FMRI allows the examination of cortical color tuning over a relatively large scale in the normal human brain, which can then provide insight into the neural basis of color appearance. Early fMRI studies identified a region of the ventral occipital cortex (thought to be hV4), which was more responsive to colors than to luminance stimuli that were isoluminant with the color stimuli (e.g., Lueck et al., 1989; Zeki & Bartels, 1999). Relatively strong responses to cone-opponent red-green and blue-yellow stimuli, as compared to response to luminance, were also observed in visual areas V1 and V2 (Barnett et al., 2021; Engel et al., 1997; Mullen et al., 2007). Similar color tuning was found in V2 and VO, which indicates that opponent-color representations are widely distributed in the cortex (Wandell, 1999).

Color selectivity of the visual cortex has also been assessed using adaptation as a tool (reviewed below). Visual areas including V1-V3, LO, hV4, VO1 and VO2 were found to selectively adapt to color contrast stimuli (Engel, 2005; Engel & Furmanski, 2001; Goddard et al., 2019; Mullen et al., 2015). Spatially distributed fMRI activation patterns have also been used to study color representation in different visual areas. Activation patterns in V1, V2, V3, V4 and VO1 can accurately decode color stimuli, suggesting that neurons in these regions respond selectively to different colors (Brouwer & Heeger, 2009; Parkes et al., 2009). Brouwer and Heeger (2009) also found that perceptually similar colors evoke the most similar pattern of activity in areas V4 and VO1, indicating a more perceptually based color representation in those regions.

In summary, neuroimaging studies have shown that cortical areas that are responsive to colors are very widely distributed, from early visual cortex to high level ventral areas. Since visual mode switching corresponds to rapid and stronger context effects, below I review studies of the neural bases of color context effects in humans, assessed with fMRI.

4.1.2 fMRI studies on color context effects

Although contextual influences on color perception have been well documented behaviorally (reviewed earlier), studies on the neural bases of context-dependent perceived color in the human visual cortex are relatively rare.

4.1.2.1 Color contrast and luminance simultaneous contrast

Some neuroimaging studies suggest that color contrast effects may not arise in the early visual cortex. When temporally modulating the luminance of the immediate surround, the perceived lightness/color changes of the center increased with the increasing amplitude of the surround modulation (Cornelissen et al., 2006). However, the fMRI responses in the early visual cortex (V1 and V2) to the center were independent of the surround modulation amplitude. These results indicate that V1 and V2 did not represent filled-in surface lightness and color. The authors argued that previously measured context-dependent neural responses in neurophysiological studies on animals were derived from the extended edge responses and were not related to the spatial filling-in of lightness or color.

However, using the Cornsweet illusion, Boyaci et al. (2007) investigated the cortical responses to context-dependent lightness variations and found that activities of human V1, V2, and V3 were all correlated with the perceived lightness, instead of the physical properties of the stimuli. Importantly, this study ruled out the possibility of the long-range edge response proposed by Cornelissen et al. (2006) by adding a control condition with a strong edge but a weak lightness effect. Different results from these studies could be because of the different experimental design and properties of the stimuli. In Cornelissen et al. (2006), the strong responses to luminance modulation of the surround might have hidden the response to illusory lightness/color.

Using fMRI, activation patterns in dorsal visual areas V3A and V3B were found to best classify appearance changes due to the WCE (Watercolor Effect, the edge-induced, filling-in illusion, reviewed earlier) versus physical changes in surface color compared to other visual areas (Gerardin et al., 2018). The classification performances of V3A and V3B were also significantly correlated with the psychophysically measured illusion magnitude of WCE across observers. This study could not exclude early visual areas from being important for the WCE, but highlighted the role of dorsal areas in color filling-in.

4.1.2.2 Color adaptation

Neuroimaging studies on both color adaptation and color contrast adaptation have identified cortical regions that may be responsible for these effects. Selective adaptation to cone-opponent colors has been examined using stimuli in cone contrast space. After adaptation to red-green stimuli, red-green test stimuli produced much less response (due to rapid neural adaptation) than luminance test stimuli in V1, although before adaptation, the two test stimuli generated equal responses. These findings suggest that a population of neurons in V1 selectively adapted to red-green cone-opponent colors (Engel, 2005; Engel & Furmanski, 2001). Engel (2005) also found that after prolonged exposure to red-green or luminance contrast stimuli, oriented either horizontally or vertically, V1 showed greater reduction in response to test stimuli that had the same color and orientation as the adaptor than to stimuli that differed in color and/or orientation. This is evidence that V1 contains neurons that are jointly selective for color and orientation. Selective adaptation to red-green contrast was also found in higher-level visual areas (Engel, 2005; Mullen et al., 2015).

In a later study, however, adaptation to red-green and luminance contrast stimuli generated almost equal signal loss when testing with red-green or luminance stimuli in V1 and V2, indicating unselective adaptation to red-green and luminance contrast in these areas (Mullen et al., 2015). Unselective adaptation between blue-yellow and luminance contrast, as well as between red-green and blue-yellow color contrast were also observed across the visual cortex including V1-V3, LO, hV4, VO1 and VO2 (Goddard et al., 2019).

Goddard et al. (2019) also examined both the psychophysical and fMRI longer-term adaptation effects and found that the color contrast adaptation continued to accumulate across the hour-long session. Neurally, such longer-term adaptation effects were found to be mainly in higher order areas such as hV4, VO1, and VO2. The differences in adaptation procedure and in stimulus properties may give rise to the different findings of selectivity across different studies, but overall, the adaptation effect is relatively robust and evident in many visual areas.

Wade and Wandell (2002) measured basic color adaptation (as opposed to color contrast adaptation) using fMRI. In this study, stimuli consisted of a fixed probe superimposed on a spatially homogeneous, full-field background whose mean level varied. This manipulation is similar to the effect of colored filters (e.g., wearing red glasses) or chromatic illumination. Effects of color adaptation were quantitatively accounted for by V1 signals, and much of the computation was explainable by gain changes in the photoreceptors.

4.1.2.3 Color constancy

As reviewed earlier, both color contrast and color adaptation effects may contribute to perceptual color constancy. Thus, cortical processes that are involved in color contrast and adaptation could also be important factors, at the neural level, in producing color constancy.

One study used stimuli designed to isolate the color constancy mechanisms (Barbur & Spang, 2008). In the test condition, which engaged color constancy mechanisms, Mondrian color patches varied in their chromaticities and luminances due to a change of illuminant; whereas in a comparison condition, the same color patches changed in luminance by the same amount, but their chromaticities remained unchanged. Comparing the differences in BOLD signal amplitude for the two conditions revealed stronger responses for the constancy condition throughout the visual cortex, in V1, V2, V3, V4 and V4α. Although the observed differences in response between the two conditions may simply be because combined changes in stimulus luminance and chromaticity induced larger responses than changes in luminance alone, this study provides a method that could be built on to measure color constancy inside the MR scanner.

Bannert and Bartels (2017) used multivariate pattern analysis to probe color constancy in visual cortex and found that activity in V1 and V4α could decode surface color across illumination changes. It is unclear why patterns of activity in V2 and V3, which receive input from V1, could not be used to decode surface color when activity in V1 could. Thus, the relative importance for primary visual cortex vs the extrastriate areas for color constancy remains unclear.

4.1.3 Pilot fMRI study on visual mode switching

This chapter presents a pilot fMRI study that aimed to explore the neural bases of visual mode switching. We used a similar behavioral paradigm as in previous mode-switching studies, in which observers wore the red glasses for many times a day for 5 consecutive days. We measured observers' brain responses to a set of color stimuli, both with and without glasses, before and after 5 days of training. Behavioral testing was conducted on each of the 5 days, with and without the glasses, to make sure that observers showed perceptual evidence of learning mode switching.

We hypothesized that a brain region may be involved in mode switching if it had changes in its response to colors when viewing through the red glasses after the 5 days of training. Alternatively, if a region showed no change in response to colors with the glasses on after training, then the region would likely not be involved in mode switching. Based on previous neuroimaging findings on color context effects reviewed above, we predicted that both primary visual cortex and the extrastriate areas might be involved in learning mode switching.

4.2 Methods

4.2.1 Observers

Four observers with normal color vision and visual acuity participated in both the behavioral and fMRI experiments. None of them had worn red glasses for extended periods of time prior to this study. Observers provided written informed consent before the start of the study. The experimental protocol was approved by the University of Minnesota Institutional Review Board and in accordance with safety guidelines for MRI research from the Center for Magnetic Resonance Research.

4.2.2 Overall Experimental Procedure

All observers participated in two fMRI scan sessions, one before they started to wear the glasses (on day 0) and one the day after 5 days of training (on day 6). In between the two scanning sessions, observers wore the red glasses for 1 hour at a time, 5 times per day, for 5 days. On each day, observers came to the lab in the morning and wore the red glasses for 1 hour, while participating in a testing session. Then, they left the lab and attended to their routine everyday activities. They were asked to put on the glasses again 1 hour after they took off the glasses in the lab. During the day, they wore the glasses for three additional 1-hr periods, each separated by 1 hour without glasses.

4.2.3 fMRI Experiment

4.2.3.1 Apparatus and Data Acquisition

MRI scanning was conducted at the Center for Magnetic Resonance Research at UMN, using a 3T Siemens Prisma system (Erlangen, Germany) with a 32-channel head coil. Functional data were acquired using a T2* weighted, slice accelerated multiband echo-planar imaging (EPI) sequence with parameters: TR = 1.5 s, TE = 30.4 ms, flip angle = 80°, FoV = 208 x 208, voxel size = 2.4 mm isotropic, slice number = 60, multiband factor = 3, phase encoding direction = AP. Anatomical data were acquired using a T1-weighted MPRAGE sequence with a voxel size of $1mm^3$ isotropic. To correct for spatial distortion, a reverse phase encoded EPI sequence was also collected.

Visual stimuli were back projected onto a translucent screen placed in the scanner bore using a NEC NP4100 projector, with resolution of 1024 x 768 pixels, and a refresh rate of 60 Hz. We were unable to calibrate the projector due to its nonlinearity. Its spectrum was relatively consistent when using only one of the three primaries, however, so, instead of doing a full calibration, we simply measured the color coordinates of hand-chosen stimuli (see Table 4.1). Observers viewed the stimuli through a mirror attached to the head coil from a distance of approximately 100 cm. Stimuli were delivered in MATLAB using the Psychophysics toolbox (Brainard, 1997).

Observers viewed phase reversing (2 Hz) radial square wave color/black gratings (1 c/deg., 6°), centered on a background image of a natural office scene (approximately 24° x 20°), separated by a 6.5° black square (Figure 4.1). Different colors were used for two sets of observers. For two of the observers (SN01, SN02), the stimuli comprised the red primary of the projector at 4 levels of intensity (approximately 4, 10, 25, 62.5 cd/m^2) and the green primary at 4 levels of intensity (approximately 4, 16, 64, 256 cd/m^2), resulting in a total of 8 conditions (Figure 4.1A). For the other two observers (SN03, SN04), the 8 conditions consisted of the projector's red primary at 4 lower intensity levels (approximately 4, 8, 16, 32 cd/m^2) and the blue primary at 4 intensity levels (approximately 3.5, 7, 14, 28 cd/m^2; Figure 4.1B). The CIE coordinates of the two sets of stimuli are shown in Table 4.1. The stimuli were selected to have logarithmic increments in luminance to produce roughly equal perceptual differences. The second set of stimuli (red and blue stimuli) were chosen to have lower intensities compared to the first set (red and green stimuli) to prevent saturation of fMRI responses. The blue and red stimuli were also selected to appear roughly equally salient at their corresponding intensity levels.

Stimulus Set 1 (Test SN01 and SN02)			Stimulus Set 2 (Test SN03 and SN04)		
CIE x	CIE y	CIE Y(cd/m^2)	CIE x	CIE y	CIE Y(cd/m^2)
0.4238	0.3429	4	0.4238	0.3429	4
0.5779	0.3496	10	0.5304	0.3454	8
0.6136	0.3506	25	0.5832	0.3498	16
0.6303	0.3515	62.5	0.6214	0.3509	32
0.3433	0.4270	4	0.2301	0.2036	3.5
0.3564	0.5268	16	0.1649	0.1206	7
0.3615	0.5674	64	0.1503	0.1021	14
0.3976	0.5785	256	0.1481	0.0991	28

Table 4.1. **CIE coordinates of the two sets of stimuli used in the fMRI experiment.** SN01 and SN02 were tested with stimulus set 1 containing four red and four green stimuli. SN03 and SN04 were tested with stimulus set 2 containing four red and four blue stimuli.

At the beginning of each fMRI scan session, we conducted a localizer scan to identify the brain regions that were responsive to the color stimuli. We used a block design paradigm which consisted of 12 stimulus blocks of 12 s each, interleaved with a 12 s interstimulus interval (ISI). Within each 12 s block, every stimulus color was presented once, in a randomized order. To ensure that the observers were paying attention to the stimuli, they were asked to indicate the intensity, on a scale of 1 to 4, of the final stimulus in each block. Observers maintained fixation on a cross located at the center of the screen during all scans in a session.

Following the localizer, data were gathered in 8 experimental runs; observers viewed the screen with natural vision in 4 runs and through MR-compatible red glasses in another 4 runs.

Observers put on and removed the red glasses in alternate runs, and viewed a set of natural images for 3 min after removing the glasses to deadapt between runs. Each run contained 18 blocks of 9 s, with a single color presented continuously in each block, and blocks separated by a 6 s fixation-only ISI. Each color was presented 8 times across 4 runs in a fully counterbalanced order, for both the glasses-on and glasses-off runs. In all runs, observers indicated their perceived intensity of the color stimulus within a block on a scale of 1-4 by pressing a button.

4.2.3.2 fMRI Data Analysis

MRI data were preprocessed with AFNI software packages (Cox, 1996) using standard procedures. Slice-timing correction, motion compensation, and distortion correction were applied. Functional images were registered to the anatomical images, and were warped into MNI standard space for the purpose of visualization and ROI definition.

A general linear model (GLM) analysis was applied to the functional data to estimate the single-trial fMRI responses, using the GLMsingle algorithm (Prince et al., 2022). GLMsingle 1) identifies a custom hemodynamic response function (HRF) for each voxel; 2) estimates beta weights using the custom HRF for each trial in the paradigm; 3) derives and uses a set of nuisance regressors to reduce noise in the data; and 4) regularizes beta estimates using ridge regression for each voxel. The beta estimates represent BOLD response amplitudes to each stimulus trial for each voxel, relative to their baseline responses when only the background image and the black square were presented.

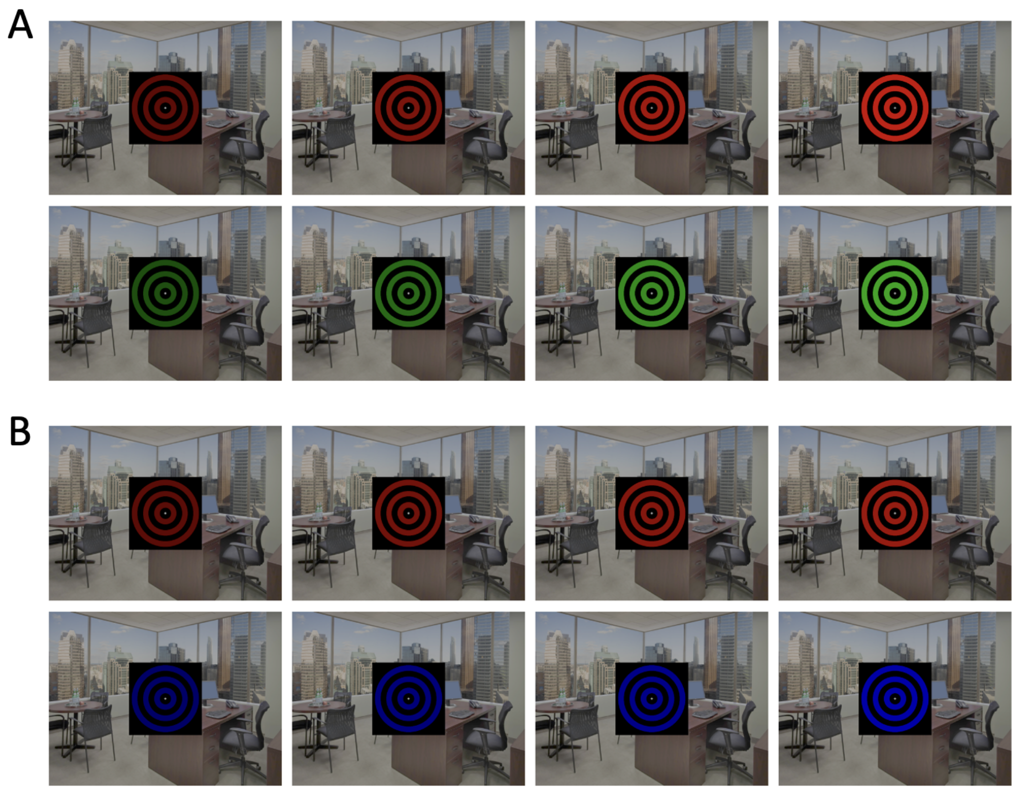


Figure 4.1. **Illustration of the stimuli used in the fMRI experiment.** The stimuli were phase reversing (2 Hz) radial square wave color/black gratings (1 c/deg., 6°), centered on a background image of a natural office scene, separated by a 6.5° black square. (A) Two observers viewed 4 intensity levels each of the red and green primaries of the projector. (B) The other two observers viewed red and blue primaries at 4 levels each.

4.2.4 Behavioral Experiment

4.2.4.1 Apparatus and Glasses

The two observers (SN01, SN02) who participated in the red/green fMRI scan session were also tested with red/green stimuli in a behavioral experiment. Visual stimuli were presented on a NEC MultiSync FP2141 CRT monitor, with screen resolution of 1024 x 768 pixels, and a refresh rate of 85 Hz. The monitor was calibrated using a Photo Research PR655 spectroradiometer. Viewing distance was kept at 50 cm with a chinrest. Observers completed all tests in a fully lit room.

The other two observers (SN03, SN04) were tested with red/blue stimuli, with the additional goal of simulating a viewing environment similar to that in the MR scanner in the fMRI experiment. Visual stimuli were back projected onto a translucent screen using a projector that was of the same model as the one used in the fMRI experiment. The distance between the projector and the screen was 150 cm, and observers viewed the screen from a distance of about 100 cm, similar to what it was during fMRI scans, through a white tube in a darkened room.

All visual stimuli were delivered in MATLAB using the psychophysical toolbox (Brainard, 1997). All 4 observers wore the same model of red glasses as the ones used in previous studies.

4.2.4.2 Procedure

During the behavioral test session, observers viewed 6° phase reversing (2 Hz) radial square wave color/black gratings (1 c/deg.), designed to be similar to the stimuli used in the fMRI experiment. The gratings were split into two halves horizontally, with one half being red/black and the other half being green/black (for two observers SN01, SN02, Figure 4.2A) or blue/black (for the other two observers SN03, SN04, Figure 4.2B). A 6.5° black square separated the gratings from the background image. To prevent simultaneous color contrast effects, a 1° black gap was placed between the two half-ring gratings (Figure 4.2).

During the test session, observers adjusted the strength of red/black "match" gratings until they appeared to be equally salient as green/black or blue/black "test" gratings. Judgment of salience or strength of color stimuli has been used to study many aspects of color perception (e.g. Kingdom et al., 2014; Switkes, 2008). Each session comprised a total of 18 blocks, with 9 blocks of a brighter test stimulus (either green with a luminance of 64 candela/m^2 or blue with a luminance of 28 candela/m^2) and 9 blocks of a darker test stimulus (either green with a luminance of 4 candela/m^2 or blue with a luminance of 7 candela/m^2). These blocks were presented in a pseudorandom order. In each block, gratings were presented for 9 s followed by a 6 s blank.

To make adjustments observers pressed the left arrow button to reduce the strength of the red stimulus, right arrow button to increase the strength of the red stimulus, and then space bar when they had set it to appear equally salient as the green or blue stimulus. Observers made as many matches as they could within 9 s (typically 3 to 9 matches) and were instructed to fixate at a cross in the center of the screen throughout the whole test. To minimize the impact of afterimages, the red/black and blue/black gratings alternated their positions after each block.

At the beginning of each test session, observers performed this task with natural vision. Then, they put the glasses on and were immediately tested again. Observers were also tested after

25 and 55 min of wearing the glasses. Between tests observers watched videos of their choice on the testing screen. After 1 hour, observers removed the glasses and were tested a last time.

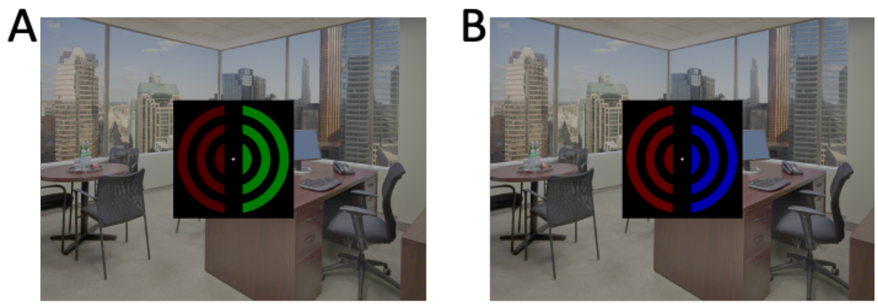


Figure 4.2. **Illustration of the stimuli used in the behavioral experiment.** The stimuli were 6° phase reversing (2 Hz) radial square wave color/black gratings (1 c/deg.), with one half being red/black and the other half being green/black or blue/black. A 1° gap was introduced between the two half-ring gratings to reduce color contrast effects. Observers' task was to adjust the strength of the red stimulus to match the salience of the green or blue stimulus. (A) Two observers were tested with red and green stimuli. (B) Two observers were tested with red and blue stimuli.

4.2.4.3 Behavioral Data Analysis

We characterized the behavioral results in terms of L cone responses produced by the match stimulus for each test stimulus. The spectra of observer' settings were multiplied by the cone fundamentals to compute cone responses, using Stockman & Sharpe (2000) fundamentals, with peaks scaled to 1. For the settings made with the glasses on, we first multiplied the spectra by the transmission spectrum of the glasses, and then multiplied by the cone fundamentals.

4.3 Results

4.3.1 Behavioral Results

4.3.1.1 A trend for adaptation to the glasses to speed up over days

When wearing the red glasses, observers reported that initially, the green and blue stimuli appeared to be much darker/weaker, but the perceived strength of red stimuli was not affected significantly. Over time, the green and blue stimuli appeared stronger. Thus, we expected that after putting on the glasses, observers' settings would be initially a weak red, but as they adapted to the glasses, the red set to match the saliency/strength of green or blue stimuli would become stronger as the appearance of the green or blue stimulus became stronger through adaptation.

This pattern is partly evident in Figure 4.3, where observers' red settings are characterized by L cone responses and are plotted as a function of test time and day. Black symbols represent settings made before putting on the red glasses on each day, and the red symbols are settings made when wearing the glasses. A higher L cone response corresponds to a brighter red stimulus on the display. We first examined effects of adaptation within the one-hour testing sessions, and observed a small trend when testing with the stronger green or blue stimulus in some observers (SN01 and SN03), visible as small rises in the red setting needed to match the salience of their appearance. Only very small changes were present when testing with the weaker stimulus.

For these same two observers, the behavioral experiment provided evidence of learned mode switching, i.e. learning to adapt to the red glasses more rapidly. That is, when they first put on the glasses, the green and blue stimuli immediately appeared to be less dark, and more saturated over days. This is reflected by the rising trend across days of the strength of the first red setting made after putting on the glasses over days. A linear regression model fit demonstrated that this increase was significant for observer SN01 both when tested with the strong green ($p < 1e\text{-}6$) and the weak green ($p < 0.01$); and for observer SN03, both when tested with the strong blue ($p < 0.001$) and the weak blue ($p < 0.05$). The changes were non-signficant for SN02 and SN04, however, there was a trend for the red setting to become stronger for SN04 when tested with the strong blue ($p = 0.07$).

Baseline settings were made before putting on the glasses on each day, preceded by many hours without glasses wear (Figure 4.3 black dots). No observer showed a significant shift in their baseline red settings over days. In addition, the variance was relatively high in baseline results within and across observers, which may indicate that the "strength" or "saliency" of a color stimulus needs to be better defined in the instructions.

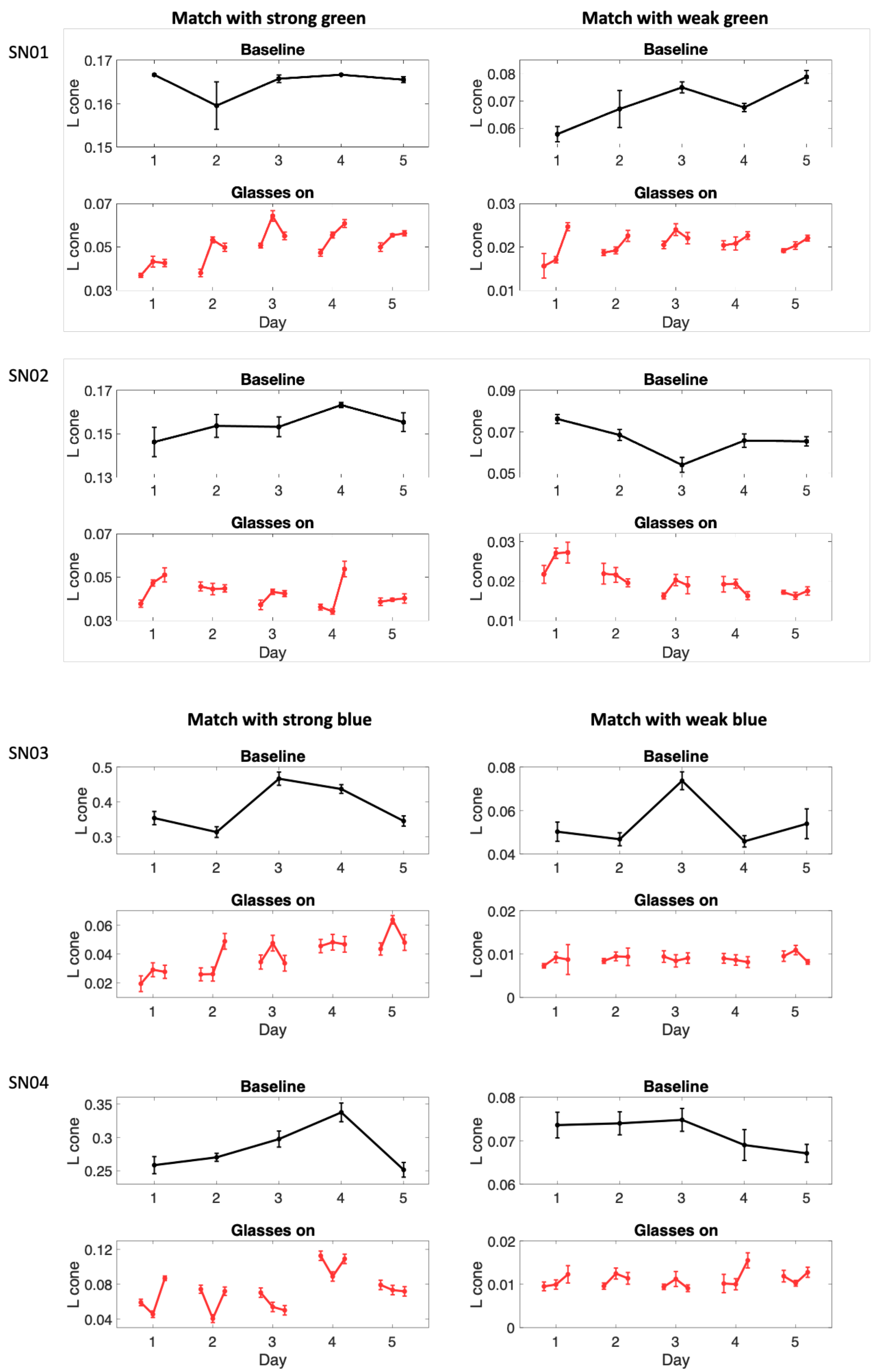

Match with strong green
Match with weak green
SN01
Baseline
Glasses on
L cone
Day
SN02
Baseline
Glasses on
L cone
Day
Match with strong blue
Match with weak blue
SN03
Baseline
Glasses on
L cone
Day
SN04
Baseline
Glasses on
L cone
Day

Figure 4.3. **Behavioral results.** Observers' red settings are measured in terms of L cone responses and are plotted as a function of test time and day. Observers SN01 and SN02 adjusted the strength of a red/black grating to match the strength of a strong or weak green/black grating. Observers SN03 and SN04 adjusted the strength of a red/black grating to match the strength of a strong or weak blue/black grating. Black symbols are settings made before wearing the glasses on each day and red symbols are setting made when wearing the glasses.

4.3.2 fMRI Results

4.3.2.1 Evaluation of Model Fitting for fMRI Data

The fMRI experimental design allowed us to observe reliable BOLD responses, which were modulated by the intensity level of the colors (see below) when viewed in a relatively complex scene (i.e. the background image and the black square). To visualize the quality of our signal and analysis, we plotted the goodness of the GLMsingle model fit for all voxels, as R^2 maps for the localizer scan and the 8 experimental scans. Figure 4.4 shows results from one observer's one scanning session. The model fitted well to the extent individual stimulus presentations produced reliable increases in BOLD signal. Large clusters of voxels were visible in visual cortex, at the back of the brain, exhibited high R^2 for the overall GLM model fit, and they overlapped in the localizer and experimental scans. R^2 maps of model fitting to other observers and scan sessions showed a similar pattern.

To examine how well the time course was fitted for each stimulus presentation, we plotted the mean fMRI time course and the mean model fit for active voxels in fMRI runs. This is shown in Figure 4.5 for the approximately 500 best-fitted voxels with the highest R^2 in the localizer scan (Figure 4.5A) and 8 experimental scans (Figure 4.5B) for one session of one observer. The fitted time course was calculated from the trial-wise estimated beta and the chosen HRF (see methods) for each voxel. The model generally fitted the time course well for all scans. Similar results were found in all observers (data not shown).

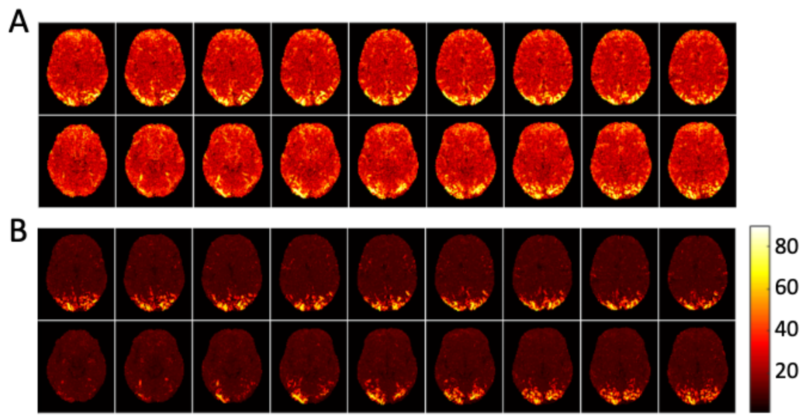


Figure 4.4. **Evaluation of fMRI model fitting.** R2 map of GLMsingle model fitting to the localizer (A) and 8 experimental scans (B) of one observer's one scan session (SN01, day 5). Responses of a good number of visual voxels were well fitted by GLMsingle. Only slices with voxels that were well fitted were shown here, which were mostly within the occipital cortex. Other areas of the brain did not contain clusters of activated voxels.

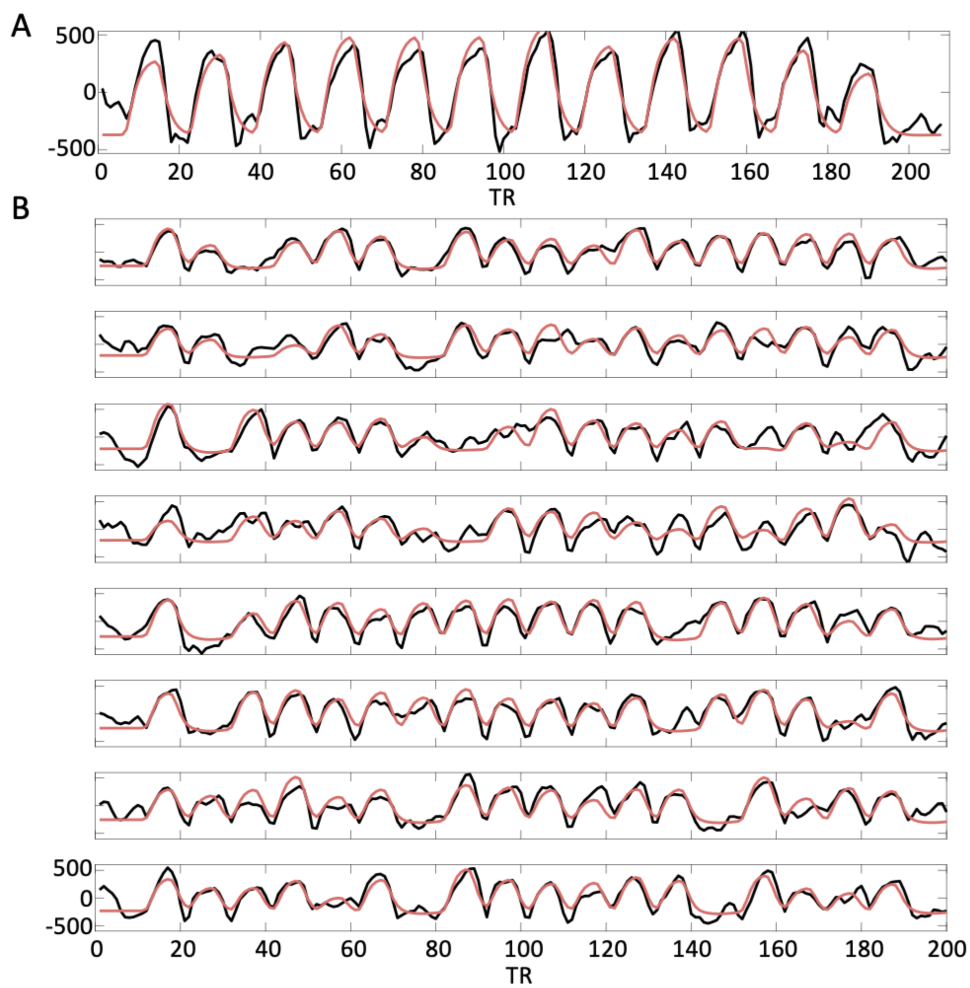


Figure 4.5. **fMRI time course and GLMsingle model fitting.** Mean fMRI time course and mean fitted time course across approximately 500 best-fitted voxels in the localizer scan (A), and the 8 experimental

scans (B) in one session of one observer (SN01, day 6). Black line represents the measured time course, and the red line represents the fitted time course.

4.3.2.2 Changes in fMRI responses after learning mode switching

Overall, fMRI responses to colors increased as the stimulus intensity level increased, both when wearing and not wearing the glasses. Figure 4.6 plots the percent signal change as a function of color intensity, for all scan sessions for each observer. Two observers (SN01, SN02) were tested with red and green stimuli of 4 intensity levels each, and the other two observers (SN03, SN04) were tested with red and blue stimuli of 4 intensity levels each. Each data point represents the mean signal across 8 presentations for each stimulus, averaging across selected voxels. For this first plot all "active voxels" in visual cortex were used, i.e., those that were well-fitted ($R^2 > 30$) and had an average response greater than zero across all blocks/trials in both the localizer scan and the experimental scans. This yielded approximately 500 voxels per observer and likely spanned early and later dorsal and ventral visual areas. Beta weights for each trial were averaged across voxels, then across stimulus type, and then plotted, and error bars represent standard error of the mean across 8 presentations for each stimulus. Filled circles are responses to colors before 5 days of training and open circles are responses after training. Darker solid lines are responses to colors under natural viewing, and brighter dashed lines are responses to colors when viewing through the red glasses. The hue of the symbol corresponds to the stimulus hue, red, green, and blue respectively.

The graphs show a rising trend of fMRI response as the intensity of the stimulus increases, in most conditions (before and after training; glasses on and off; different color stimuli) for all 4 observers. This highlights that the experimental paradigm allowed us to observe intensity-dependent fMRI responses. Such a trend was less obvious in a few conditions for some observers (especially SN04), which may be due to the lower SNR in those scans. Below, we examined different visual areas and found that the intensity-dependent response was more prevalent in lower-level areas.

Before training, observers’ brain responses to green and blue stimuli when wearing the glasses were much lower than without wearing the glasses. This was expected because when viewing through the red glasses, green and blue stimuli appeared much darker than under natural viewing, which can be predicted by the glasses’ transmittance. This effect was more pronounced for stimuli with lower intensity levels compared to those with higher intensity levels. On the other hand, the glasses had a very small effect on the responses to red stimuli, as expected since the glasses did not greatly alter the perceived strength of red stimuli.

The fMRI results also display neural correlates of mode-switching. Behaviorally, after experiencing the red glasses for 5 days, observers learned to switch visual modes and perceived the green and blue stimuli to be stronger when first put on the glasses. Similarly, on day 6, the brain responses to greens and blues seen through the glasses increased and was less different from when not wearing glasses, compared to day 0. This can be seen by comparing the green and blue dotted curves from day 0 to day 6, with most showing an increase in response, particularly for the lowest intensities. The increase was significant for observer SN02 for the lowest and the second highest intensity, as well as for observers SN03 and SN04 for one of the medium intensities (with t-tests; all $p < 0.05$). Responses to red stimuli were less affected by wearing the glasses and did not change significantly over days.

These patterns are consistent across observers and are also reflected by the mean responses across observers. Figure 4.7 plots the mean responses to red stimuli across all four observers, and mean responses to green and blue stimuli across two observers. To compensate for the differences in overall response amplitudes across observers, we scaled each observer's responses for all stimuli in all conditions by dividing by their response to the brightest red stimulus under natural viewing before training. We did not conduct statistical tests, however, of means across observers due to the small sample sizes ($N = 2$) in this pilot work.

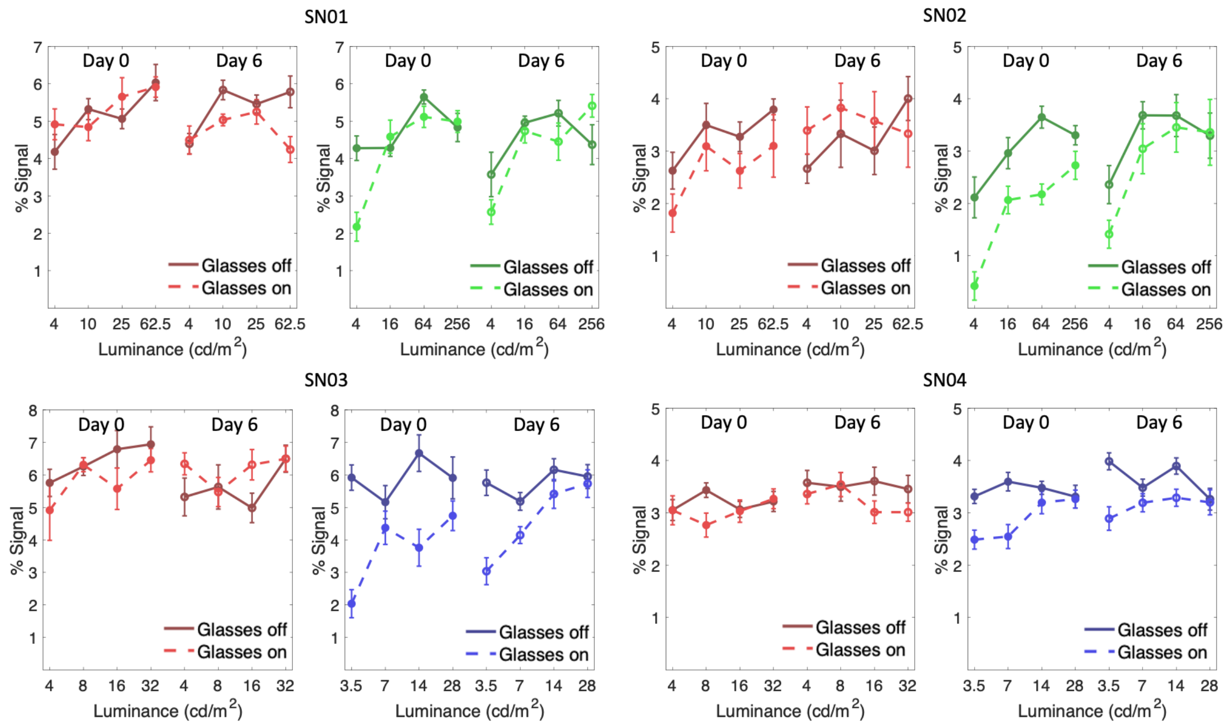


Figure 4.6. **"All active voxels" fMRI results for each observer.** Brain responses measured as percent signal change are plotted as a function of stimulus intensity (luminance). Filled circles are responses to stimuli before learning, and open circles are responses after learning. Solid lines are responses to stimuli under natural viewing, and dashed lines are responses to stimuli seen through the glasses. The symbol hue corresponds to the stimulus hue, red, green, and blue respectively. Each data point represents mean response across selected voxels and averaged across 8 presentations of each stimulus type under each condition. Error bars are standard errors of the mean across stimulus presentations.

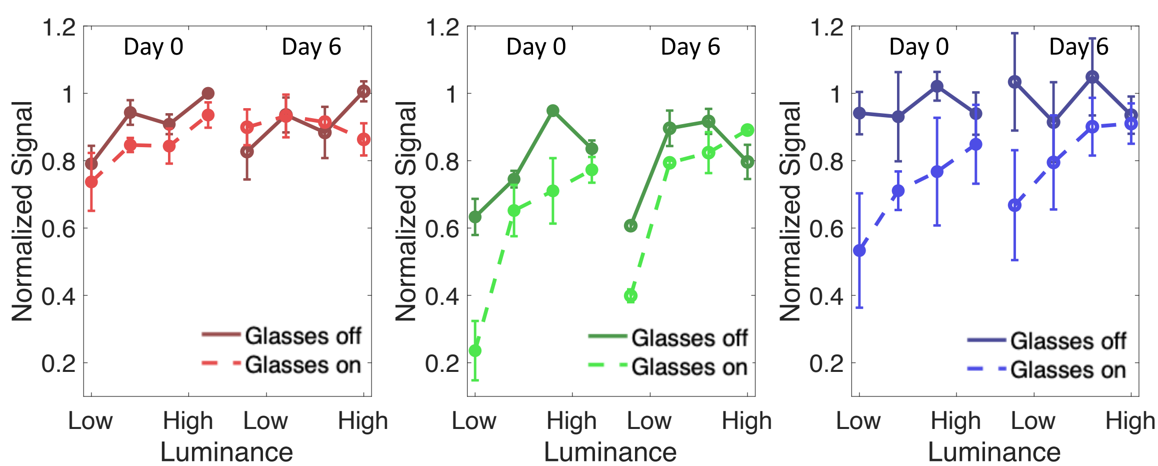


Figure 4.7. **Mean normalized fMRI responses across observers.** Mean responses to red stimuli were averaged across all four observers, whereas responses to green and blue stimuli were averaged across two observers. Symbol meanings are the same as in Figure 4.6. Error bars are standard errors of the mean across observers.

4.3.2.3 Both primary and higher-level visual areas are likely to be involved in mode switching

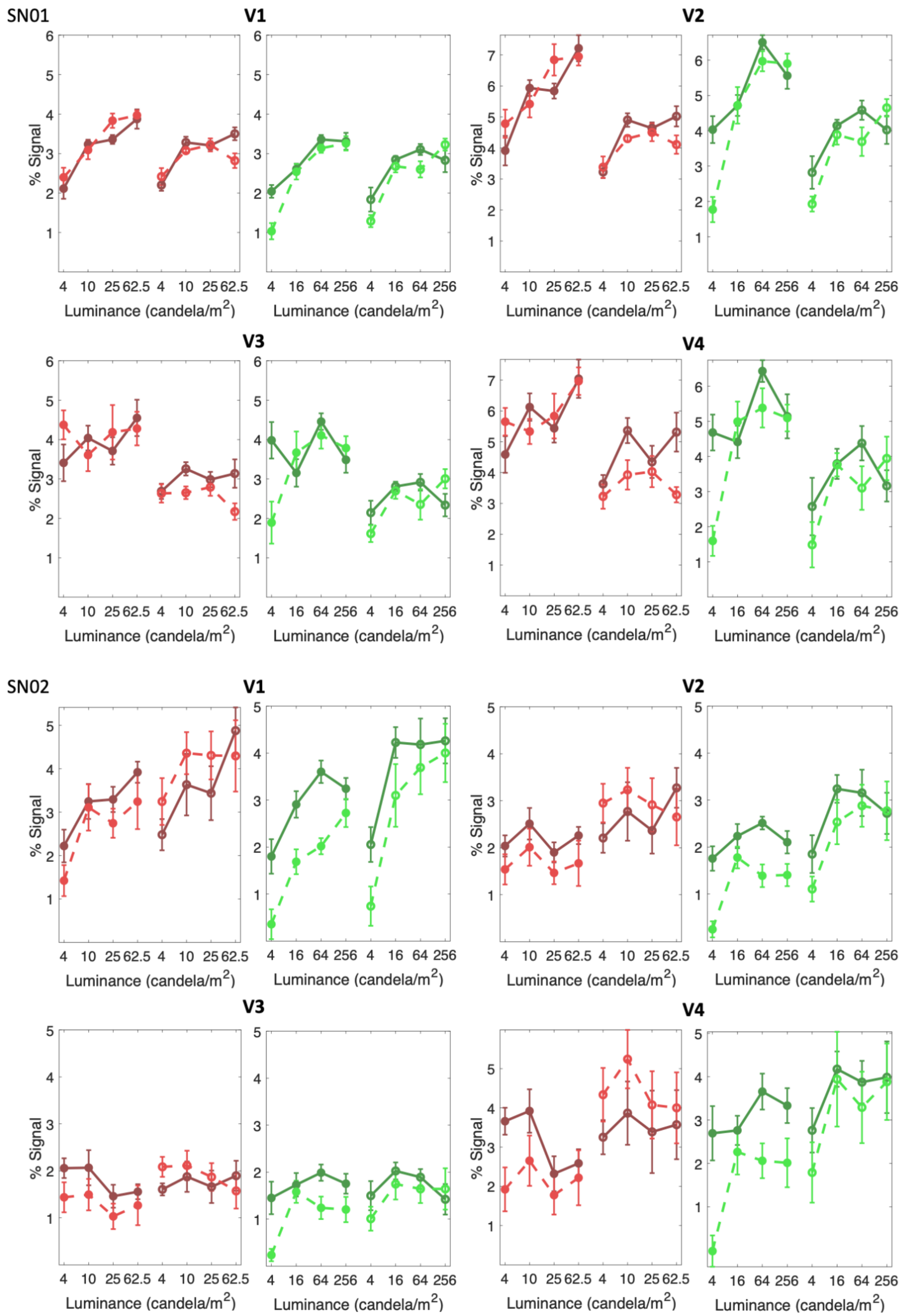
To evaluate the role of different visual areas in mode switching, we defined retinotopic visual areas in our observers using a probabilistic atlas (Wang et al., 2015). We used a probability threshold set at 30 percent of subjects, a relatively lenient criterion, because we also included an additional step of voxel selection: As before, we then selected voxels that were reasonably well-fitted by GLMsingle ($R^2 > 20$) and had an average response greater than zero across stimulus presentations, in both the localizer and the 8 experimental scans within a scan session.

Figure 4.8 plots the mean fMRI responses of areas V1, V2, V3 and V4, both with and without wearing the glasses, before and after 5 days of training for each observer. Figure 4.9 shows the mean responses averaged across observers for each visual area. As before, responses to red stimuli were averaged across 4 observers and responses to green and blue stimuli were averaged across two observers. Observers' responses were normalized by dividing their response to the brightest red when glasses were off before training.

In most conditions, fMRI responses increased as the intensity level of the stimulus increased, and this effect was more pronounced in V1 than in other areas. This is in accordance with previous findings that V1 response increases as the stimulus becomes stronger (e.g., Boynton et al., 1999).

As described earlier, wearing glasses caused the brain responses to green and blue stimuli to decrease substantially on day 0. As observers learned to adapt more rapidly to the glasses over 5 days, fMRI responses to greens and blues increased, approaching the response levels when glasses were off. Such effects were observed in all visual areas V1, V2, V3 and V4, indicating that all these areas are likely to be involved in mode switching. Future work can test more observers and perform statistical tests on a larger sample size to provide more robust and reliable conclusions.

V3 responses were less affected by the glasses and were of lower amplitudes overall, compared to V1, V2, and V4, which could be because neurons in V3 are less sensitive to color. V4 responses in observer SN04 showed a different pattern and of lower amplitudes, which may be because the V4 ROI we used did not align well with the V4 area of this observer.


SN01
V1
V2
V3
V4
SN02
% Signal
Luminance (candela/m^2)
4 10 25 62.5 4 10 25 62.5
4 16 64 256 4 16 64 256

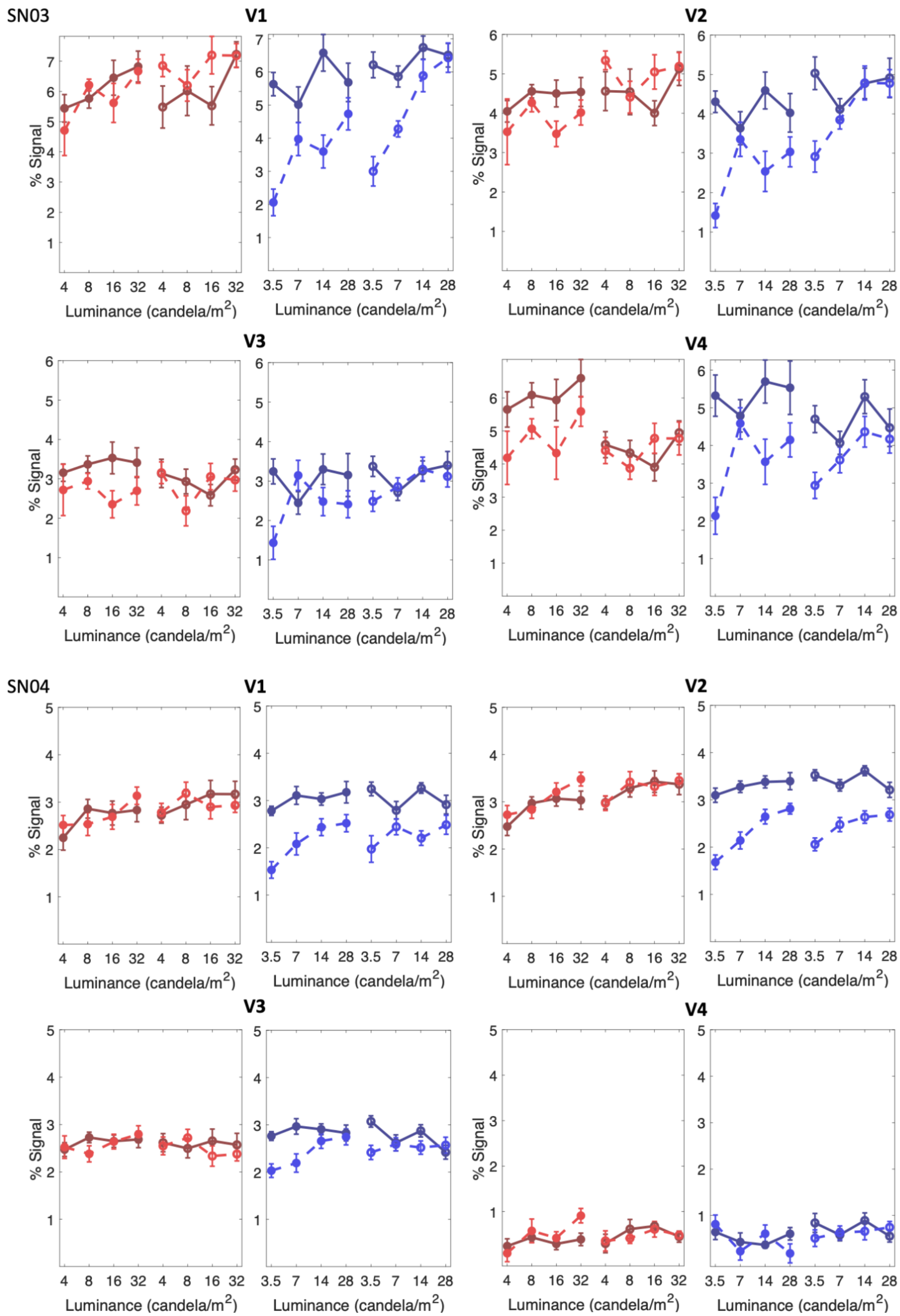


Figure 4.8. **fMRI responses in different areas V1, V2, V3, and V4 for each observer.** Symbol meanings are the same as those in Figure 4.6.

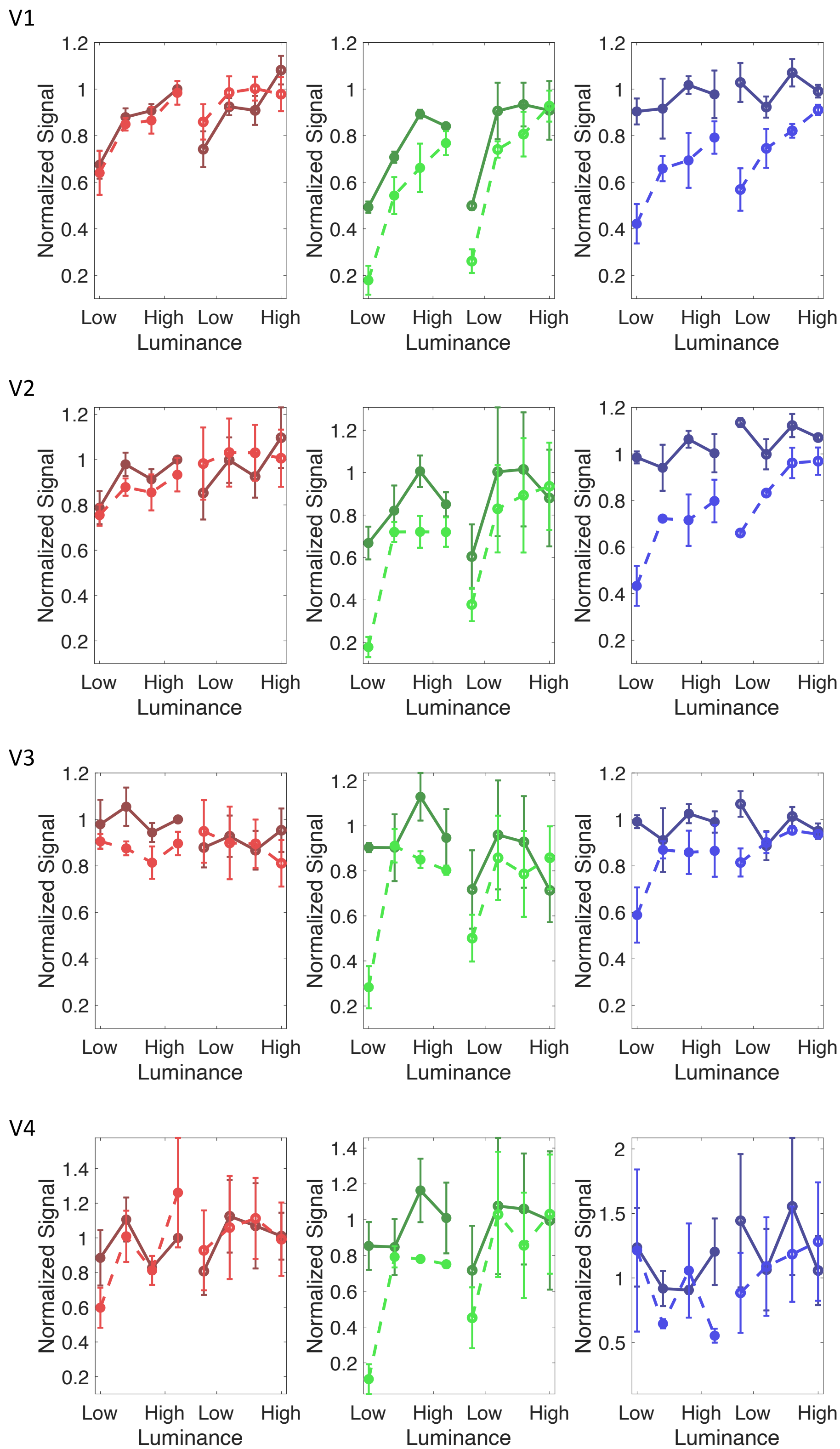


Figure 4.9. **Mean normalized fMRI responses in areas V1, V2, V3, and V4 across observers.** Symbol meanings are the same as in previous figures. Error bars are standard errors of the mean across observers.

4.4 Discussion

The goal of this pilot study was to develop a paradigm to explore the neural mechanisms of visual mode switching. Our aim was to identify brain areas whose responses to colors seen through the red glasses changed after learning mode switching. We piloted the study on four observers, where two of them were tested with red and green stimuli and the other two were tested with red and blue stimuli. Observers showed decreased fMRI response to green or blue stimuli when they first wore the glasses, and the response increased after experiencing with the glasses for 5 days. Such a change in response pattern was found in many visual areas including primary visual cortex and higher level visual cortices. Responses to red stimuli seen through the glasses also may have increased somewhat in early visual areas after 5 days, but to a lesser extent than blues and greens.

Our findings suggest that the brain areas that may be involved in mode switching are widely distributed, including both striate and extrastriate cortex. Previous neuroimaging studies showed mixed results on the role of V1 in producing color context effects (e.g. Cornelissen et al., 2006; Engel & Furmanski, 2001; Perna et al., 2005; Wade & Wandell, 2002; See review above), and our results provide evidence for the importance of V1 in context-dependent neural responses and perception. In addition, middle areas V2 and V3 also appeared to contribute to visual mode switching. Our results also further support the argument that high-level visual areas, e.g. V4, are important for context-dependent processing (Barbur & Spang, 2008; Bannert & Bartels, 2017; Goddard et al., 2019). However, it is unclear where the effects arise initially. Future work could investigate whether the changes observed in later visual areas are due to changes in input from earlier visual areas (or for earlier areas even LGN and retina), or if feedback information from later areas influences the activity in early stages of visual processing.

4.4.1 Limitations and Next Steps

The fMRI paradigm piloted in this study appeared to be effective for exploring the neural bases of mode switching. There are several future directions that could be pursued. First, only four observers participated in this pilot study, and they were presented with two different sets of stimuli. A next step would be to test a larger number of observers using the same stimuli to allow adequate statistical power to draw meaningful conclusions. With more data gathered, we could also build computational models to further quantify fMRI response changes, which could then be correlated with behavioral measurements. Furthermore, multivariate analyses could be used to identify brain regions that exhibit different activation patterns prior to and after learning, which may differ from regions detected with univariate analyses. Lastly, by measuring responses to a larger number of colors, we could test and model which color direction shows the largest change in neural responsiveness and how that correlates with our perception.

Why did we not see strong behavioral results as in past work? All four observers verbally reported that they learned to mode switch; i.e. that the world seemed much less red when initially putting the glasses on by the fifth day. However, observers' red settings made when wearing the glasses were very far away from those set with glasses off, even after 5 days of training. There are many possibilities of the lack of a behavioral effect.

The learning effect in the previous chapters could be modeled by a change in relative gain of the photoreceptors, i.e. L/M and L/S. In the current experiment, observers adjusted only the red primary, which scaled the L and M cones simultaneously. Thus, we were likely measuring a change in the sum of L and M cones with the current setup, which was of a lower magnitude compared to the relative gain change. For instance, when there is a change in the L/M ratio from 1 to 1.5, it corresponds to a 50% increase. However, in terms of L+M, this change would correspond only to a 25% increase, from 2 to 2.5. In addition, perceptually, much of the compensation to the red glasses could be that colors regain their hue and saturation, e.g., a blue stimulus appearing purple initially and bluer as people adapt; or a green stimulus appearing dark grayish-green and becoming more saturated green over time. But these effects may not change the saliency/strength of a color stimulus and so may not have been captured by the task.

It is worth noting that both during the hour of testing and over the 5 days of training, observers' perception of the red stimuli could also have changed, and this may also have reduced adaptation and learning effect we observed. However, even if the red stimuli were strengthened by mode switching and adaptation, the effects were expected to be much smaller than for green and blue stimuli, which should have allowed us to observe strong behavioral effects within and across days.

Another possible reason that we did not see stronger effects in the behavioral and fMRI data could be that the projector used in this study had different characteristics than the monitors used for our past work. We noticed that when wearing the glasses, other displays (e.g., laptop, phone, CRT monitor) as well as objects in the natural world appeared quite dim and reddish initially, and brighter and less reddish gradually as we adapted. However, stimuli or images displayed by the projector appeared relatively normal immediately and did not change their appearance much over time. While we can only speculate as to the cause of this phenomenon, it could be due to the broadband spectrum of the projector's primaries and its high brightness level, which could produce high color constancy immediately upon donning the glasses. So, the "projector world" may not be suitable for inducing the mode switching effect, and future experiments could be conducted using a different display.

4.4.2 Significance

This work provides a fMRI paradigm that could be used to study the neural bases of visual mode switching, which will further deepen our understanding of how context can alter cortical processing, producing context effects. With such a paradigm, we could gather a rich data set whose explanation will require extending classical neural models of visual function to include mode switching. It is possible that this deeper understanding of the neural bases of mode switching could aid the optimization of perceptual training programs for unique visual environments, such as those experienced by radiologists and pathologists searching for abnormalities in clinical images. It's also possible that it could help with optimizing treatments for some visual disorders.

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Appendices

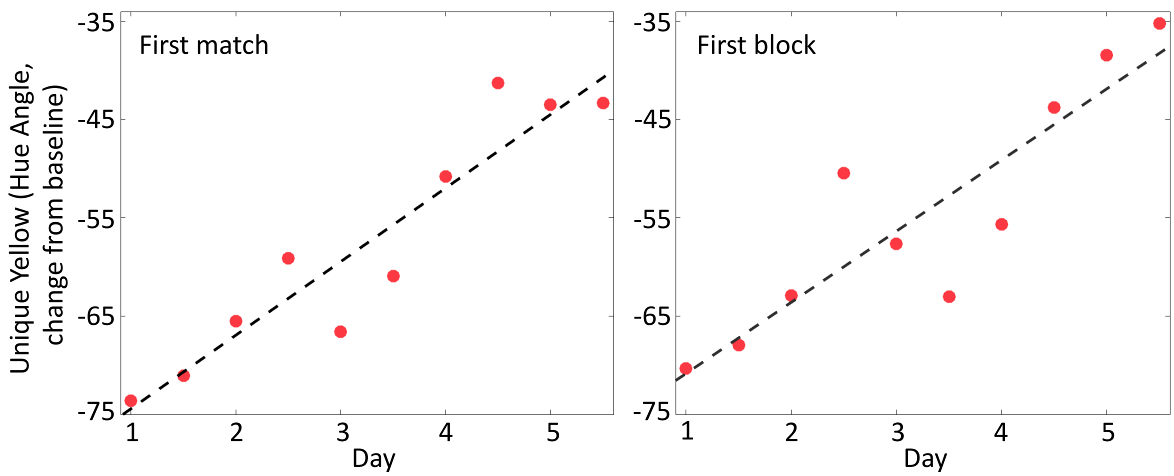

Figure A2.1. **Rapid adjustment effect analyzed from the first match and the first block.** Red dots in the left scatter plot show rapid adjustment analyzed using the first match with the glasses on in each session. The black dashed line is the least-square fit; the rapid effects shifted significantly across days ($p < 0.01$). The red dots in the right scatter plot show rapid adjustment from the first 1 min block of each session with the glasses on. The black dashed line is the least-square fit. The rapid effects shifted significantly across days ($p < 0.001$).

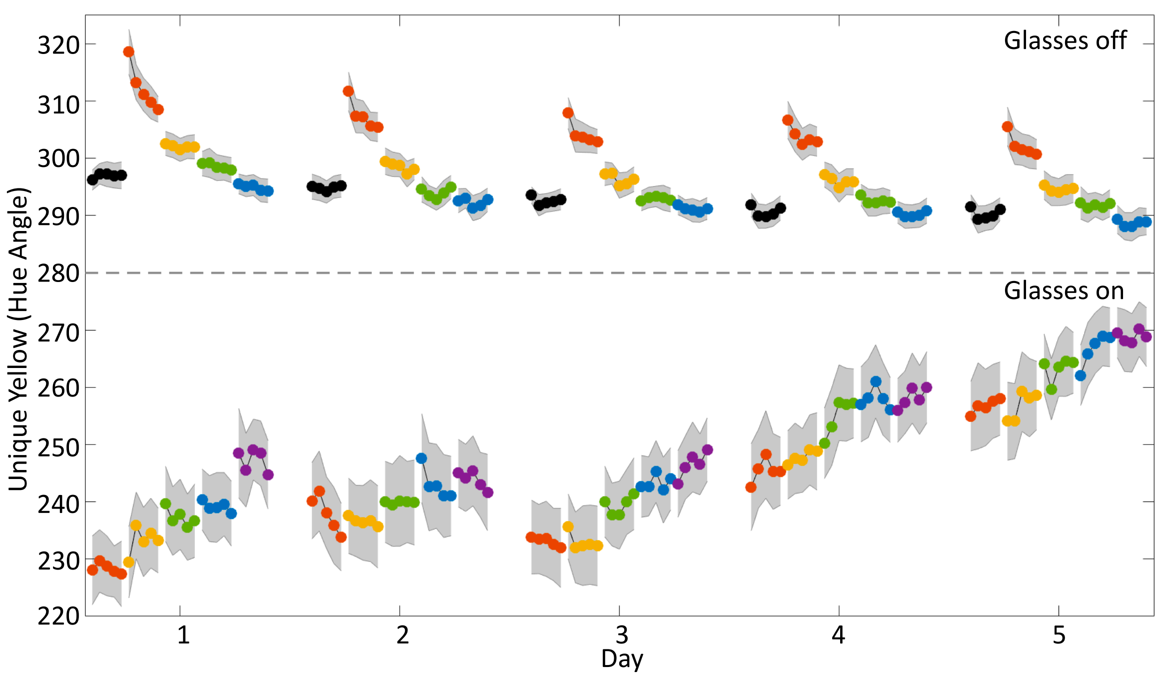

Figure A2.2. **Block-by-block results in the main experiment.** Morning and afternoon sessions within a day were averaged. The upper section of the figure shows unique yellow settings made with the glasses off. The black dots are baseline settings made immediately before putting on the glasses. The lower section of the figure shows unique yellow settings made with glasses on. Each dot in this figure represents the mean setting of a one-minute block, and 5 connected dots show the 5 blocks of each test. The first matches from tests 2-5 with glasses on in each session were influenced by the transition to the test display after breaks so were excluded when calculating the means. This did not affect the overall pattern of the results. Note that there were different amounts of time between the tests (See Figure 2.1C), during which observers were observing uncontrolled stimuli, so one cannot simply connect the lines to get accurate adaptation and de-adaptation time courses.

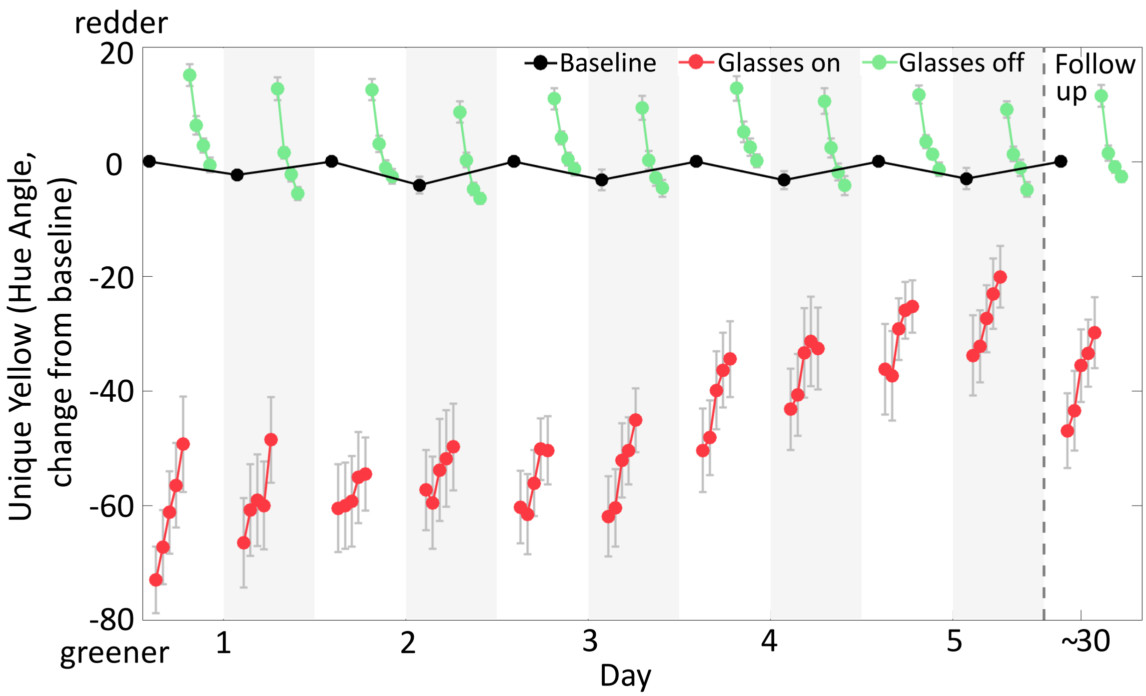

Figure A2.3. **Baseline-corrected results of the main experiment and the follow-up tests.** Mean unique yellow settings represented in hue angle are plotted as a function of time for 5 days and the follow-up test. Data were normalized by subtracting the baseline value for each morning test session, taken immediately before putting the glasses on in the morning. The black dots are baseline settings, made at the beginning of each test session with glasses off. The white background indicates morning sessions, and the light gray background indicates afternoon. The red dots plot settings with glasses on and the green dots are settings after removing the glasses. Successive symbols are plotted for each 5 min test. The gray bars represent standard errors of the mean, computed across participants (N = 11). These baseline-corrected results showed an identical overall pattern across days as the uncorrected data, though some effects became slightly larger.

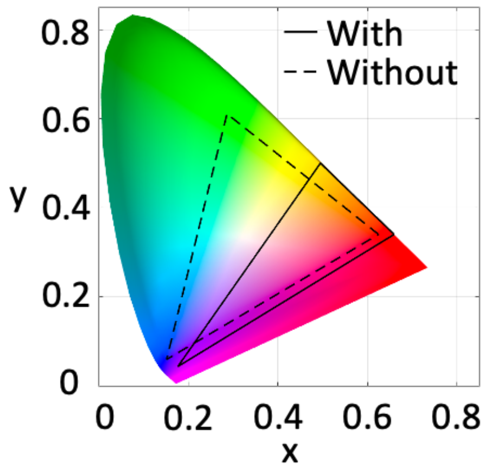

Figure A3.1. **Display gamut.** The gamut of the laptop display used in Experiment 2 without (dashed line) and through (solid line) the glasses, plotted in CIE color space. The glasses compressed the gamut and shifted it toward red chromaticities.

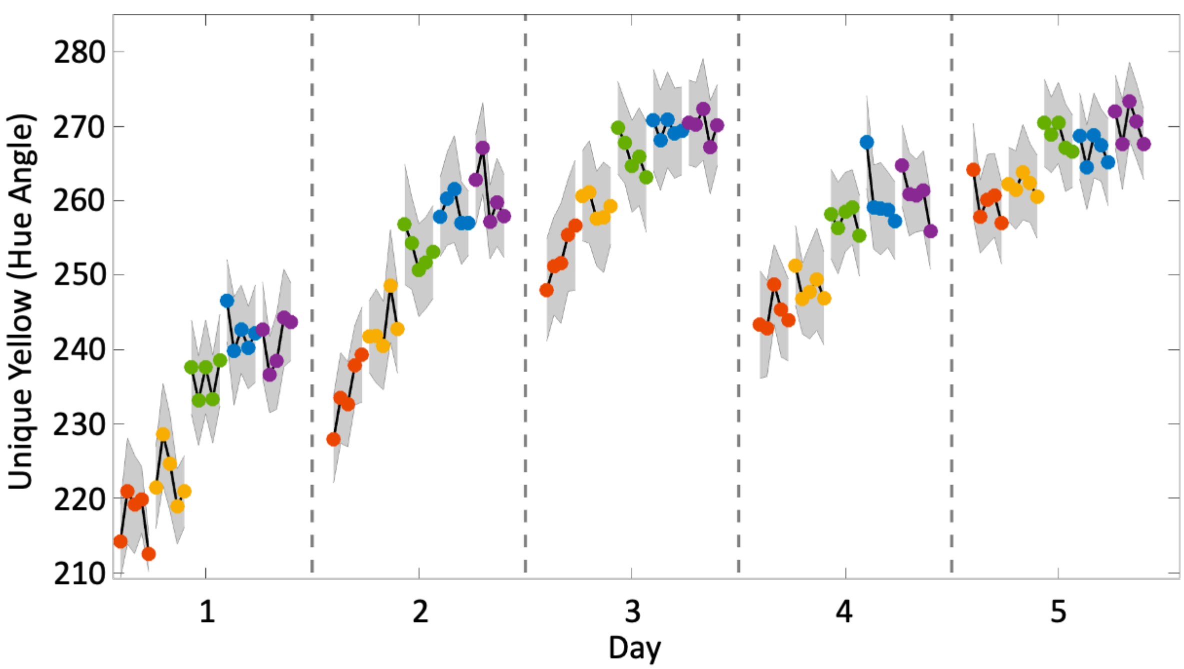

Figure A3.2. **Block-by-block results during the first hour of wearing the glasses on 5 days in Experiment 1.** Each dot in this plot represents the mean setting of a 1-min block, and 5 connected filled circles show the 5 blocks of each test. The first settings from tests 2-5 in each session were influenced by the transition to the test display after breaks so were excluded when calculating the means. This did not affect the overall pattern of the results. Note that there were different amounts of time between tests (See Figure 3.1D), when participants were viewing uncontrolled stimuli, so one cannot simply connect the lines to get an accurate adaptation time course.

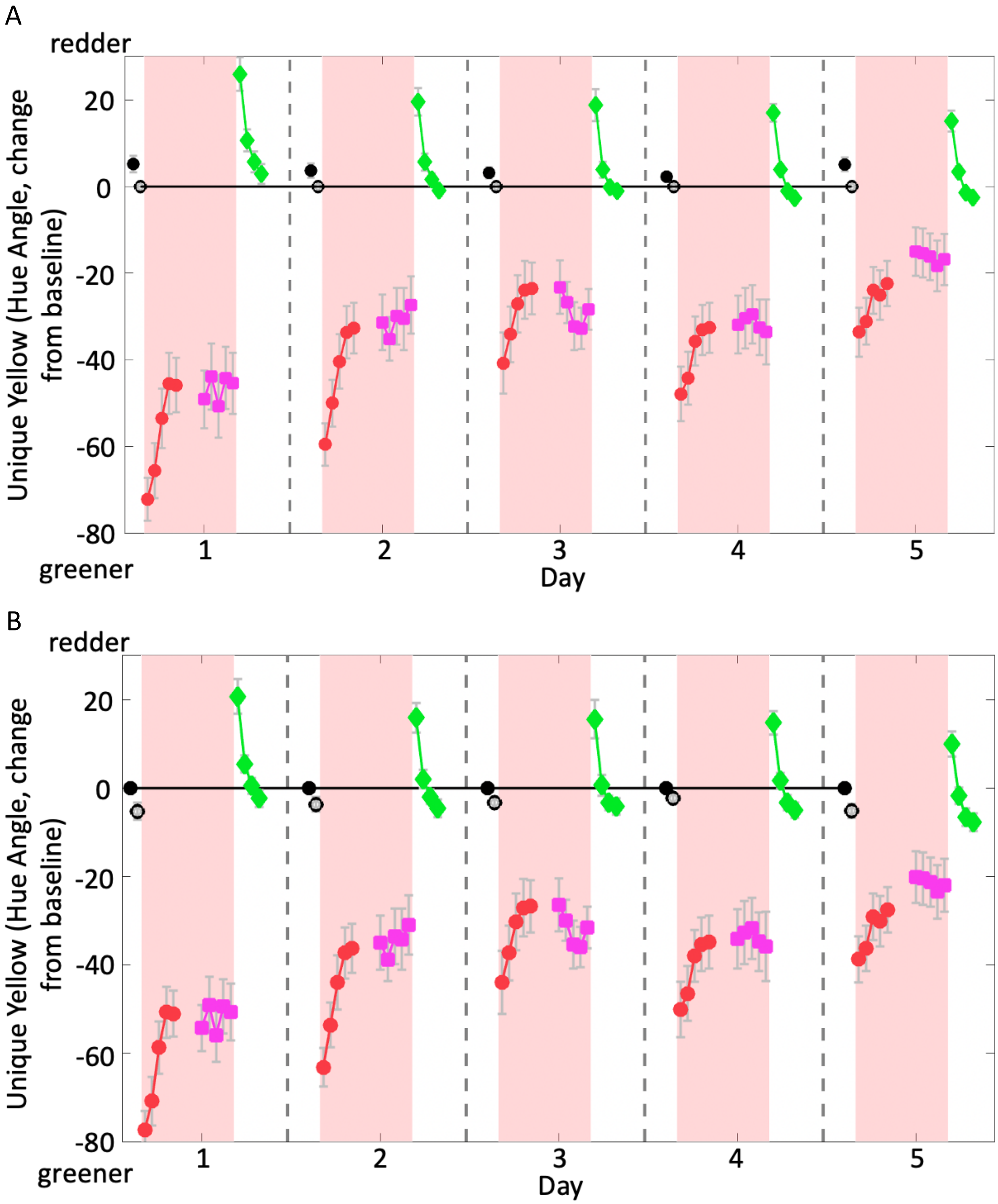

Figure A3.3. **Baseline corrected results of Experiment 1 (N = 12).** Mean unique yellow settings in hue angle are plotted as a function of time for 5 days. The white background indicates tests when not wearing the glasses, and the light red background indicates tests when wearing the glasses. The black filled circles are settings made after dark adaptation in the darkened room with no background image on the display. The black 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. Data were normalized by subtracting the baseline value, taken before wearing the glasses each day, from all settings within the day, to correct their effects. (A) Correct for the baseline setting under room light, tested with the background image provided. (B) Correct for the baseline setting after dark adaptation, tested in a darkened room with no background image on the screen.

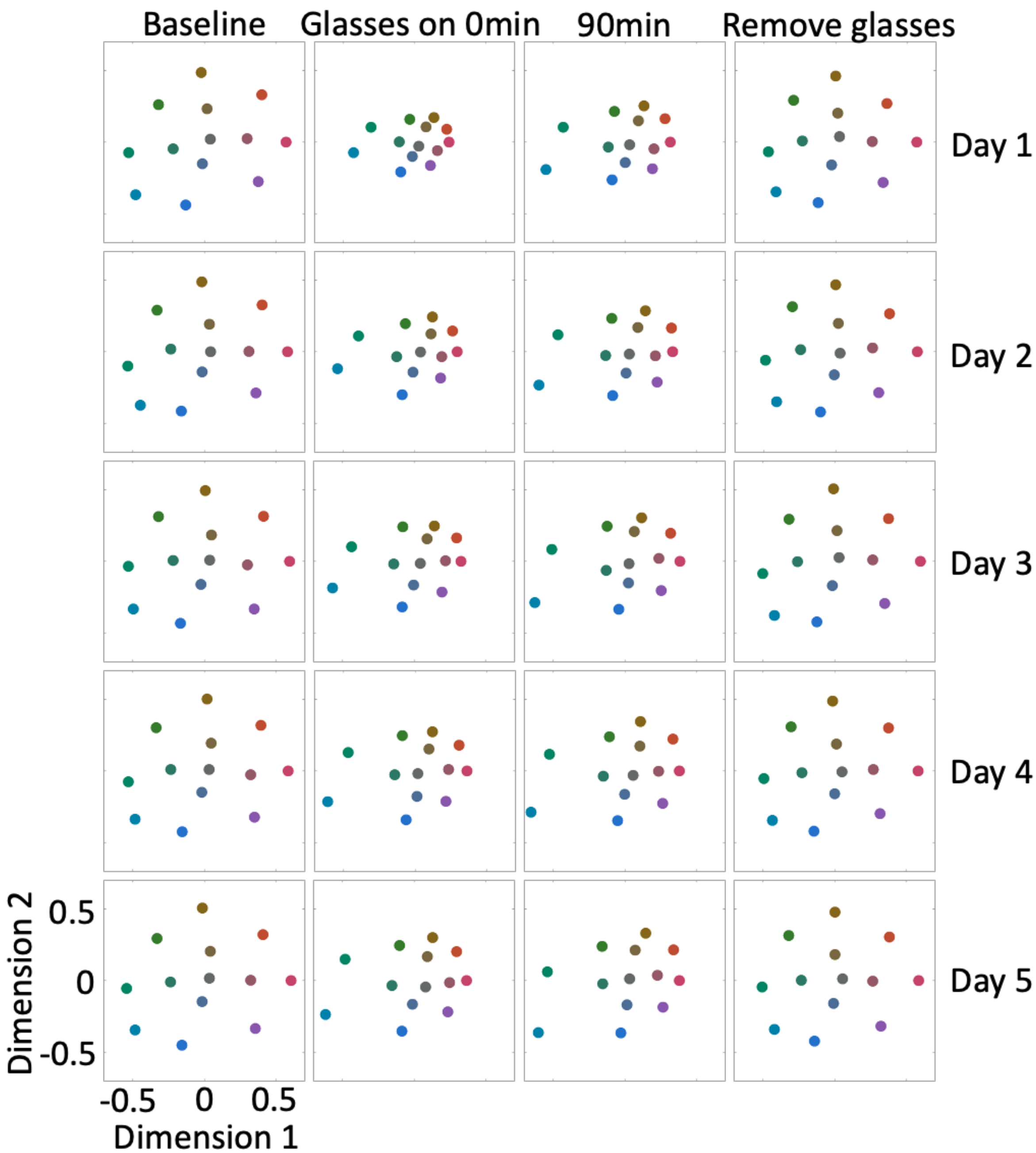

Figure A3.4. **Perceptual color spaces reconstructed using MDS from difference ratings.** Results in the second test sessions on 5 days are shown here (Figure 3.6 shows first test session). Results are shown for tests performed before wearing the glasses, immediately after putting on the glasses, 90 min after putting on the glasses, and immediately after removing the glasses. Perceptual color spaces were rotated to best coincide with the glasses-off stimuli in CIELAB color space.

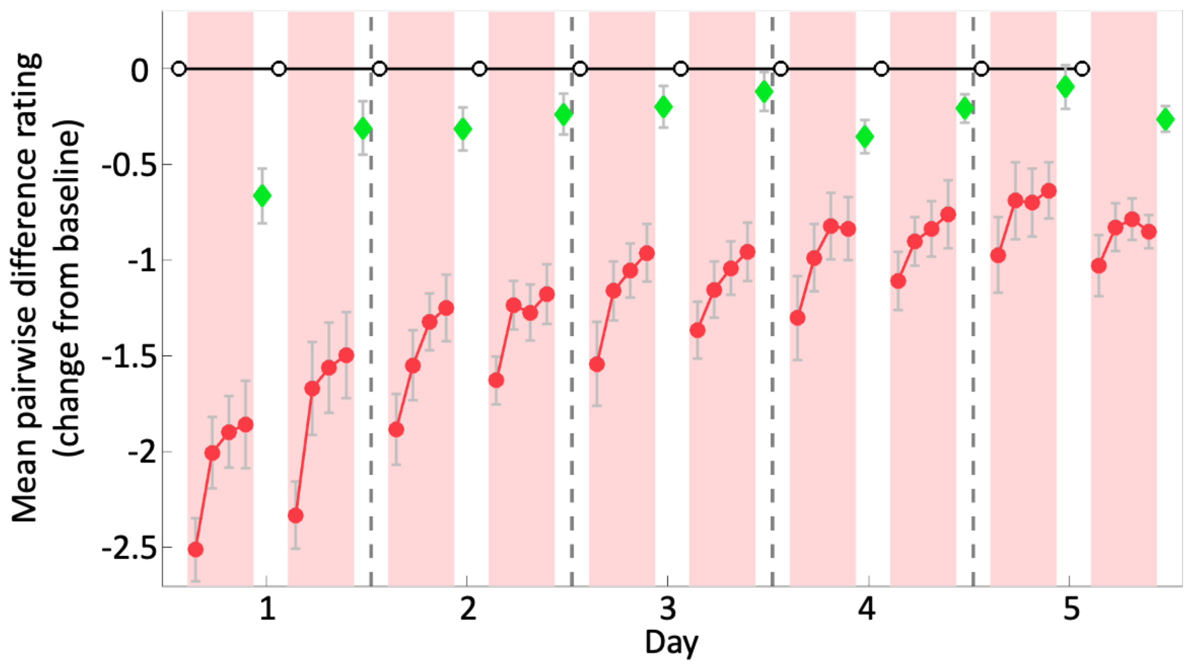

Figure A3.5. **Baseline-corrected results of Experiment 2 (N = 13).** Mean pairwise difference ratings, computed as the average rating across all pairs within a test, are plotted as a function of test time and day. The white background indicates tests when not wearing the glasses, and the light red background 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 glasses on and the green diamonds are ratings after removing the glasses. Data were normalized by subtracting the baseline rating before wearing the glasses from all settings within the session. The gray bars plot standard errors of the mean across participants. The baseline-corrected results showed a very similar overall pattern across days as the uncorrected results.