

Adjusting to a sudden “aging” of the lens

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Color perception is known to remain largely stable across the lifespan despite the pronounced changes in sensitivity from factors such as the progressive brunescence of the lens. However, the mechanisms and timescales controlling these compensatory adjustments are still poorly understood. In a series of experiments, we tracked adaptation in observers after introducing a sudden change in lens density by having observers wear glasses with yellow filters that approximated the average spectral transmittance of a 70-year-old lens. Individuals were young adults and wore the glasses for 5 days for 8 h per day while engaged in their normal activities. Achromatic settings were measured on a CRT before and after each daily exposure with the lenses on and off, and were preceded by 5 min of dark adaptation to control for short-term chromatic adaptation. During each day, there was a large shift in the white settings consistent with a partial compensation for the added lens density. However, there was little to no evidence of an afterimage at the end of each daily session, and participants' perceptual nulls were roughly aligned with the nulls for short-term chromatic adaptation, suggesting a rapid renormalization when the lenses were removed. The long-term drift was also extinguished by brief exposure to a white adapting field. The results point to distinct timescales and potentially distinct mechanisms compensating for changes in the chromatic sensitivity of the observer. © 2016 Optical Society of America

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1. INTRODUCTION

The crystalline lens of the human eye selectively absorbs UV and short-wavelength light, and this absorption increases steadily with age [1]. As a result, the light spectrum reaching the retina is continuously changing as we age. For example, an infant's lens may transmit 25 times more light at 400 nm than the lens of an average 70-year-old [2]. If there were no adjustment of neural responses, then the dramatic losses of short-wavelength sensitivity would strongly affect color appearance, reducing the “bluish” content of the light and thus biasing the spectrum to appear yellower [3]. However, color judgments and achromatic settings are instead remarkably stable throughout our lifetimes [4–6]. In particular, young and old observers choose very similar physical spectra when selecting the stimulus that appears white to them, even though the spectra of the retinal stimuli on which they base these judgments are markedly different. Such findings point to mechanisms of color constancy that strongly compensate for age-related changes in lens pigment density (and other age-related optical and neural changes) [6,7], as well as adjusting more generally to changes in the observer or the environment [8]. However, the basis for the compensation remains poorly understood.

One simple mechanism that can adjust to most of the effects of a spectral bias is adaptation in the photoreceptors. If the sensitivity of each cone class decreases as the light it receives increases (von Kries adaptation), then this will effectively renormalize the cone responses for the current average, maintaining the perception of gray. Calibration for differences in macular pigment density, which introduces spatial changes in sensitivity to short wavelengths between the fovea and nearby periphery, includes compensation acting as early as the receptors [9]. However, this scaling alone cannot correct for all spectra, and color appearance remains more similar for differences in lens or macular pigment than predicted by receptor changes alone, implicating additional processes beyond the receptors [10–13].

The adjustments could also occur over many timescales. Chromatic adaptation can very rapidly adjust to changes in the stimulus [14–16]. However, the stabilities of color percepts between old and young observers, or between the fovea and nearby periphery, persist after observers are dark-adapted to remove adaptation to the immediate stimulus context, and thus include calibrations with a longer time constant than conventional short-term adaptation [6,9]. Moreover, because the

brunescence of the lens occurs very gradually, the mechanisms of compensation might themselves adjust very slowly, and there are theoretical advantages for tying the rate of adaptation to the rate of stimulus change (e.g., so that slow but persistent changes are tracked by adjustments that build up and decay slowly) [17]. The natural environment can also vary slowly in its color properties, for example, as the seasons cycle [18], and recent evidence suggests that color vision exhibits long-term adaptation tied to these seasonal changes [19]. Distinct forms of long-term chromatic adaptation have been experimentally induced by exposing observers for extended periods to chromatically biased environments or to artificially colored lenses [20,21]. For example, extended periods of exposure to a red-biased stimulus can lead to shifts in the wavelength that appears unique yellow, and these aftereffects can last for days. When these long-term aftereffects are assessed in the presence of a short-term chromatic adapting stimulus, the effects may be additive [22].

In a previous study, Delahunt *et al.* [23] examined compensation for an aging lens by measuring the changes in color appearance following cataract surgery. The patients ranged in age from 63 to 84 years and had nuclear sclerotic cataracts. Following replacement of the lens with an intraocular lens, achromatic settings took months to return to near their presurgery settings. These slow drifts are distinct from the short-term normalization that also occurs when subjects are exposed to an adapting field, or when cataract patients are adapted to an external stimulus [24]. Delahunt *et al.* isolated the long-term component by measuring the white settings while observers were dark-adapted, thus removing the adaptation to the immediate “extrinsic” light environment in order to reveal the underlying “intrinsic” white balance of the observer. Their results suggest that there is substantial plasticity in the color coding of the senescent visual system and that this includes processes that normalize color appearance over both short and very long timescales.

In the present study, our aim was to extend the experiments of Delahunt *et al.* [23] by testing complementary conditions, in which the lens pigment density was suddenly increased rather than decreased, and in younger rather than older adults. To do this, observers wore glasses with yellow lenses that approximated the lens transmittance of an older observer. Thus our experiments introduce a sudden rather than gradual “aging” of the lens, and we sought to measure the properties and time course of the adjustments to the change. The cataract study tracked these changes over weeks and months but could only test the patients at a small number of widely spaced intervals. Our aim was also to examine more short-term adaptations, over periods of hours or days, and the extent to which these might recalibrate color percepts.

2. METHODS

A. Participants

Observers included author KT and 11 additional college students (18 to 35 years of age) at the University of Nevada, Reno. All had normal color vision, as assessed by the Cambridge Colour Test [25], and normal or corrected-to-normal visual acuity. Different observers were tested in different subsets of experiments. None had been exposed to the lenses prior to this study. Each observer participated with informed consent, and

all procedures followed protocols approved by the university’s Institutional Review Board.

B. Stimuli

Stimuli were presented on a SONY 20Se monitor using a Cambridge Research Systems VSG board, allowing for a high color-resolution display. The monitor was calibrated using a Photo Research PR 655 spectroradiometer, with gun outputs linearized through look-up tables. Probe stimuli were uniform 2-deg fields of 25.42 cd/m² presented on a black background, and were presented for 250 ms at 1.5 s intervals. In experiments involving adaptation, the adapting stimuli were 4 deg fields, displayed first for 1 min, then at every interstimulus interval for 1.5 s in order to top up the adaptation. Observers viewed the display binocularly at a distance of 114 cm in an otherwise dark room.

C. Lenses

Adapting lenses were commercially available high-definition night vision glasses made by Idea Village. Black baffling was added to the frames to exclude light from the periphery. The lens transmittance was measured by placing the lens in front of the spectroradiometer and recording the light from an equal-energy white light produced by an Agile Light Source (Gooch and Housego). Figure 1 shows that the transmittance was similar to the lens of a 70-year-old at shorter wavelengths.

D. Procedure

For most experiments, observers wore the lenses for 8 h per day for 5 consecutive days. The lenses were worn during daylight hours, and the participants engaged in their normal activities. Testing was done on each day at different periods, including immediately before or after the glasses were first worn or removed or at intervals during the day.

All settings involved determination of the observer’s white point under different states of adaptation and with the lenses either on or off. Most settings were collected using a staircase that varied the chromaticity of the probe along the axis extending along a “blue–yellow” line defined by the gun coordinates passing through a nominal white point of Illuminant E with or without the lenses. On each trial observers reported whether the probe appeared “too blue” or “too yellow,” with the achromatic setting determined by the mean of the last six of eight reversals. As noted below, for some conditions the staircase procedure was replaced with a method of adjustment in order to allow more rapid estimates. In each case the observer repeated the settings six times, and each white setting reported is an

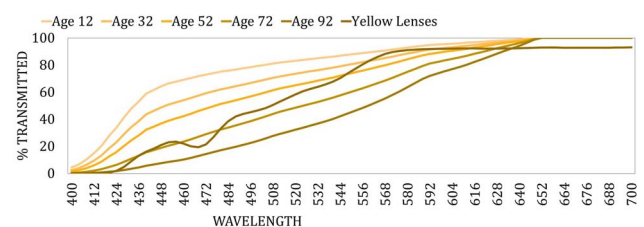


Fig. 1. Measured transmittance of the lenses worn by observers compared to estimates of the average transmittance of the crystalline lens for observers of different ages (from [1]).

average of these settings. The repeated settings typically required 10 min or more to complete, and no trend was observed across repetitions (suggesting that the adaptation state remained stable at least over this time). Moreover, except where noted, all settings were preceded by 5 min of dark adaptation in order to extinguish short-term adaptation to the immediately recent context.

Results are presented using a modified version of the MacLeod–Boynton chromaticity diagram [26], scaled so that the origin corresponds to a nominal white point of Illuminant C and so that sensitivity is roughly equated along the LM and S axes [27]:

$$LM = (L_{mb} - .6568) * 2754,$$

$$S = (S_{mb} - .01825) * 4099.$$

Within this space the bluish–yellowish axis of the stimuli falls approximately along the negative diagonal.

3. RESULTS

A. Color Shifts Introduced by the Lens

Figure 2 illustrates the color biases when observers first put on the lenses. The filled star marks the yellow chromaticity of the nominal white stimulus after filtering through the lens. Triangles show the value that observers selected when viewing the isolated test patch in a dark room when the glasses were first introduced. These are strongly shifted toward blue chromaticities to cancel the yellow from the lens. However, if the same settings are instead made in a normally lit room, there is almost no shift in the achromatic settings. This effect has been known since Monge, who observed that viewing the world through a colored filter has much less effect on color appearance than the spectral filtering alone would predict, and it illustrates the profound constancy that occurs immediately and is afforded by the spatial context [28]. Thus when wearing the lenses in their daily activities, much of the spectral shift was already

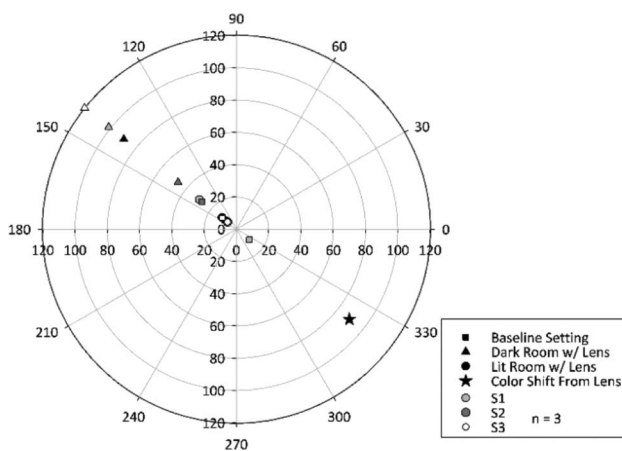


Fig. 2. Achromatic settings with lenses on or off, prior to adaptation to the lenses. Points plot the chromaticities of the white settings for the test stimulus in the dark context without (squares) or with (triangles) glasses; circles show the settings with glasses and room lights on. Star shows the chromaticity of the monitor white point through the glasses (filled). Black symbols represent the means across three observers; gray to white symbols represent individual observers.

discounted by the spatial contrast effects, and similarly should be discounted in observers who differ in the density of their natural lens pigment.

B. Adaptation to the Lenses

In the remaining experiments, we restricted the settings to dark contexts in order to measure the underlying renormalization of the white point. Achromatic settings were collected at the beginning and end of each 8 h interval, both with and without the yellow lenses. Note again that prior to the settings, observers were first dark-adapted for a period of 5 min. Thus the settings in this case represent the underlying white balance remaining after the immediate adapting context was extinguished [23].

Figure 3 summarizes the settings for six observers and averaged across the 5 days. There were large individual differences in the magnitude of the color settings. However, for all observers, wearing the lenses produced a large shift toward yellow in appearance that was reduced by ~50% on average by the end of the day. This represents substantial discounting of the lens bias during the course of the day, namely, so that the stimulus required to appear achromatic needed less short-wave radiance.

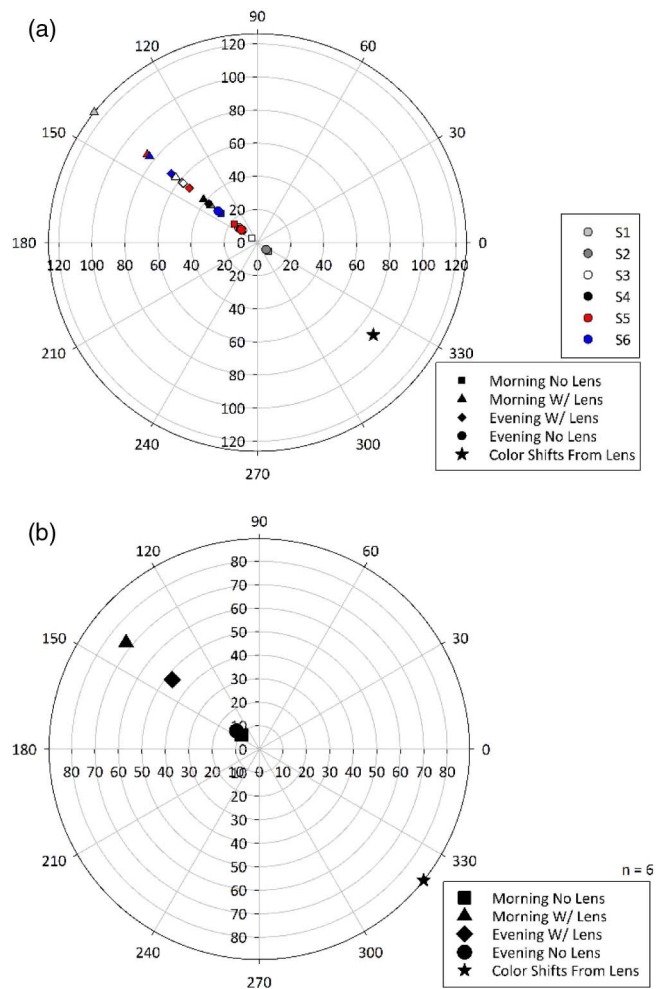


Fig. 3. Achromatic settings at the beginning and end of each day and before or after removing the lenses. Settings are averaged across the 5 days. (a) Individual settings for each observers. (b) Settings averaged across all six observers.

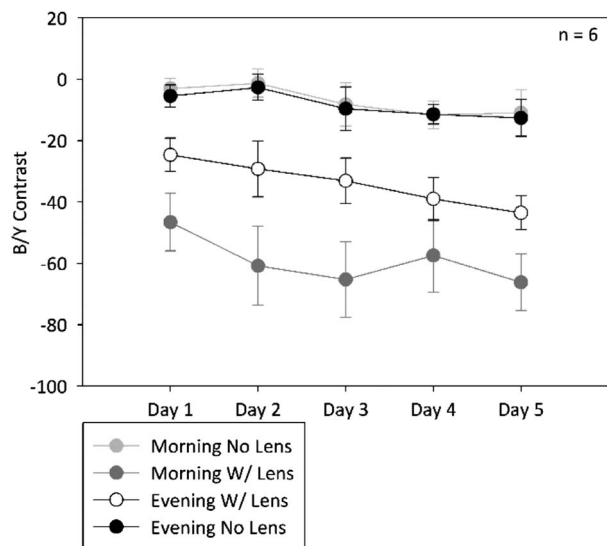


Fig. 4. White settings with or without the lenses at the beginning and end of each day, averaged across observers.

Surprisingly, however, when the glasses were removed the settings returned to very close to the morning baseline. That is, the sensitivity bias resulting from adaptation to the glasses did not induce an expected “bluish” aftereffect.

This pattern is further illustrated in Fig. 4, which plots the settings as distances or “contrasts” along the blue–yellow testing axis, with negative values corresponding to the blue direction. In this case the settings are averaged across the observers to also show the effects on each of the 5 days. Again there is a consistent and substantial discounting of the lens filtering by the end of each day, with no evidence of an aftereffect when the lens was removed. Moreover, there was no evidence for a buildup of the adaptation across successive days. In fact, the figure suggests a trend toward weaker adaptation as the days progressed, though this trend was not significant [$F(4, 25) = .383$, $p = .819$]. The results thus suggest that significant compensation occurs within each day but did not transfer across days or lead to a prolonged aftereffect at the end of the day.

C. Adaptation during the Course of Single Days

To further assess the time course of the adjustments, we performed a second series of measurements with a different subset of observers, this time sampling the achromatic settings at 2 h intervals. Observers again wore the glasses for a total of 8 h while engaged in their daily activities, and measurements were again preceded by 5 min of dark adaptation and measured in a dark room.

Figures 5 and 6 show the settings for four observers averaged across the 5 test days or for each day averaged across observers, respectively. There were again large individual differences in the achromatic settings and the strength of the adaptation. For comparison, the settings for each observer have therefore been normalized relative to their individual baseline level (morning, before wearing the lenses), such that a value of 1 corresponds to no change in the baseline while a value of 0 represents complete compensation. Much of the adjustment in the dark-adapted

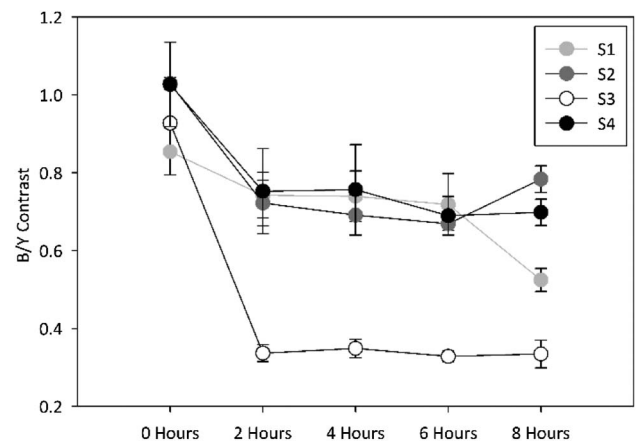


Fig. 5. Shifts in white settings within each day (relative to the morning setting without lenses). Individual plots show the settings for different observers averaged across the 5 test days.

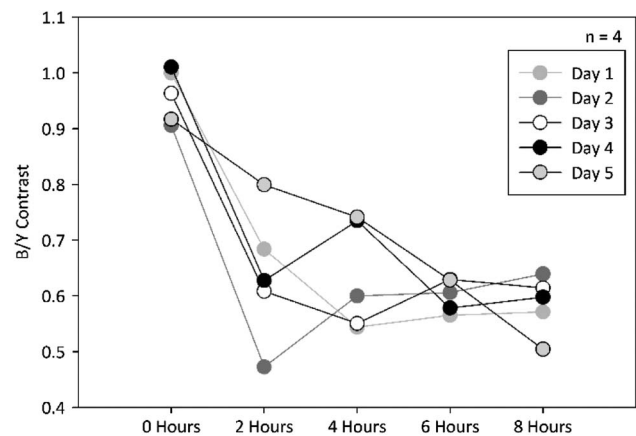


Fig. 6. Same settings as Fig. 5, but averaged across observers to show the buildup of adaptation within each of the 5 days.

white points occurs within the first 2 h. Further, as before, there is no evident trend for the adaptation to build up across successive days.

D. Renormalization of the White Point and Short-Term Chromatic Adaptation

If the slow daily drifts in the achromatic settings reflect peripheral changes in chromatic sensitivity, then there should be corresponding drifts in the null points for simple chromatic adaptation. That is, what appears white to the observer at the end of the day should also be the chromaticity that does not produce a short-term color afterimage when observers view that chromaticity. Alternatively, if the drifts reflect changes in criterion rather than sensitivity—or if the sensitivity changes arise after sites of short-term chromatic adaptation—there should be a dissociation between the observer’s subjective null and their short-term adaptation null. This comparison was previously used by Webster and Leonard [9] to show that the long-term normalization for differences in macular pigment density

occurs at or before early retinal sites of conventional chromatic adaptation.

To assess this for the current context, observers again adapted by wearing the lenses for the full day and made achromatic settings with or without the lenses. However, in this case, these settings were immediately followed by brief adaptation to adapting fields chosen to bracket and include their dark-adapted white points. Specifically, observers first dark-adapted for 5 min and then made six settings. These settings were used to define a set of five blue–yellow adapting chromaticities that ranged from -40 to $+40$ in contrast increments of 20 and were centered on the dark-adapted settings. Observers adapted to each level shown in a 4-deg field for 60 s, and then adjusted the chromaticity of the 2-deg test field until it again appeared achromatic, with top-up to the adapting chromaticity between each test pulse. Because of the prolonged testing, we also modified the experiment so that a method of adjustment was used to set the white point during each adapting condition, with six settings taken before moving immediately to the next adapting condition. The adaptation sequence varied as (1: dark adapt; 2: adapt to the dark-adapted white setting [0 contrast]; to -20 ; $+20$; $+40$; -40).

Figures 7 and 8 illustrate the resulting settings for three observers. In these plots the dashed lines show the contrast of the stimulus that appeared achromatic when dark-adapted, while the symbols plot the settings in the presence of each bracketing adapting level. The neutral point for the short-term adaptation was estimated by linear fits to the adapted settings to estimate the level that intercepts the dark-adapted white point. This defines the null for the chromatic adaptation—that is, the stimulus level that did not bias the observer’s dark-adapted white point. These “sensitivity nulls” deviate somewhat from the subjective white points, but in general strongly covary with the dark-adapted “perceptual nulls.” This suggests that a large part of the longer-term renormalization to the lens reflects actual changes in chromatic sensitivity that occurs at or before the sites controlling conventional short-term chromatic adaptation. In turn, this implies an early retinal locus for at least part of the adjustment.

E. Interactions between Long-Term and Short-Term Adaptation

In the preceding experiment we selected the adapting fields so that they were at or near the level the observer perceived as

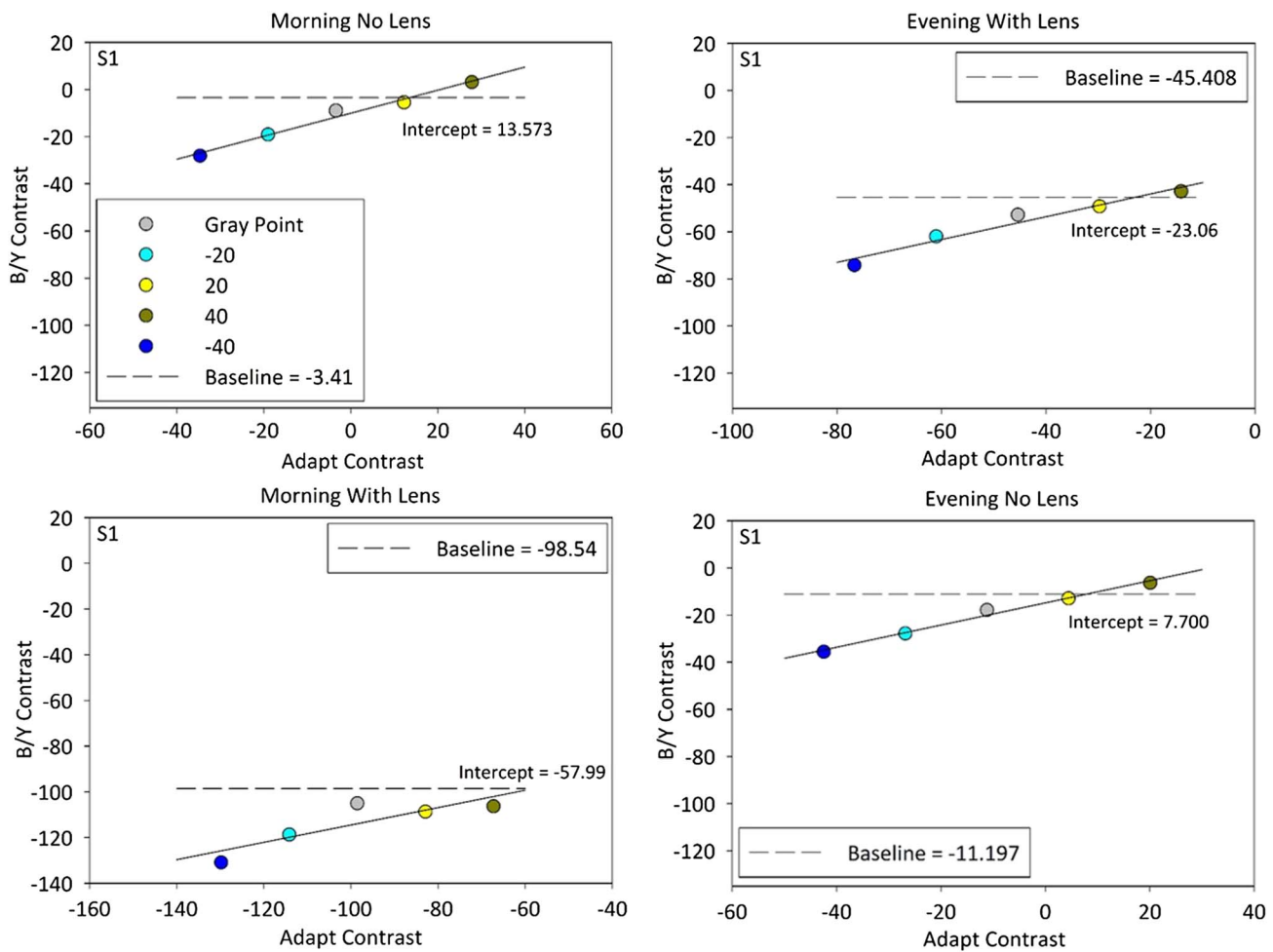


Fig. 7. Dark-adapted achromatic setting (dashed line) and white settings in the presence of different adapting levels (contrast along the blue/yellow axis). Panels show settings with or without the glasses on for one observer.

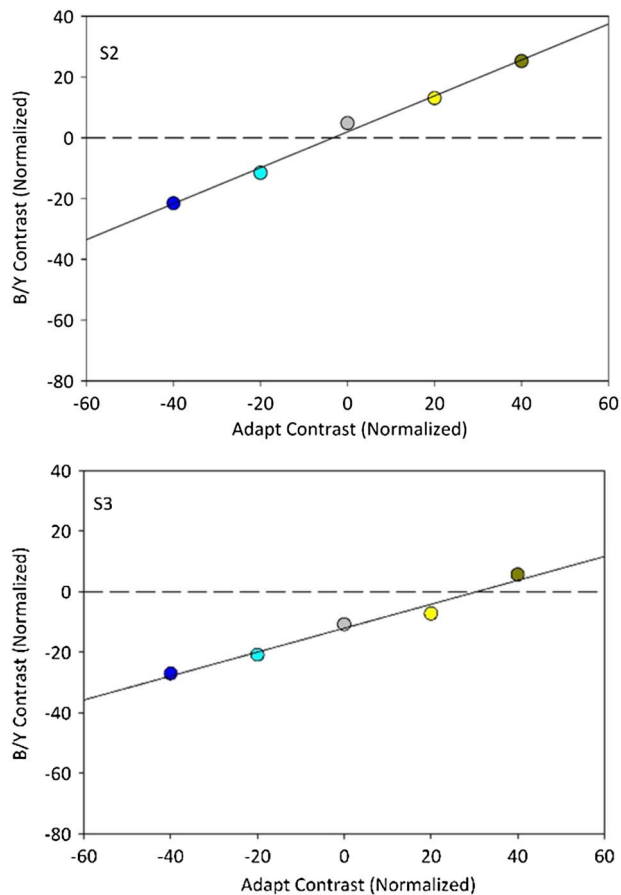


Fig. 8. Short-term adaptation settings for two additional observers, plotted relative to their dark-adapted settings at the end of the day, with lenses on.

white, in order to assess correspondences between the null points for each task. In the final experiment we instead tested for interactions between long- and short-term adaptation by briefly adapting observers to a strongly biased stimulus. This condition followed from several previous studies that have tested for distinct adaptation effects at different timescales by testing for “spontaneous recovery” [29]. In this paradigm, a long-term aftereffect is briefly extinguished by exposure to an opposing adapting stimulus. Recovery of the original aftereffect when the counteradaptor is removed indicates that two different mechanisms with different timescales contribute to the aftereffects. This pattern has been found for a wide variety of sensory and motor aftereffects [30–34].

In our case we measured the white settings after wearing the lenses for 8 h and then de-adapted observers by briefly (1 min) exposing them to the original nominal white stimulus on the monitor (i.e., a stimulus with the chromaticity of Illuminant C). The observers continued to wear the lenses throughout, and the nominal white appeared yellowish to them because they were not completely adapted to the lenses. Note this is different from most previous studies of spontaneous recovery because the brief adaptation was to a stronger stimulus (one that should look too yellow) rather than the opposite (blue) stimulus. This was done in part because strong blue adapting

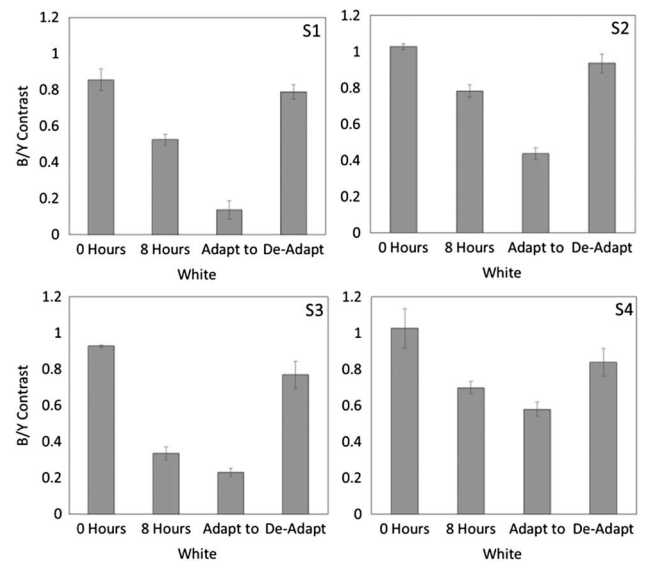


Fig. 9. Adaptation settings for four observers averaged across their six settings. Bars show the mean dark-adapted settings with the glasses on at the beginning (0 h) or end (8 h) of the day, the settings while adapted to the Illuminant E chromaticity on the screen (adapt to white), and then the settings after 5 min of readaptation to dark (de-adapt). Error bars represent the standard error of the means.

stimuli could not be readily achieved because the required blue chromaticities were too strongly filtered by the lenses.

Figure 9 plots the settings for four observers. For each there is a significant drift in the dark-adapted setting during the course of the day, again replicating the partial longer-term normalization ($0 > 8$ hours, $p = .004$). Subsequent brief exposure to the “yellow” adapting field increased the adaptation ($8 > \text{adapt}$, $p = .02$). However, after a further 5-min period of dark adaptation the settings surprisingly return to near the morning levels (0 vs. de-adapt, NS), and are weaker than the initial evening settings (de-adapt > 8 hours, $p = .04$). Thus rather than showing recovery to the long-term adapt level, the de-adapting stimulus appeared to extinguish the long-term effect.

4. DISCUSSION

The visual system undergoes profound optical and neural changes across the lifespan, and thus requires continuous recalibration in order to maintain the stability of perception [7,35]. The fact that many aspects of perception remain constant is thus a testament to the integrity of compensatory processes themselves in the face of visual aging [36], and basic mechanisms of color and form adaptation may be largely robust to age [37,38]. Here we examined mechanisms of adaptation that might be engaged to compensate for age-related changes in the density of the human lens. Our results expand on previous studies to suggest that this compensation may include a variety of mechanisms operating over different timescales.

Delahunt *et al.* [23] found that normalization of achromatic settings reflected extremely slow drifts occurring over a period of months. The present study was restricted to much briefer timescales but points to multiple adjustments within these

intervals. In particular, our study suggests at least three distinct processes adjusting to a change in spectral sensitivity within moments after it occurs. This includes a pronounced anchoring effect from simultaneous contrast [39,40], which acts to discount the spectral shift almost immediately, and potentially two forms of adaptation that operate over the course of minutes or hours. Both appear to operate at much shorter timescales than the sluggish renormalization observed in cataract patients, and thus suggest the possibility of at least three stages of adaptation.

The nature of the slower adjustment we found during the course of the day remains enigmatic. On the one hand, the changes behaved like a simple yet slow change in chromatic sensitivity. Consistent with this, we found that the drifts in the achromatic percepts were accompanied by drifts in the null points for short-term chromatic adaptation (Figs. 7 and 8). Yet on the other hand, these surprisingly did not lead to an aftereffect when the lenses were removed (Figs. 3 and 4). Moreover, when we introduced brief adaptation to a different stimulus, this acted to largely cancel the longer-term drift, returning the achromatic percepts to near their baseline settings (Fig. 9). This interaction suggests that the two processes are distinct, but in a way that has not conventionally been observed in studies of spontaneous recovery [29,32]. In particular, there was no evidence of a rebound to the longer-term adapted state. Moreover, the brief adapting stimulus we used might have been expected to augment rather than counteract the long-term drift [22], since it involved a stronger (yellow) rather than countering (blue) adapting stimulus; yet the effect was instead to extinguish the longer-term effect. These properties raise the possibility that the drifts in the dark-adapted settings during the course of each day were too labile to reflect conventional forms of chromatic adaptation, and in this regard instead behaved more like criterion than sensitivity changes. Yet regardless of their bases, our results again point to multiple distinct mechanisms contributing to stabilizing color appearance in the face of changes in the observer.

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