



Habitual wearers of colored lenses adapt more rapidly to the color changes the lenses produce



Stephen A. Engel^{a,*}, Arnold J. Wilkins^b, Shivraj Mand^c, Nathaniel E. Helwig^a, Peter M. Allen^{c,d}

^a University of Minnesota, Department of Psychology, Minneapolis, MN, USA

^b University of Essex, Department of Psychology, Colchester, UK

^c Anglia Ruskin University, Department of Vision and Hearing Sciences, Cambridge, UK

^d Anglia Ruskin University, Vision and Eye Research Unit, Cambridge, UK

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ABSTRACT

The visual system continuously adapts to the environment, allowing it to perform optimally in a changing visual world. One large change occurs every time one takes off or puts on a pair of spectacles. It would be advantageous for the visual system to learn to adapt particularly rapidly to such large, commonly occurring events, but whether it can do so remains unknown. Here, we tested whether people who routinely wear spectacles with colored lenses increase how rapidly they adapt to the color shifts their lenses produce. Adaptation to a global color shift causes the appearance of a test color to change. We measured changes in the color that appeared “unique yellow”, that is neither reddish nor greenish, as subjects donned and removed their spectacles. Nine habitual wearers and nine age-matched control subjects judged the color of a small monochromatic test light presented with a large, uniform, whitish surround every 5 s. Red lenses shifted unique yellow to more reddish colors (longer wavelengths), and greenish lenses shifted it to more greenish colors (shorter wavelengths), consistent with adaptation “normalizing” the appearance of the world. In controls, the time course of this adaptation contained a large, rapid component and a smaller gradual one, in agreement with prior results. Critically, in habitual wearers the rapid component was significantly larger, and the gradual component significantly smaller than in controls. The total amount of adaptation was also larger in habitual wearers than in controls. These data suggest strongly that the visual system adapts with increasing rapidity and strength as environments are encountered repeatedly over time. An additional unexpected finding was that baseline unique yellow shifted in a direction opposite to that produced by the habitually worn lenses. Overall, our results represent one of the first formal reports that adjusting to putting on or taking off spectacles becomes easier over time, and may have important implications for clinical management.

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1. Introduction

To cope with frequent changes in the environment, the visual system adjusts itself continuously, altering aspects of neural response in order to keep us seeing well. This visual adaptation happens at many different rates. Some adjustments, such as initial phases of adapting to changes in overall light levels, happen relatively quickly. Others, like adjusting to the visual changes produced by a new pair of glasses, appear to take hours or days.

Why do some types of adaptation occur relatively slowly? One possible reason is that some environmental changes may be

relatively subtle. For these shifts it might take the visual system more time to acquire evidence that the world has indeed changed (e.g. Wark, Fairhall, & Rieke, 2009). Another possibility is that some environmental changes may be relatively rare or unexpected. For these, vision may require extra evidence to be gathered before adapting extensively (e.g. Todorovic, van Ede, Maris, & de Lange, 2011).

For many repeatedly encountered environmental changes, it would be advantageous if one could learn to adapt to them rapidly. For example, people who wear spectacles often remove and replace them many times a day. Repeated slow adaptation could become burdensome, and indeed many regular lens wearers report that while the initial adjustment to a new prescription takes time, re-adaptation is almost instantaneous. Formal studies of rapid visual re-adaptation to spectacles for optical correction are

* Corresponding author.

E-mail address: engel@umn.edu (S.A. Engel).

inconclusive however (Vinas, Sawides, De Gracia, & Marcos, 2012; Yehezkel, Sagi, Sterkin, Belkin, & Polat, 2010; see Section 4).

Here, we examined observers with a different sort of prescription. Colored lenses (here termed filters) are sometimes prescribed for reduction of symptoms of “visual stress”, which include photosensitivity and difficulty reading (Wilkins, Huang, & Cao, 2004). The filters produce large changes in the average spectrum of light reaching the eyes.

Vision is known to adapt to such changes in spectral power. For example, illuminating the surround of a constant test patch with lights of different colors produces large changes in test appearance (e.g. Chichilnisky & Wandell, 1999; Rinner & Gegenfurtner, 2000; for a review see Foster, 2011). Some of this color adaptation happens immediately, and so is often labeled color contrast, while some of it arises more gradually (Fairchild & Reniff, 1995; Rinner & Gegenfurtner, 2000; Shevell, 2001). In the present study, wearing reddish filters made a reddish test light appear more neutral in color. The most common explanation for such adaptation is that the rest of the image, which appears more reddish than usual and is relatively dominated by longer wavelength light, causes a reduction in the strength of signals from the long wavelength cones relative to the strength of signals from the other cone types, through some sort of scaling process (for reviews, see Foster, 2011; Rieke & Rudd, 2009). Note that such adaptation partially compensates for the tint produced by the filters, making the visual world more “normal”, as reddish colors become more neutral (Webster & Leonard, 2008). Greenish filters produce effects in the opposite direction.

If the visual system can learn to adapt to spectacles, then observers who routinely wear colored filters should show larger and more rapid color adaptation than naïve observers wearing those same filters. We tested this possibility, measuring adaptation by recording the effects of a large, uniform surround on the color appearance of a central target. Observers wore and removed colored filters, which changed the spectral power of the surround. Appearance of the target was measured by having participants set it to be “unique yellow”, a shade that appears to contain neither any red nor any green (Jameson & Hurvich, 1955). As subjects adapted to the donning or removal of the spectacles, the appearance of the target changed over time, and this adaptation was tracked through repeated measurements of unique yellow. We found more rapid and larger adaptation to colored filters in habitual wearers than in control participants.

2. Materials and methods

2.1. Participants

Nine habitual wearers of colored filters and nine age-matched control participants were recruited. Five of the habitual wearers used reddish filters, and four habitually wore greenish ones. Habitual wearers had been prescribed their filters for visual stress, and had been using them for an average of approximately 14 months (range 3–34). They estimated that they wore their filters an average of 6.5 h per day (range 2–12). We selected participants who used reddish and greenish filters for consistency, and because these colors should have a large effect on unique yellow. The habitual wearers ranged in age from 17 to 69 years (mean 33.7), and each was matched with a control participant close in age (mean pairwise age difference = 0.8 years). Participants' visual acuity was either normal or corrected to normal with lenses that were worn throughout the experiment. Participants were recruited through the University Eye Clinic at Anglia Ruskin University, where experimental procedures were approved by the Faculty Research Ethics Panel. The work was conducted in accordance with

the Code of Ethics of the World Medical Association (Declaration of Helsinki).

2.2. Apparatus

A computer-controlled white LED light source projected through an interference monochromator (manufacturer, Jobin Yvon, model H10UV), and exited in a vertical slit 6 mm high and 0.5 mm wide viewed through a 24 mm long, 17 mm diameter black tube which created a circular black surround in which the vertical slit was central. The end of the tube was surrounded by white cardboard 450 mm high and 290 mm wide, with its width subtending 42 degrees, lit by overhead “white” T12 multiband fluorescent room lights. The mean luminance of the surround was 99 cd m⁻², and the mean luminance of the monochromator was approximately 290 cd/m² at 555 nm, the peak of the luminosity function. Participants viewed this display from a distance of 0.5 m, so that both eyes could see the slit (45 min by 3.4 min) through the tube (Fig. 1). At this distance and position, the slit luminance was approximately 390 cd m⁻². Individually prescribed colored filters were worn by the habitual wearers in their own spectacle frames. Control colors for the habitual wearers and all colors for the control participants were worn in a custom-made trial lens frame.

2.3. Color parameters

Each participant's individually prescribed colored filters differed in transmission spectrum, but the transmission was greatest either for long (red), or middle (green) wavelengths. Seen without filters, the surround had CIE 1976 UCS (*u'*, *v'*) coordinates of 0.223, 0.509. When measured through the reddish filters, the surround had *u'* coordinates that ranged from 0.272 to 0.290, and *v'* coordinates that ranged from 0.483 to 0.524. When measured through the greenish filters, the corresponding ranges were 0.135–0.169, and 0.520–0.545 (Fig. 1B).

The ratio of L to M cone absorptions for the surround with and without filters was calculated from the normalized cone spectra of Stockman and Sharpe (2000). The L/M ratio of the surround without filters was 1.22. The ratio when wearing reddish filters ranged from 1.41 to 1.54, and the ratios for the greenish filters ranged from 0.92 to 1.02. Note that of course the wavelength of monochromatic light for the test stimulus was not altered by the filters. Its radiance however, was reduced, on average, by 57% for the reddish filters and 85% for the greenish filters. Unique yellow settings are not affected by changes of this magnitude at this light level (Shevell, 2003).

2.4. Procedure

Participants were asked to judge the colored line produced by the monochromator as either “reddish” or “greenish”. During each trial, the line flashed for 100 ms, which was followed by a 4900 ms response interval. The next trial then started immediately. The wavelength of light viewed on successive trials was adjusted using a one-up/one-down staircase procedure to estimate the wavelength where each response was equally likely, a color termed unique yellow.

Unique yellow was affected by the surround over a time course that we measured using the “method of a thousand staircases” (Fig. 1C; Cornsweet & Teller, 1965; Mollon & Polden, 1980; Rinner & Gegenfurtner, 2000). The experiment was divided into 24 one-minute runs. Each began with the participant either placing filters over their eyes, or removing the filters, in both cases with their eyes closed. Participants then opened their eyes, on instruction from the experimenter, who simultaneously pressed a key to start the computer-controlled staircase procedure. Twelve trials

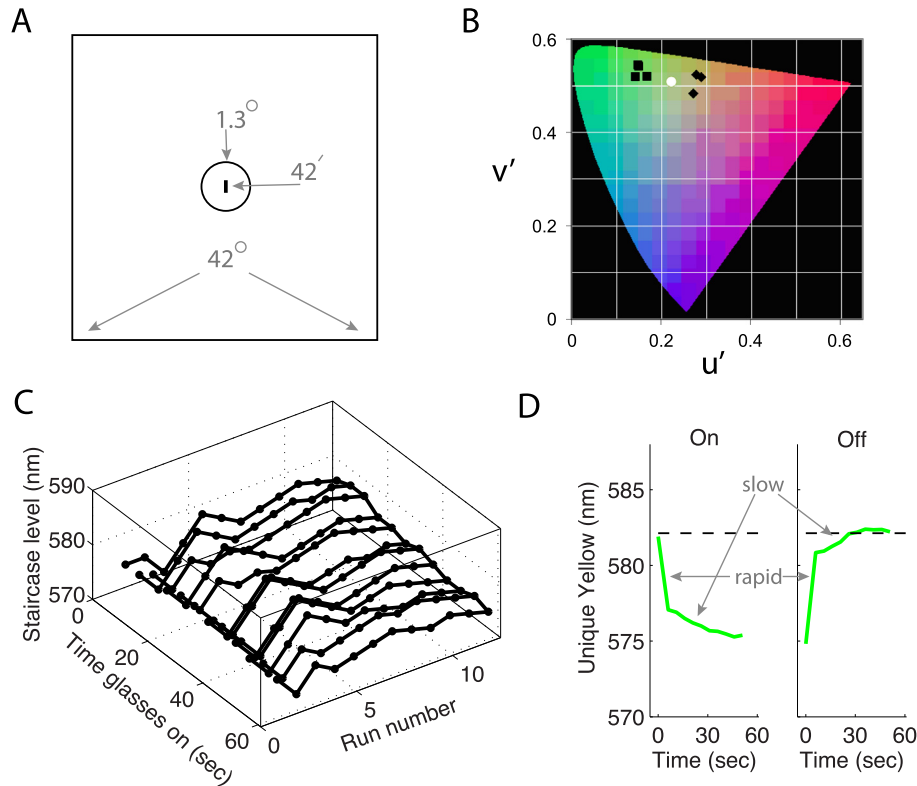


Fig. 1. A) Stimulus configuration. Subjects judged a $42'$ test slit of light surrounded by a 1.3° black tube and a neutral, 42° uniform field. B) Filter chromaticities. The neutral surround is marked with a white diamond. Its chromaticity seen through the subjects' red filters are shown as diamonds, and seen through green filters are shown as squares. Note some subjects used identical filters, so the number of symbols is less than the number of subjects. C) Psychophysical methods. Subjects judged the test light in 12 runs of 12 trials each with filters on and off. Each run was one trial in one of 12 staircases that estimated unique yellow at 5-s intervals following donning or removal of the filters. The plot shows example staircases for one subject wearing green filters. D) Sample results. Unique yellow estimates for control subjects wearing green filters changed over time as subjects adapted to donning and removal of filters. The adaptation time courses showed an initial rapid change, and a later slow one. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

were performed in the run, separated by the 4900 ms response period, where subjects adapted while remaining fixated without a test stimulus being present. Each of the twelve trials was controlled by an individual staircase and estimated unique yellow at a different 5 s interval following the start of adaptation. Upon completion of the twelve trials, participants then immediately closed their eyes, and switched viewing conditions as quickly as possible (removing or replacing their filters, aided by the experimenter and accomplished in less than 2 s). They then began the next trial and upon finishing twelve, they continued for a second set of trials with filters on, yielding the second data point in each of the twelve staircases. They continued to alternate between filters on and filters off for a total of 24 runs. These yielded 12 trials per staircase with both filters on and filters off, and each staircase estimated unique yellow at successive 5 s intervals beginning approximately 1 s after opening of the eyes.

To aid convergence to threshold, the “steps” of each staircase began at 4 nm, and its step size was reduced to 2 nm and then 1 nm following 2 reversals in that staircase. Each staircase started at a preliminary estimate of unique yellow made in two runs using a single conventional up-down staircase of 20 trials taken without filters preceding the main experiment.

Habitual wearers performed one block of 24 runs using their prescribed filter, then following a short break performed a second 24 min block of runs using a control filter; for participants who wore reddish filters this was a greenish filter. The same greenish filter, roughly in the center of the range shown in Fig. 1B, was used for all habitual reddish wearers, while a reddish control filter, again from near the center of the distribution in Fig. 1B was used for

participants who habitually wore greenish filters. An age-matched control participant was paired with each habitual wearer, and was tested with the same filters used for that habitual wearer.

2.5. Analysis

Unique yellow was estimated at each of the twelve time points following donning or removal of the filters (Fig. 1C). To do so, trials from the current and subsequent two time points were combined into a single psychometric function (of percent “reddish” responses vs wavelength). Unique yellow was estimated by fitting a cumulative normal function to the psychometric curve and calculating the 50% point of the function. This procedure did not produce estimates for the last two time points; other methods of estimating unique yellow that did (e.g. fitting a function from just one trial) showed comparable, but noisier results.

Plotting unique yellow estimates as a function of time yielded a time series of data (Fig. 1D). Because subjects alternated between filters off and filters on conditions, the final point of each was an estimate of the starting point of the other. Thus, to construct complete time courses for each condition, we prepended the final time point of the opposite condition.

2.6. Models

To characterize adaptation, we fit a simple bilinear model to the time series data. The *rapid* component of adaptation was estimated as the linear trend between the first and second points of the

timecourse (Fig. 1D), while the *slow* component of adaptation was the linear trend in all the following points.

To test our hypotheses, we fit three nested versions of the model to the data. The **reduced** model contained terms capturing overall rapid and slow adaptation, along with terms that allowed adaptation to green filters to be different than adaptation to red filters. Adaptation was modeled as identical in each group of subjects, however. The **basic** model contained two additional terms that allowed adaptation to habitually worn colors in habitual wearers to differ from adaptation in other conditions (i.e. non-habitual colors in habitual wearers and both colors in control subjects). One term was added for each of slow and fast adaptation. The **extended** model contained two additional terms that allowed slow and fast adaptation to be generally greater, regardless of filter color, in habitual wearers than in controls.

All three models contained terms to capture baseline levels of unique yellow, which were allowed to differ between subject groups. They also contained a term to allow baselines to differ for red and green glasses in the habitual wearers of green glasses (see Fig. 2); these terms allowed all models to fit better, but did not affect the overall pattern of results.

The models were fit simultaneously to the time series data in all 6 conditions (3 subject groups $\times$ 2 filter colors) using linear mixed effects modeling, an instantiation of the General Linear Model. For each subject a baseline, a rapid adaptation effect, and a slow adaptation effect were modeled as random factors. The other factors were modeled as fixed effects. Formally, let the data μ_i be a vector that concatenated all time series of unique yellow values, for every subject in every condition. The fixed effects of the reduced model can then be expressed as:

$$\mu_i = \beta_1 + \beta_2 b + (\beta_3 + \beta_4 g) t_{i,fast} + (\beta_5 + \beta_6 g) t_{i,slow}$$

where μ_i is the time series data, $t_{i,fast}$ and $t_{i,slow}$ are linear trend indicator variables for the fast and slow adaptation over time in the bilinear model (see below). β_1 is the modeled global baseline unique yellow, β_2 is the shift in baseline for the red and green groups, and the indicator variable b is -1 for the habitual-red group, 1 for the habitual-green group, and 0 for the control group. β_3 and β_5 model fast and slow adaptation, respectively. β_4 , β_6 , and the indicator variable g (1 when green filters were worn, 0 otherwise) model the increase in adaptation effects for green filters over red ones. To fit the model we inverted the sign of the net fast and slow adaptation for green filters (where adaptation's effects were to decrease unique yellow) but not red filters (where its effects were positive).

The basic model contained two additional terms, β_7 and β_8 , which modeled changes in fast and slow adaptation for habitually worn colors, as controlled by the indicator variable h , which was 1 for habitual red wearers and red glasses, habitual green wearers and green glasses and 0 otherwise:

$$\mu_i = \beta_1 + \beta_2 b + (\beta_3 + \beta_4 g + \beta_7 h) t_{i,fast} + (\beta_5 + \beta_6 g + \beta_8 h) t_{i,slow}$$

The extended model contained two more terms, β_9 and β_{10} , which modeled changes in fast and slow adaptation for habitual wearers, regardless of color, as controlled by the indicator variable p , which was 1 for both habitual red and habitual green wearers and 0 for control subjects:

$$\mu_i = \beta_1 + \beta_2 p + (\beta_3 + \beta_4 g + \beta_7 h + \beta_9 p) t_{i,fast} + (\beta_5 + \beta_6 g + \beta_8 h + \beta_{10} p) t_{i,slow}$$

To minimize parameters, donning and removing filters were modeled as producing equivalent effects in opposite directions. For example unique yellow shifted towards greenish when greenish filters were put on, and shifted in the opposite reddish direction when the filters were taken off, and all models assumed these shifts were equal in magnitude. Accordingly, $t_{i,fast}$, which indicated

when in the time series the linear fast adaptation component was present, was set to 0 for the first time point and 1 for the remaining ones while the filters were on, and 1 for the first timepoint with filters off, and 0 for the remaining points in the filters-off time series. This modeled one linear trend from timepoint $1-2$ (e.g. increasing) for donning filters, and its equal and opposite trend for removal (e.g. decreasing). $t_{i,slow}$ provided the linear trend for the slow component, and was $\{0,0:9\}$ for the timepoints when the filters were on, and $\{9,0:0\}$ for timepoints with filters off. This modeled the slow linear trend over timepoints $2-10$ when the filters were worn, and its equal and opposite when they were removed.

Random effects were modeled in a standard way; each subject was allowed a random intercept (baseline unique yellow value) and slope (over time; both fast and slow adaptation) as samples from normal distributions whose means, variances, and covariances were estimated by the linear mixed effects modeling procedure.

2.7. Statistical inferences

To formally test for the statistical reliability of our results we used three procedures within the LME framework. First, we conducted nested models tests, which comprised analyses of variance between the nested models. These determined which of two models fit the data best, given their differing number of free parameters. Second, we examined the t value associated with each parameter in the basic model, which we compared to a Z distribution given that the number of degrees of freedom of the full model was quite high (~ 700). Third, we conducted linear contrasts between parameters of the model, which again were compared to the Z distribution.

3. Results

Participants judged unique yellow at 5 s intervals during 1 -min runs following the placement or removal of their colored filters (Fig. 1). Unique yellow estimates were relatively stable. The last three points of the “filters off” runs, where adaptation had generally stabilized, had a mean standard deviation of less than 1 nm, averaged across filters and participants.

Unique yellow changed dramatically as participants adapted to the donning or removal of colored filters. Fig. 2 (upper) plots estimated unique yellow as a function of time following placement and removal of reddish (longer-wave length) and greenish (shorter-wavelength) filters, averaged from the nine control participants. The reddish filters shifted unique yellow to longer wavelengths, closer to colors that appear reddish under neutral conditions, as expected from a scaling process that normalizes the image (see above). Greenish filters, as expected, shifted colors in the opposite direction. These effects were strong even at the first measured time-point, indicating that much of adaptation was very rapid, even in control participants. A slower and smaller change in unique yellow continued over the course of the trial. These two phases of adaptation are consistent with measurements of its time course made in past work (Rinner & Gegenfurtner, 2000). When participants removed their filters, unique yellow shifted in the opposite direction, and this time course again had both rapid and slow components.

Fig. 2 (lower) plots the data for habitual wearers of red and green filters, who adapted more rapidly and strongly than controls. Note that the habitual red wearers using their red filters and the habitual green wearers using their green filters both showed “L”-shaped curves with large rapid and minimal slow adaptation. This pattern was evident both when the filters were donned and

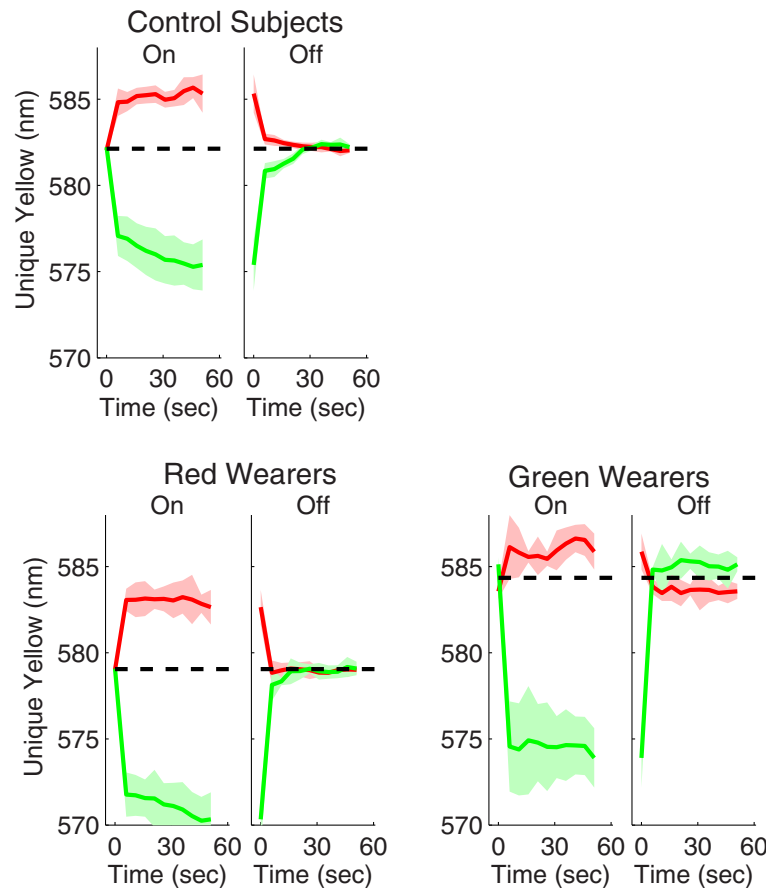


Fig. 2. Results. Unique yellow estimates as a function of time for reddish filters (red lines) and greenish filters (green lines) in three subject groups. Left panels show unique yellow after donning the filters, and right panels show it after removing the filters. The dotted lines show baseline unique yellow, and shaded regions indicate $\pm$ one standard error of the mean. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

when they were removed. In contrast, the control subjects showed smaller rapid and greater slow adaptation for both colors of filters.

To estimate the statistical reliability of this pattern, we fit bilinear models to the time series of unique yellow settings using linear mixed effects model fitting. We call the models bilinear because they estimated rapid adaptation as the slope of the first two points of the time series, and estimated slow adaptation as the slope of the remaining time points. The *reduced* model contained terms for these slopes along with parameters that allowed this adaptation to be larger for green than red filters in general, an effect evident in Fig. 2. The *basic* model added two parameters that allowed rapid and slow adaptation to differ only for the habitual filter colors of habitual wearers. The *extended* model added two parameters to allow adaptation to be greater for habitual wearers overall, regardless of filter color. The models are formally described in Methods, above. They essentially implemented a repeated measures analysis of variance while allowing full modeling of the time courses.

Fig. 3 plots average data along with model fits. To allow data to be averaged across filter colors, estimated baselines were subtracted and the signs of the time series for green filters were inverted. Habitual color refers to data averaged from red filters for red habitual wearers and green filters for green wearers. Nonhabitual color refers to data averaged for the other filters for habitual wearers.

The reduced model fit an identical adaptation timecourse to each condition, effectively serving as a null hypothesis against which we tested our hypothesis that habitual wearing of filters affected adaptation. As can be seen, despite capturing the overall

trends of adaptation well, the reduced model produced an especially poor fit for habitual wearers' habitually worn filters.

The basic model added parameters that allowed adaptation in such cases to differ, and its fit falls substantially closer to the data. The basic model accounted for 99% of the variance in the mean data plotted in Fig. 3, while the reduced model accounted for 92%, and this difference was highly reliable (nested models test, chi-square = 70.091, $p < 0.0001$).

The better fit of the basic model indicated that adaptation was greater for habitual wearers when wearing their habitual color. The model contained a parameter that explicitly modeled the increase in fast adaptation for habitual colors, and the boost was estimated to be 2.4 nm, a parameter value that was reliably greater than 0 ($t = 8.4$, $p < 0.0001$). The model contained another parameter that modeled the increase or decrease in slow adaptation for habitual colors of habitual wearers, which was estimated to be a decrease of 0.75 nm, a value reliably less than 0 ($t = 2.0$, $p < 0.05$). A planned contrast indicated that total adaptation (fast + slow) was also greater for habitually worn colors in habitual wearers than other conditions ($t = 3.1$, $p < 0.002$). Note that all tests were two-tailed, but not corrected for multiple comparisons.

Fig. 3 also shows a small trend for habitual wearers to adapt more rapidly in general, as indicated by increased adaptation to their non-habitual color compared to controls. This trend was statistically unreliable, however. The extended model contained all the parameters of the basic model, but added two that allowed habitual wearers to differ in rapid and slow adaptation for both kinds of filters tested. While the extended model fit the data a little better than the basic model (Fig. 3, dotted gray lines, 99.5% of

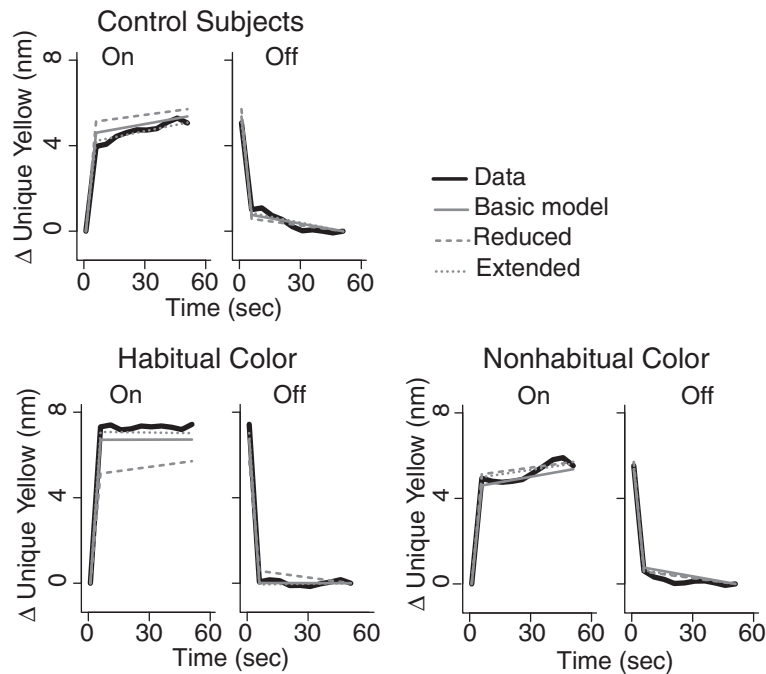


Fig. 3. Grand average time series data and model fits. Data from green and red filters were averaged by subtracting baseline unique yellow values and inverting the sign of the data from green filters. The upper panel plots results from control subjects. The bottom two panels show results from habitual wearers separately for their habitually worn filters (i.e. red filters for red wearers and green filters for green wearers; left) and the other filter tested (i.e. green filters for red wearers and red filters for green wearers). Details of the three models are described in the text.

variance explained), it did not do so more than expected given its increase in number of parameters, which is the null effect in the nested model test (chi-square = 0.73, $p < 0.5$).

As also can be seen in Fig. 2, the baseline value of unique yellow for red and green filter-wearers also differed from that of controls. The models also accounted for baselines (see Methods) and this unexpected trend was reliable ($t = 2.3$, $p < 0.03$). The baseline shifts are in the opposite direction of the shift produced by the filter-wearers' habitually worn color, and possible accounts for them will be discussed below. Finally, Fig. 2 also shows a trend for more complex interactions; specifically, the red and green wearers showed different amounts of adaptation relative to controls for their non-habitual colors. Our data, with only 4 and 5 habitual wearers in each color group, did not contain sufficient power to investigate this trend.

4. Discussion

Habitual wearers of colored spectacles showed larger and more rapid effects of adaptation to the color changes those filters produce than did control participants. The amplitude of relatively rapid adaptation was reliably larger in habitual wearers, while the amplitude of slower adaptation was smaller. Spectacles wearers of all types report anecdotally that adjusting when they put their lenses on, or take them off, becomes easier over time. Our results suggest that this is indeed the case for wearers of colored lenses.

Habitual wearers alternate many times a day between two different visual environments, the natural one, and the filtered one. Adaptation presumably places the visual system in a more optimal state for functioning in each environment. For example, for changes in the color of illumination, whose effects are similar to those produced by the filters here, adaptation helps colored surfaces retain their appearance despite large shifts in the light they reflect to the eye (e.g. Brainard & Radonjic, 2014; Foster, 2011). Our results suggest that experience allows the visual system to

increase the efficiency with which it alternates between adapted states, presumably gaining their benefits more rapidly.

Our “rapid” adaptation measurements pooled data over the first ~10 s after the filter changed. This is because our procedure that estimated unique yellow combined data from three temporally adjacent staircases. Limiting the estimation procedure to a single staircase allowed us to estimate effects ~1 s after subjects donned or removed their filters. Results of such analyses were qualitatively similar to those shown above (i.e. habitual wearers showed larger effects) but were noisier. Careful prior measurements of the time course of color adaptation have shown the existence of a near instantaneous “color contrast” process, a second very rapid process that occurs in the first second of adaptation, as well as a slower process that extends over many seconds (Rinner & Gegenfurtner, 2000). Our “rapid” effects are likely dominated by the first two of these, as they are generally larger than the slower effects. Our “slow” effects should tap only the slower adaptation process.

Three prior studies have documented long-term adaptation to colored environments for exposures lasting between 7 and 21 days using unique yellow judgments (Belmore & Shevell, 2008, 2011; Neitz, Carroll, Yamauchi, Neitz, & Williams, 2002). All three used unique yellow judgments, and adapting to reddish or greenish environments shifted unique yellow by 2–5 nm in the same direction as did wearing those colored filters in our experiment. Some subjects in these experiments wore colored filters; others were in a room lit with colored lights, or had experience on colored computer displays. However, all participants were tested only immediately before each day's experience with the colored environment, following prolonged exposure to the uncolored environment. Because of the single testing session, it is unclear whether participants learned to shift between two adaptive states or whether they simply remained in one state that was affected by the filter wearing. Additionally, even if the subjects' visual systems learned to switch between two adaptive states, corresponding to the environment with and without filters, it is not clear which state would have been adopted during testing. In these studies, the test was

preceded by dark adaptation and presented on a dark background, which effectively eliminated cues as to which environment was present. Other studies of long-term adaptation to colored environments similarly show large effects, but do not address whether the visual system can learn to switch between states (Delahunt, Webster, Ma, & Werner, 2002; Delahunt, Webster, Ma, & Werner, 2004; Eisner & Enoch, 1982; Werner, Delahunt, Ma, & Webster, 2003; Willmann et al., 2010).

A recent study measured effects of 5 days of wearing colored filters and found no change in adaptation speed or magnitude (Tregillus, Werner, & Webster, 2016). However, adaptation was first measured after 30 minutes of filter wearing, by which time the effects observed here may no longer have been evident. Alternatively, it is possible that greater than 5 days experience is needed to produce changes in adaptation.

Our habitual wearers showed a trend towards baseline values – that is unique yellow values after adapting relatively completely to the unfiltered environment – that were shifted in the opposite direction from the effects of wearing their filters. One admittedly speculative cause of the baseline effects is the presence of some homeostatic process; specifically, if wearing the filters caused the gain of some neural population to increase relative to some “neutral” point, then to maintain a fixed overall level of gain, it may be set lower than neutral when the filters were not worn.

While we attribute our results to subjects' experience with filters, the lenses were prescribed to aid with an underlying condition, visual stress. It is therefore possible in principle that our results were due simply to the condition. It is unlikely, however, that visual stress is associated with stronger color adaptation generally, as indicated by the failure of the extended model, which contained parameters to capture such effects, to significantly improve the fit to our data. In addition, one of our subjects was tested longitudinally, both before and after 6 months of wearing green filters (Fig. 4). The results show the same trends as our across group comparison: Filter wearing increased rapid and decreased slow adaptation for the habitually worn color (green, though for this subject small changes may also be present for the non-prescribed color).

Adaptation to mean color change has effects at multiple levels of the visual hierarchy. Some effects may arise in the first few synapses in the retina, and some may arise in retinal output layers, where signals from the different cone classes are combined (for reviews, see Hood, 1998; Rieke & Rudd, 2009). Color adaptation likely affects cortical stages of color processing as well (Rinner & Gegenfurtner, 2000). These possibilities are not mutually exclusive, and it will be of great interest to determine which can be modified by experience.

How did experience with the filters lead to changes in the speed and strength of adaptation? Modern theories propose that adaptation is controlled by an inference process in which the visual system first uses its input to infer the nature of the environment, and then adjusts its function accordingly (Grzywacz & de Juan, 2003; Kording, Tenenbaum, & Shadmehr, 2007; Wark et al., 2009). Within this framework, experience with the filters may have had several possible effects, which break down along the components of a Bayesian optimal decision process. The visual system may have learned that filtered scenes are simply more likely in general (i.e. they have higher prior probability). It may also have learned to more efficiently extract evidence that the scenes are filtered (giving them a higher likelihood). A third possibility is that the visual system learned that one filtered scene is likely to be followed by similar ones for a long time (i.e. it is costly to not adapt). These possibilities are not mutually exclusive, and future work could determine which account for the changes in adaptation seen here.

Rapid re-adaptation to prescriptions is unlikely to be unique for color. A number of studies have documented faster re-adaptation to prisms that rotate or displace the visual field, but most of this adaptation is sensorimotor rather than strictly visual (Redding, Rossetti, & Wallace, 2005), and habitual wearing of spectacles may not produce such rapid sensorimotor re-adaptation (Schot, Brenner, Sousa, & Smeets, 2012). Prior work is more suggestive for adaptation to astigmatism. Normal observers can adapt to wearing cylindrical lenses (that produce an astigmatism), showing a reduction in perceptual distortions over a 4 h session (Yehezkel et al., 2010). A subset of participants in this study was re-adapted a second day, and appeared to return quickly to near their previous adapted state. However, interparticipant variability made the rapid re-adaptation unclear statistically (though greater adaptation by the end of the second session was reliable).

Uncorrected astigmatic subjects also show adaptation to their uncorrected state, where the anisotropic blur produced by their astigmatism appears isotropic (Sawides et al., 2010). However, it is not clear whether long-term wearing of spectacles alters this effect (Vinas et al., 2012), and no study has examined if adaptation to astigmatism arises rapidly when spectacles are removed and then reapplied. Our results suggest that such rapid re-adaptation is in fact likely to occur.

Adapting to a new prescription is an important determinant in whether it is worn, and some patients even experience difficulties adapting to a correct prescription (Hrynychak, 2006). It is possible that individuals differ in their ability to learn to re-adapt rapidly to the donning and removal of spectacles. Identifying such

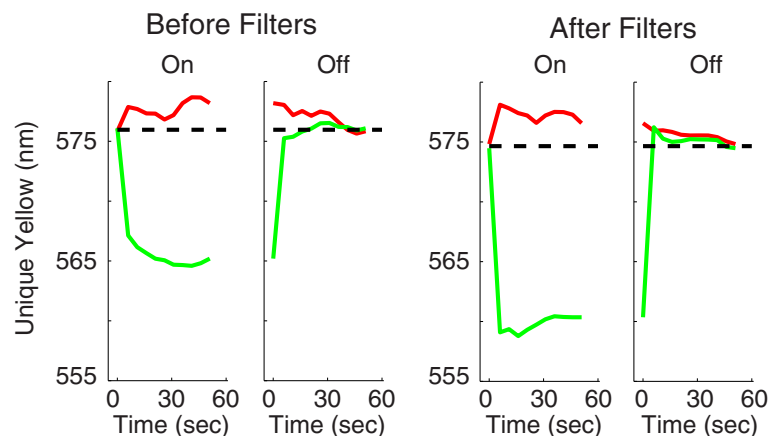


Fig. 4. Unique yellow for a single subject before being prescribed green filters and about 6 months after wearing the filters approximately 6 h daily. Plotting conventions are as in Fig. 2.

individuals, and intervening to improve their adaptability, could aid the management of optical correction in patients.

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