

# Individual and age-related variation in chromatic contrast adaptation

Institute for Mind & Biology, University of Chicago,  
Chicago, IL, USA

**Sarah L. Elliott**

Department of Ophthalmology & Vision Science, University of California, Davis, Sacramento, CA, USA



**John S. Werner**

Department of Ophthalmology & Vision Science, University of California, Davis, Sacramento, CA, USA



**Michael A. Webster**

Department of Psychology, University of Nevada, Reno, Reno, NV, USA



Precortical color channels are tuned primarily to the LvsM (stimulation of L and M cones varied, but S cone stimulation held constant) or SvsLM (stimulation of S cones varied, but L and M cone stimulation held constant) cone-opponent (cardinal) axes, but appear elaborated in the cortex to form higher-order mechanisms tuned to both cardinal and intermediate directions. One source of evidence for these higher-order mechanisms has been the selectivity of color contrast adaptation for noncardinal directions, yet the degree of this selectivity has varied widely across the small sample of observers tested in previous studies. This study explored the possible bases for this variation, and in particular tested whether it reflected age-related changes in the distribution or tuning of color mechanisms. Observers included 15 younger (18–22 years of age) and 15 older individuals (66–82), who adapted to temporal modulations along one of four chromatic axes (two cardinal and two intermediate axes) and then matched the hue and contrast of test stimuli lying along eight different directions in the equiluminant plane. All observers exhibited aftereffects that were selective for both the cardinal and intermediate directions, although selectivity was weaker for the intermediate axes. The degree of selectivity increased with the magnitude of adaptation for all axes, and thus adaptation strength alone may account for much of the variance in selectivity among observers. Older observers showed a stronger magnitude of adaptation thus, surprisingly, more conspicuous evidence for higher-order mechanisms. For both age groups the aftereffects were well predicted by response changes in chromatic channels with linear spectral sensitivities, and there was no evidence for weakened channel tuning with aging. The results suggest that higher-order mechanisms may become more exposed in observers or conditions in which the strength of adaptation is greater, and that both chromatic contrast adaptation and the cortical color coding it reflects remain largely intact in the aging visual system.

Keywords: human aging, contrast adaptation, color mechanisms

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## Introduction

Chromatic sensitivity shows age-related losses at several sites in the visual pathways. For example, when optical factors (Weale, 1988; Werner, 1982; Winn, Whitaker, Elliott, & Phillips, 1994) are taken into account, measures of detection (Hardy, Delahunt, Okajima, & Werner, 2005; Werner, Bieber, & Scheffrin, 2000) and discrimination (Scheffrin, Shinomori, & Werner, 1995; Shinomori, Scheffrin, & Werner, 2001) for chromatic stimuli reveal age-related functional losses at precortical sites. The sensitivity losses in the short (S), medium (M), and long (L) wavelength sensitive cone pathways (Werner et al., 2000; Wuerger,

Xiao, Fu, & Karatzas, 2010) are consistent with functional changes in the receptors themselves and/or in their post-receptoral pathways (Werner & Steele, 1988). Discrimination thresholds for targets varied along cone-specific (Knoblauch, Vital-Durand, & Barbur, 2001) or cone-opponent pathways (Scheffrin et al., 1995) reveal age-related increases consistent with a reduction in the ability of cones to capture quanta or changes in the level of neural noise (Scheffrin et al., 1995; Shinomori et al., 2001).

Yet despite these losses in detection and discrimination, the color appearance of suprathreshold chromatic stimuli shows relatively little change with age. Losses in contrast sensitivity for spatio-chromatic gratings (Har-

dy et al., 2005) disappear at suprathreshold levels (Delahunt, Hardy, Okajima, & Werner, 2005), paralleling the contrast constancy found for different spatial frequencies (Georgeson & Sullivan, 1975). Spectral unique hues (Scheffrin & Werner, 1990; Wuerger et al., 2010), the loci of achromatic points (Werner & Scheffrin, 1993), and the appearance of broadband surfaces (Scheffrin & Werner, 1993) similarly show little change in the elderly.

The stability of suprathreshold color vision across the life span demonstrates that the visual system can recalibrate color appearance to compensate for sensitivity changes resulting from optical screening or declines in the peripheral neural signals. This recalibration may include a number of distinct adjustments, such as changes in the relative weighting of the cones, the response gain of the cones, or the postreceptoral mechanisms. The adjustments may also operate over multiple timescales, from the rapid sensitivity changes underlying conventional chromatic adaptation (Fairchild & Lennie, 1992; Rinner & Gegenfurtner, 2000; Webster & Wilson, 2000), to longer-term adjustments when observers are exposed to a chromatically-biased environment (Belmore & Shevell, 2008; Neitz, Carroll, Yamouchi, Neitz, & Williams, 2002), or to changes in their own optics, for example after cataract surgery (Delahunt, Webster, Ma, and Werner, 2004).

Most studies of both changes and invariances of color vision with aging have focused on precortical mechanisms to examine cone-specific and early cone-opponent stages of color-coding. In addition, processes of chromatic adaptation in older adults, whether short- or long-term, have been examined only at sites preceding binocular combination (Delahunt et al., 2004; Delahunt et al., 2005). At least some of these long-term adjustments could arise as early as the photoreceptors (Webster & Leonard, 2008). The focus of this study was cortical color coding and its short-term adaptation at the level of the cortex, by measuring the changes in color appearance when observers are adapted to chromatic contrast (variations in color around a fixed mean chromaticity). Adapting to a field that is modulated in color over time induces large changes in the threshold for detecting colors and in the perceived contrast and hue angle of suprathreshold colors (Krauskopf, Williams, & Heeley, 1982; Webster & Mollon, 1994). This adaptation shows interocular transfer and pattern selectivity that is consistent with a cortical locus of the response changes (Webster, 1996). Moreover, while cells in the magnocellular pathway strongly adapt to luminance contrast, geniculate cells that convey chromatic information exhibit little contrast adaptation (Solomon, Peirce, Dhruv, & Lennie, 2004), while this chromatic contrast adaptation is clearly manifest in primary visual cortex (Engel & Furmanski, 2001; Tailby, Solomon, Dhruv, & Lennie, 2008).

Adaptation to chromatic contrast has provided an important tool for characterizing cortical color coding (Eskew, 2009; Webster, 1996). The losses in chromatic sensitivity following adaptation are strongest along the LvsM (stimulation of S cones varied, but L and M cone stimulation held constant) and SvsLM (stimulation of S cones varied, but L and M cone stimulation held constant) geniculate axes, and these aftereffects were the basis for defining the geniculate axes as the *cardinal directions* of color coding (Krauskopf et al., 1982). Subsequent work showed that this form of adaptation is also selective for multiple, intermediate directions and provided evidence for *higher-order* chromatic mechanisms, each tuned to a different direction in the volume of color-luminance space (Krauskopf, Williams, Mandler, & Brown, 1986; Webster & Mollon, 1991, 1994). These higher-order mechanisms have been revealed in a variety of psychophysical tasks suggesting that they are not a consequence of the adaptation alone (Eskew, 2009; Krauskopf, 1999). They are also evident in physiological measurements showing a broader range of chromatic tuning preferences in cortical cells compared to cells in the lateral geniculate nucleus (LGN) (Conway & Livingstone, 2006; Horwitz, Chichilnisky, & Albright, 2007; Johnson, Hawken, & Shapley, 2001; Lennie, Krauskopf, & Sclar, 1990; Wachtler, Sejnowski, & Albright, 2003). Thus these higher-order mechanisms appear to reflect a general and important transformation of the representation of color in the cortex. However, the degree to which these mechanisms emerge and impact color coding remains uncertain. For example, both observers and tasks vary widely in the extent to which they appear to recruit or depend on mechanisms tuned to noncardinal directions (Eskew, 2009). The present study explored some of the potential factors underlying this observer variation as measured by the task of color contrast adaptation with the specific goal of examining age-related differences in cortical color coding. Little is known about the integrity of higher-order color mechanisms with aging or whether the processes of chromatic contrast adaptation that have revealed them might themselves change with age. Age-related visual losses (e.g., in intracortical connectivity) that compromise cortical visual processing might differentially affect the selectivity or adaptability of higher-order color mechanisms compared to mechanisms with selectivity to the cardinal axes that is derived from earlier stages. In the spatial domain, there is evidence that aging may differentially compromise visual coding and adaptation in central compared to precortical sites of the visual system. Significant age-related changes in the processing of stimuli defined by second-order characteristics, such as stereopsis (Laframboise, De Guise, & Faubert, 2006), bilateral symmetry (Herbert, Overbury, Singh, & Faubert, 2002), motion defined by contrast (Habak & Faubert, 2000) or percent coherence (Billino, Bremmer,

& Gegenfurtner, 2008), and perceived shape defined by texture (Habak, Wilkinson, & Wilson, 2009) have been reported. Stimuli defined by second-order characteristics (Chubb & Sperling, 1988; Cavanagh & Mather, 1989) are thought to target cortical mechanisms separate from those underlying the initial processing of first-order stimuli (Baker & Mareschal, 2001).

Psychophysical adaptation experiments have also suggested that age-related changes may be stronger in higher-order visual mechanisms. One recent study measured bandwidths for degree of face rotation following adaptation to frontal or side views of a face (Wilson, Mei, Habak, & Wilkinson, 2011), a task specific to the ventral pathway. The aftereffects suggested age-related deficits in face view transformations consistent with a 1.7-fold increase in bandwidths for face orientation. An age-related increase in bandwidth for face selectivity is consistent with the age-related increase in fMRI adaptation and reduction in discrimination thresholds for distinct face-pairs (Goh, Suzuki, & Park, 2010). Single-unit recordings with aging primates further supports a physiological decrease in selectivity for many stimulus features, such as direction of motion (Liang et al., 2010; Schmolesky, Wang, Pu, & Leventhal, 2000) and orientation (Schmolesky et al., 2000). The increase in bandwidth across multiple stimulus dimensions, whether measured psychophysically or physiologically, is generally accompanied by an increase in neural noise, both of which may result from an age-related decrease in cortical inhibition (Leventhal, Wang, Pu, Zhou, & Ma, 2003; Schmolesky et al., 2000).

In sum, there is good reason to suspect that cortical mechanisms of color perception might also be compromised with age. To examine cortical color coding, the current study compared both the selectivity and strength of chromatic contrast adaptation in a group of younger and older observers. A large set of observers was tested because previous studies have revealed large individual differences in the selectivity of the aftereffects even in the small sample of observers tested (and intriguingly, these tended to show weaker selectivity in the *senior* authors) (Krauskopf et al., 1982; Webster & Mollon, 1994). As a result, it remains unclear what the general characteristics are for chromatic contrast adaptation, how much they might differ between color-normal observers, or whether they reliably change with age.

## Methods

### Observers

Fifteen younger (mean age 21, age range 18–22, seven male) and 15 older phakic observers (mean age

72.6, age range 66–82, eight male) participated. Observers were undergraduate students at the University of California, Davis (UCD) and/or were recruited from the UCD Eye Center through advertisements. All were tested monocularly using their preferred eye (i.e., the eye with superior visual acuity and health, or by individual preference). Refractive errors did not exceed  $\pm 4.5$  diopters (D) sphere or  $\pm 2.0$  D cylinder for any observer. Corrected Snellen acuity was equal to or better than 20/25 in the tested eye. The presence of abnormal ocular media and retinal disease were ruled out for each observer by conventional eye screening, including a slit lamp examination and ophthalmoscopy. Color fundus photographs of the macula and optic disk were evaluated by a retinal specialist. All participants had no more small drusen than is considered normal for their age and no abnormal vascular, retinal, choroidal, or optic nerve findings. All observers had intraocular pressure of  $< 21$  mm Hg, and all were normal trichromats based on testing with the Farnsworth D15 Color Vision Test, the Neitz anomaloscope, the HRR pseudoisochromatic plates, and the Cambridge Trivector Colour Test. Written informed consent was obtained following the Tenets of Helsinki and with approval of the Institutional Review Board of the University of California, Davis, School of Medicine.

### Apparatus and stimuli

Visual stimuli were generated on a ViSaGe Visual Stimulus Generator (Cambridge Research Systems, Rochester, England) and were presented on a 17-inch EIZO FlexScan T566 CRT. The frame rate was maintained at 100 Hz. Gamma correction was controlled through the ViSaGe software but luminance and chromaticity output were checked and monitored using a Minolta colorimeter (CS-100 Chroma Meter). Errors in the ViSaGe calibrations were corrected in the experimental software. The stimulus configuration included two uniform  $2^\circ$  fields centered  $0.25^\circ$  above and below a central fixation cross (Figure 1a). Narrow black borders ( $0.04^\circ$ ) delimited the fields from a background of the same average luminance ( $30 \text{ cd/m}^2$ ) and *gray* chromaticity of Illuminant C (CIE  $x, y = 0.310, 0.316$ ).

Colors presented within the fields were specified in a cone-opponent space (Derrington, Krauskopf, & Lennie, 1984; MacLeod & Boynton, 1979), with chromaticities defined by their angle ( $\sim$ hue) and contrast ( $\sim$ saturation) relative to the origin, defined as the zero contrast gray background. For a standard observer, hue angles of  $0$  and  $90^\circ$  (the cardinal axes) corresponded to an increase in L-cone excitation along the LvsM axis and an increase in S-cone excitation along the SvsLM axis, respectively (Figure 1b, CIE chromaticity

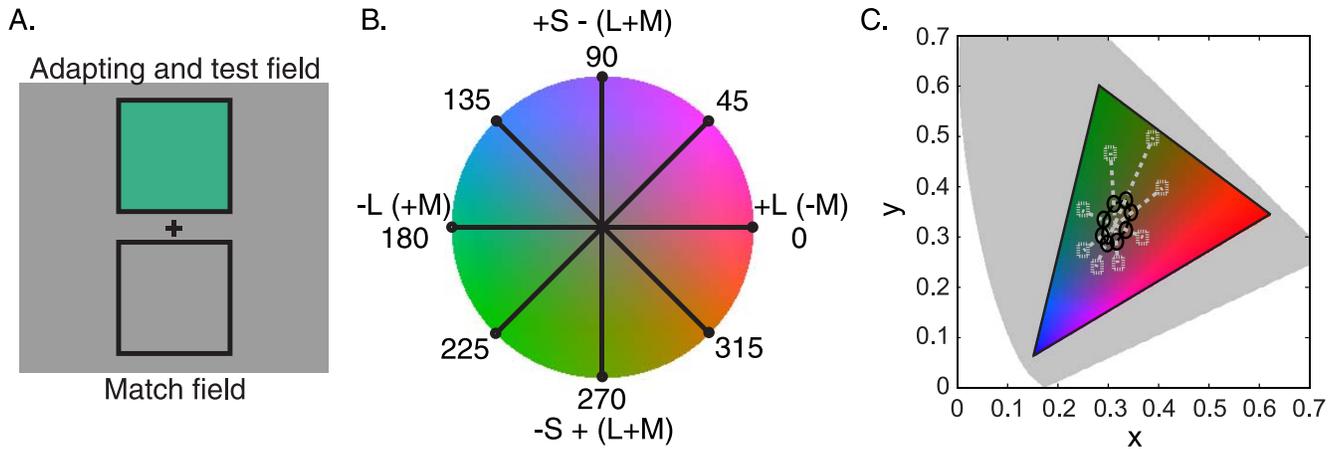


Figure 1. (a) Spatial arrangement for the asymmetric matching task (Webster & Mollon, 1994). Observers viewed modulation along one chromatic axis of the color space (b) in the 2° field above fixation. Test stimuli were presented in the same field and observers matched the perceived color by adjusting the contrast and hue of the matching stimulus presented in the neutral-adaptation field below fixation. (b) An equiluminant plane of a three-dimensional cone-opponent space. (c) The test (black symbols) and adaptation (white symbols) CIE chromaticity coordinates. The colored triangle illustrates colors within the CRT gamut.

coordinates shown in Figure 1c). Equiluminance was established for each observer using minimum motion photometry (Anstis & Cavanagh, 1983) with a 1 cpd grating varying along either the LvsM or SvsLM axis.

Contrasts along the LvsM and SvsLM axes were nominally scaled to equate the strength of contrast adaptation effects along the cardinal axes based on previous measures (Webster & Mollon, 1994, 1995). The resulting units correspond approximately to multiples of the contrast detection thresholds (though they were not directly based on threshold measurements) and were related to the  $r$ ,  $b$  coordinates of the MacLeod-Boynton chromaticity diagram according to the following equations:

$$\text{LvsM contrast} = (r_{mb} - 0.6568) \times 1,955$$

$$\text{SvsLM contrast} = (b_{mb} - 0.01825) \times 5,533$$

where 0.6568 and 0.01825 are the MacLeod-Boynton coordinates of Illuminant C and 1,955 and 5,533 are the contrast scaling constants for the LvsM and SvsLM axes, respectively.

## Procedure

Observers were seated in a dark room 186 cm from the CRT and their heads were stabilized with the use of a chin rest. An opaque eye patch was used to cover the nontested eye. Younger observers wore their habitual correction throughout the experiment. Older observers were refracted for the test distance by adding +0.50 D to their habitual distance correction. Observers were instructed to maintain fixation in the middle of the screen throughout the experimental procedure.

Aftereffects were measured using an asymmetric matching task under five adaptation conditions. The first corresponded to adaptation to the gray (zero-contrast) background. The remaining four involved adaptation to chromatic flicker along one of the cardinal axes (0–180 and 90–270°), or two intermediate axes (45–225 and 135–315°). Adapting stimuli were modulated sinusoidally at 2 Hz at a contrast spanning  $\pm 80$  units. The initial adaptation period was 120 s (or 30 s for the gray condition) and was presented in one of the two fields. The matching field remained gray during the adaptation. Following this, 1-s test pulses were shown in the same adapting field and interleaved with 4 s of re-adaptation. Test stimuli included eight equally spaced chromaticities (at intervals of 45°) with a fixed contrast of 30 units (Figure 1b). Observers used two pairs of buttons to match the contrast and hue to the concurrently presented test field. Hue and contrast changed by 1° and unit, respectively, for each button press.

During a single session, observers maintained adaptation to one axis and completed eight matching trials, one for each of the eight test stimuli. The chromaticity coordinates were randomized in the matching field prior to each match and the order of test chromaticities was randomized and blocked based on the axis of adaptation. In one daily session, observers completed one setting for each combination of test and adapting stimulus. The settings were repeated four times, requiring four visits to the lab (plus one visit for individual calibrations and a practice session). To control for retinal asymmetries, the location of the adaptation and test stimulus (top or bottom field) vs. the matching stimulus was counter-balanced each day. Daily sessions began with matches

following adaptation to the gray background and the order of the four adapting axes was randomized and blocked by day.

### Data analysis

Hue and contrast are unique perceptual dimensions and were adjusted independently by the observers during the asymmetric matching task. Therefore, hue (polar angle of the match) and contrast (radius of the match) matching values were analyzed separately. Unless otherwise stated, hue and contrast aftereffects were assessed with multiple repeated-measures analyses of variance (RMANOVA) with age group (young vs. old) as the between subject factor and axis of adaptation (0–180, 45–225, 90–270, or 135–315°) as the repeated measures factor. Each RMANOVA included two-way comparisons between the four axes of adaptation. All  $p$ -values for the comparisons are reported with a Bonferroni correction.

## Results

### Control experiments

Before turning to the adaptation effects, control experiments and analyses are presented to ensure that any individual or age-related differences in the adaptation could not be attributed simply to differences in color or contrast sensitivity or to differences in the ability to perform the color matching task. These included the following tests.

#### Contrast sensitivity for the different chromatic axes

To confirm that contrasts were perceptually equated for the younger and older observers (who could potentially differ in their relative sensitivity to the LvsM and SvsLM signals), all observers completed a contrast matching task (Switkes & Crognale, 1999). The contrast of a test color, defined by either pole of the LvsM axis, was compared to a fixed contrast of 30 units in a reference color corresponding to either pole of the SvsLM axis. The two stimuli were presented simultaneously in the two stimulus fields, with the location of the reference and test counterbalanced. A two-alternative forced-choice staircase was used to estimate the stimulus level at which the contrast (i.e., perceived saturation relative to the gray background) of the two different hues appeared equal. The mean chromatic contrast match for each observer across the four separately matched  $\pm$ LvsM and  $\pm$ SvsLM pairs is plotted in Figure 2. The mean for each observer was used to scale the contrast along the LvsM axis in the

experimental paradigm. The mean match for the younger and older age group was  $27 \pm 1.42$  units and  $27 \pm 1.12$  units, respectively, and thus did not significantly differ ( $F_{(1,28)} = 0.01$ , NS, confirmed across the four separately matched pairs). Therefore, any average age-related change in perceived contrast is not selective for a specific axis in the chromaticity space and any potential age-related errors in contrast scaling were not a major concern for the experimental task.

### Adaptation and individual differences in contrast sensitivity

As Figure 2 illustrates, there were consistent individual differences in the relative perceived strength of signals along the two cardinal axes. Two observers (who were not part of the main experiment) participated in a pilot experiment to examine how aftereffects might be influenced by errors in the scaling of the axes for individual observers. In this case both the relative and absolute scaling of the LvsM and SvsLM axes were varied over a wide range (e.g., such that the ratio of LvsM to SvsLM varied from 0.25 to 4.0). Changes in perceived contrast along both cardinal axes following adaptation to one of the axes was then assessed for stimuli defined by the new nominal contrasts. However, these large scaling changes had surprisingly little effect on the measured aftereffects, consistent with a largely multiplicative effect of the contrast adaptation. Thus the measured magnitude of the adaptation is relatively robust to errors in the scaling for the different observers (though scaling differences could still impact the effective direction of intermediate axes in the space, since these are defined by the relative signals along the two cardinal axes; Webster & Mollon, 1994).

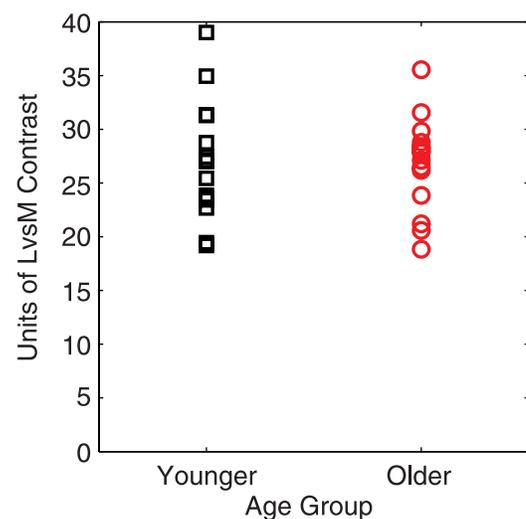


Figure 2. The mean chromatic contrast match for each younger and older observer across the four separately matched  $\pm$ LvsM and  $\pm$ SvsLM pairs.

### Age-related differences in the cardinal axis directions

A further potential factor that could impact the measured adaptation effects was that the stimulus directions that isolated the cardinal axes might differ between observers because of differences in their spectral sensitivities (Smithson, Sumner, & Mollon, 2003; Webster, Miyahara, Malkoc, & Raker, 2000). In particular, the MacLeod-Boynton color space used for defining the axes is based on a standard observer corresponding to the Smith and Pokorny cone fundamentals (Smith & Pokorny, 1975). These assume an ocular media density of a standard 32-year-old observer, and thus will underestimate the average lens pigment density of the older observers (Pokorny, Smith, & Lutze, 1987). To assess the impact of density differences on the cardinal axes, the lens model of Pokorny et al. (1987) and the energy spectrum of the CRT was used to estimate the predicted tilt in both the LvsM and SvsLM axes. Compared to the 32-year-old standard, where LvsM = 0–180° and SvsLM = 90–270°, axes defined for the younger observers were predicted to be shifted by –1 and –2, respectively, while the older were tilted by a maximum of +7 and +9°. While this could potentially alter the estimates of selectivity for the different adapting axes, it is in fact within the range of variation observed in empirical measurements of the cardinal axes (Webster et al., 2000), and thus is unlikely on its own to introduce substantial age-related differences in the measured adaptation effects. Consequently, the chromatic axes for all observers were based on the same standard observer (though, as noted in [Methods](#), equiluminance was determined empirically for each individual).

### Color matches under neutral adaptation

The final control was included as part of the main adaptation experiment and involved matching the test and comparison stimuli under neutral adaptation to the gray background. Note that for this condition the two stimuli were shown under the same adaptation state, and thus the settings should in theory correspond to a physical match. The settings therefore indicate how well the observers could perform the match. The results are shown in [Figure 3](#), where the symbols plot the mean matches made by each of the young (black squares) or old (red circles) observers. The matches in perceived color for all observers were within close range of the contrast and hue defining the eight equiluminant test stimuli. Only three younger observers showed a small but significant increase (by an average 2–5.5 units) in matched contrast from the test contrast (presumably reflecting a weak criterion bias in how they set the match), while the selected hue angles did not differ significantly from the test angle for any of the 30 observers. Thus all observers were good at discrimi-

nating small differences in the colors and could accurately perform the task.

The pattern of variability in these matches can potentially reveal a number of important features about the color mechanisms underlying the discriminations and were therefore explored in detail. In [Figure 3](#) the error bars show the standard deviation of the mean matches for each age group. To avoid clutter the bars have been displaced toward (old, red) or away (young, black) from the origin. Separate estimates of the variability were obtained for the mean hue angle (independent of contrast) or the contrast (independent of hue), and thus the bars are shown as crosses.

The individual differences suggest that observers were more sensitive to some dimensions of the stimulus than others. In particular, the variability between the observers follows a very similar pattern to the within-observer variations reported in a study of color contrast discrimination. Krauskopf and Gegenfurtner (1992) found that when observers were adapted to a neutral background, discriminating a suprathreshold color change in the background was generally worse when the stimulus was a change in contrast rather than hue. Thus the discrimination ellipses they measured were generally oriented along radii extending from the adapting to the test color (i.e., along the contrast axis). This is seen in the present data by the standard deviations in the settings, which tend to be larger along the radial contrast axis than the hue axis. This pattern is present both for test stimuli lying on and in between the cardinal axes, suggesting that discrimination depends on more than two chromatic mechanisms even under a fixed state of neutral adaptation. If discrimination were instead mediated only by the independent signals in the two cardinal mechanisms, then discrimination ellipses should instead remain oriented along one or the other cardinal axis and the contrast and hue error bars in [Figure 3](#) should approach equal values along the intermediate axes.

A number of comparisons were conducted to assess the relative variance in the settings for the young and old observers. These are summarized in [Table 1](#) (not corrected for multiple comparisons). For both age groups, individual differences were larger overall in contrast than in hue, though this selectivity was weaker for the older observers. Specifically, significantly greater variance in contrast than hue was found for each axis for younger observers, but only along two axes (90–270 and 135–315) for the older observers (comparisons one through eight). The variance of contrast matches did not differ for the younger and older age groups (nine). However, older observers were less consistent in their hue settings (10). Variability in the hue settings was also greater for both age groups along the intermediate compared to the cardinal axes (12 and 14), while also greater for contrast for the

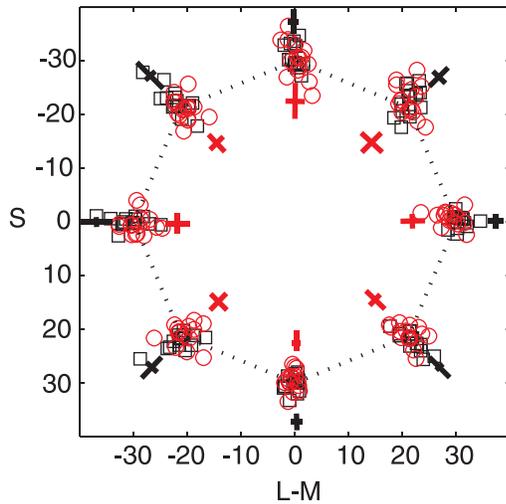


Figure 3. Mean matches plotted for individual young (black squares) or old (red circles) observers under neutral adaptation. The error bars show the standard deviation of these means for each age group (black and red for young and older, respectively), and are plotted as the Cartesian distances from the mean match along either the hue or contrast axis. To avoid clutter the bars have been displaced toward (old, red) or away (young, black) from the origin.

young but not the older group (11 and 13). Finally, both younger and older participants were more sensitive to the hue differences—but not the contrast differences—in the blue and yellow tests (135 and 315) when compared to the orthogonal reddish-greenish tests (45 and 225), even though these stimuli were composed of the same component signals along the cardinal axes (but combined in opposite phase) (15–18).

To summarize, matches under neutral adaptation suggest that (a) both age groups exhibit variability consistent with higher-order mechanisms; (b) the reduced evidence for these mechanisms in the older observers is reflected by a selective loss in sensitivity to hue differences in the stimuli; (c) for both age groups selectivity is greater for cardinal than intermediate directions, consistent with a bias or preferential representation along the cardinal axes; and (d) there is an asymmetry in color coding between the intermediate axes so that sensitivity is enhanced for detecting hue changes relative to the blue-yellow axis, an asymmetry reported in a number of other measures of color discrimination (Boynton, Nagy, & Eskew, 1986; Danilova & Mollon, *in press*; McDermott, Malkoc, Mulligan, & Webster, 2010). These features all parallel the properties of color discrimination as assessed in a single observer (Krauskopf & Gegenfurtner, 1992). Although older observers exhibited a selective reduction in sensitivity to hue differences, the similarity of matches under neutral adaptation for the two age groups also suggest that these properties of color coding are largely preserved in the older observers.

### Contrast adaptation

#### Selectivity for cardinal vs. noncardinal axes

The remaining sections focus on how the color matches were affected by adaptation to the different adapting axes, and whether these aftereffects differed between the two age groups. For the subjects as a whole, the basic aftereffects parallel previous reports in showing changes in color appearance that are selective

	Comparison	Variance: Group 1	Variance: Group 2	F	df	p
1	Contrast vs. hue 0–180; young	5.07	1.05	4.83	29	<0.00001
2	Contrast vs. hue 45–225; young	6.42	2.12	3.03	29	0.002
3	Contrast vs. hue 90–270; young	3.50	0.92	3.79	29	0.0003
4	Contrast vs. hue 135–315; young	8.78	0.83	10.5	29	<0.00001
5	Contrast vs. hue 0–180; old	4.75	2.82	1.68	29	NS (0.08)
6	Contrast vs. hue 45–225; old	5.27	5.48	0.96	29	NS (0.46)
7	Contrast vs. hue 90–270; old	7.12	1.85	3.84	29	0.0003
8	Contrast vs. hue 135–315; old	4.85	2.43	2.00	29	0.034
9	Young vs. old contrast	5.89	5.59	1.05	119	NS (0.39)
10	Young vs. old hue	1.26	3.29	0.41	119	<0.00001
11	Intermediate vs. cardinal – contrast young	7.51	4.22	1.78	59	0.014
12	Intermediate vs. cardinal – hue young	1.70	0.99	1.72	59	0.019
13	Intermediate vs. cardinal – contrast old	5.12	6.05	0.85	59	NS (0.26)
14	Intermediate vs. cardinal – hue old	4.03	2.61	1.54	59	0.049
15	45–225 vs. 135–315 hue; young	2.12	0.83	2.54	29	0.007
16	45–225 vs. 135–315 contrast; young	6.42	8.79	0.73	29	NS (0.20)
17	45–225 vs. 135–315 hue; old	5.48	2.42	2.26	29	0.016
18	45–225 vs. 135–315 hue; old	5.27	4.85	1.09	29	NS (0.41)

Table 1. Comparisons of the relative variance in mean neutral settings for the observers.

for each adapting axis (Webster & Mollon, 1991, 1994). Specifically, adaptation to each axis produced the largest changes in perceived contrast along the adapting axis and biased the perceived hue of test stimuli away from the adapting axis and toward the orthogonal axis (with no systematic change in hue along the adapting or orthogonal axis). This can be seen in Figure 4, which plots the mean matches to the test stimuli (top panel) and rotations in the perceived hue of the test stimuli (i.e., the difference in hue angle between the match and test stimulus; bottom panel) for the two age groups. The selective changes in perceived contrast and hue are consistent with adaptation in multiple, higher-order color mechanisms (Krauskopf et al., 1986; Webster & Mollon, 1991, 1994).

To characterize the aftereffects, ellipses were fit to each of the 120 data sets (30 observers  $\times$  4 adapting axes) by minimizing the sum of squared deviations between the observed and predicted values. For each fit, one axis of the ellipse was forced to align with the axis of the adaptation. The length of this axis was used as an estimate of the strength of the adaptation, while the aspect ratio (or ratio of lengths for this axis and the orthogonal axis) provided an estimate of the selectivity of the adaptation. Figure 4 (top panel) shows examples of these fitted ellipses and illustrates that they provided a close approximation to the observed matches.

Aspect ratios for the ellipse fits were  $< 1$  for all observers, with the exception of the 135–315° axis for

one observer (where it equaled 1.0). This indicates that adaptation was always selective for the specific adapting angle and is again consistent with multiple, higher-order color mechanisms (Krauskopf et al., 1986; Webster & Mollon, 1991, 1994). Figure 5 plots the aspect ratios (top panel) and adaptation (minor) axis values (bottom panel) of the fitted ellipses against each axis of adaptation for the 15 younger (black squares) and 15 older (red circles) observers. The values for each age group are displaced slightly from the axis of adaptation for ease of comparison between the two age groups. The ratios ( $F_{(3,84)} = 20.93, p < 0.001$ ) and minor axis ( $F_{(3,84)} = 5.64, p < 0.01$ ) values varied with the axis of adaptation. Aspect ratios were more biased for the cardinal compared to the intermediate axes for all but 3 observers, suggesting greater selectivity for the cardinal axes overall. This difference is illustrated in Figure 6a, which plots the mean aspect ratio of the cardinal axes against the mean aspect ratio of the intermediate axes for each observer. The greater selectivity for the cardinal axes was confirmed by two-way comparisons, revealing significant differences between each cardinal vs. each intermediate axis ( $p < 0.01$ ), but no mean difference in cardinal (0–180°) vs. orthogonal cardinal (90–270°) or intermediate (45–225°) vs. orthogonal intermediate (135–315°). Notably, two-way comparisons for the minor axis fits did, however, reveal a significant difference between the two intermediate axes ( $p < 0.01$ ), suggesting the strength of adaptation was higher for the 45–225 vs.

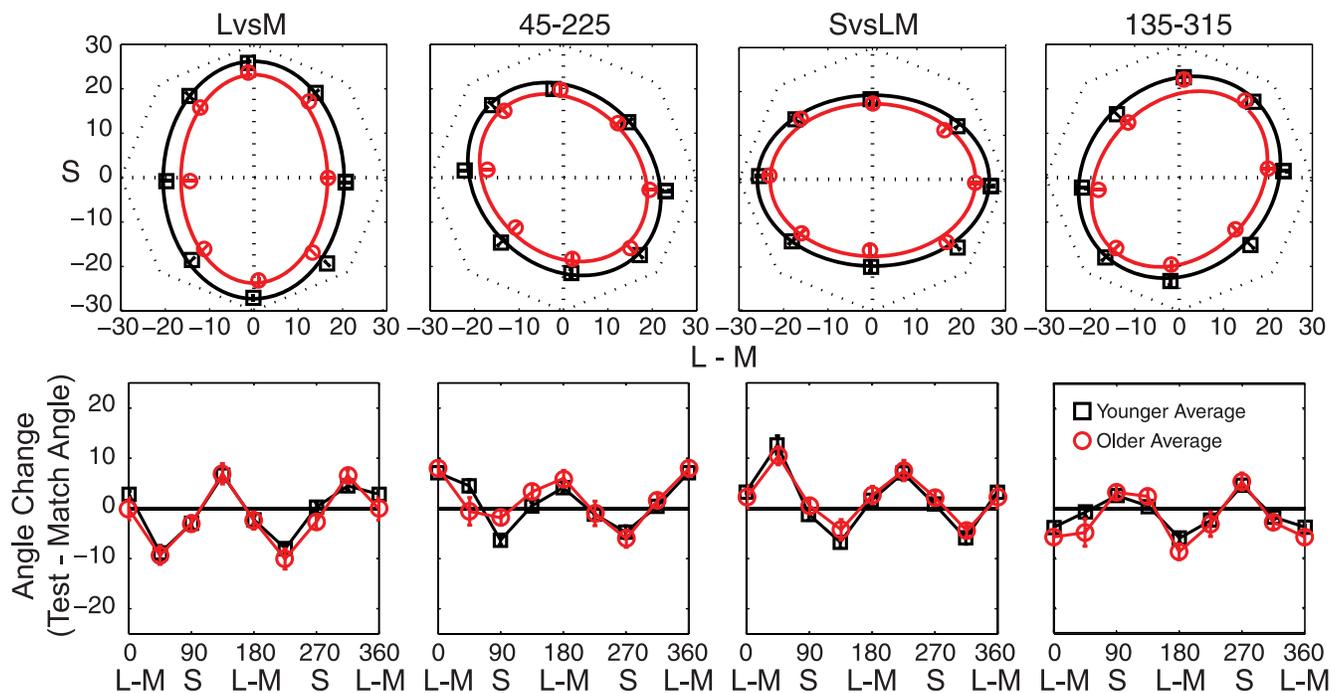


Figure 4. Mean color changes within the equiluminant plane (symbols) and the corresponding ellipse fits (solid lines) are plotted in the top panel for the two age groups. The shifts in perceived hue (test hue angle – matched hue angle) for the two age groups are plotted in the bottom panel. Each axis of adaptation is shown separately. Black and red symbols are for the younger and older age groups, respectively. Error bars are  $\pm 1$  SEM for contrast matches in the top panel, and for matched hue angle in the bottom panel.

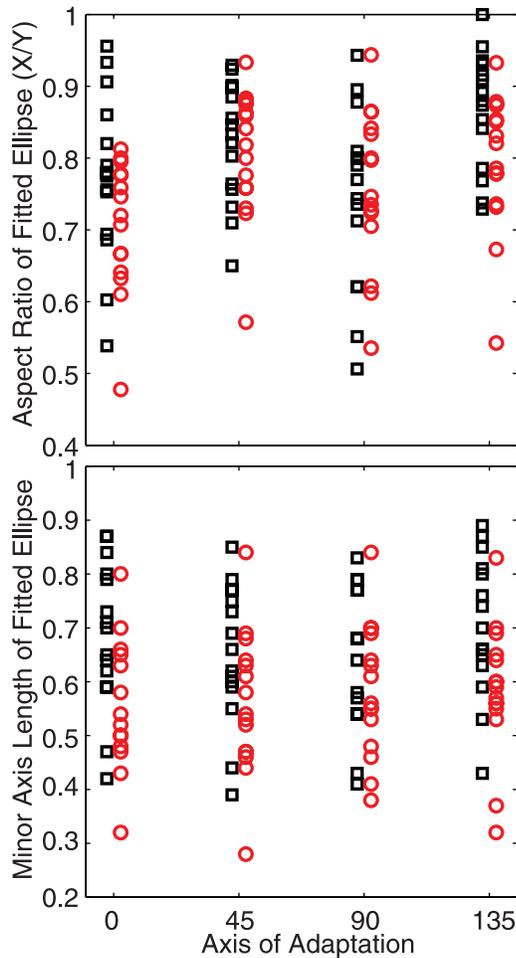


Figure 5. Black and red symbols denote younger and older observers, respectively. The top panel illustrates the aspect ratios of the fitted ellipses; the bottom panel illustrates the minor axis fits for each individual observer plotted as a function of the axis of adaptation. Black and red symbols are shifted slightly for clarity.

135–315° axis for both age groups. This difference mirrors the asymmetry noted above for matches under neutral adaptation.

In sum, the analyses indicate that (a) adaptation to each axis produced changes in contrast and hue that were selective for that axis, consistent with adaptation in multiple, higher-order color mechanisms (Webster & Mollon, 1991, 1994); (b) aftereffects (and ellipse fits) were more selective for the cardinal axes than the intermediate axes, once more suggesting a bias in the representation for the cardinal axes; and (c) there is an asymmetry in selectivity for the two intermediate axes. These points are in agreement with the findings under neutral adaptation.

### Individual differences in adaptation

There were large individual differences within each age group in both the magnitude and selectivity of the

color changes. For example, Figures 7 and 8 show the settings made by six representative observers (three younger and three older, upper and lower panel, respectively), chosen because they spanned a range from strong (OK & BK) to moderate (EC & JS) to weak (PB & SE) aftereffects. Figure 7 plots the actual matches to the test stimuli (solid lines are the individual ellipse fits) and Figure 8 plots the rotations in the perceived hue of the test stimuli (similar to Figure 4, bottom panel). Table 2 lists the aspect ratios and minor axis value for each example observer in Figure 7 as well as age group means (shown in Figure 4).

As Figure 5 illustrates, across all observers there was roughly a three-fold variation in the strength of the adaptation (as measured by the minor axis of the fitted ellipse) and a two-fold range in the selectivity (as measured by the aspect ratio). On the assumption of two chromatic channels tuned to the cardinal axes, adaptation to either cardinal axis should produce a loss in sensitivity restricted to that axis. That is, there should be a correlation between the area of the fitted ellipse and its aspect ratio for the two cardinal axes, which not surprisingly there was ( $r = 0.78$ ,  $p < 0.0001$ ). Under the assumption of *only* two chromatic channels, however, an unselective change along the intermediate axes is predicted since sensitivity should decrease by roughly the same magnitude within the two cardinal mechanisms. In this case, no correlation is expected between the size and shape of the ellipse. Yet instead, there was a strong correlation between area and aspect ratio for both the young ( $r = 0.79$ ,  $p < 0.0001$ ) and old ( $r = 0.78$ ,  $p < 0.0001$ ) age groups for the two intermediate axes. This relationship is shown in Figure 6b, where the aspect ratio is plotted as a function of the area of the ellipse for the two intermediate adapting axes. Specifically, the selectivity of adaptation was greater in observers who showed a stronger adaptation effect. In fact differences in adaptation magnitude alone could account for more than 60% of the variance ( $r^2$ ) in the selectivity for intermediate axes. These results thus suggest that the tendency to exhibit higher-order mechanisms could be largely predicted simply by how *adaptable* the observer is.

### Age-related differences

Despite the substantial individual variability within each age group, some clear age-related differences emerged. Perceived contrast was reduced to a greater degree for the older age group compared to the younger age group regardless of the axis of adaptation, as assessed by comparing the minor axes of the fitted ellipses ( $F_{(1,28)} = 5.20$ ,  $p < 0.05$ ). Thus the strength of adaptation was *greater* overall for older compared to younger observers, a difference that is evident in the

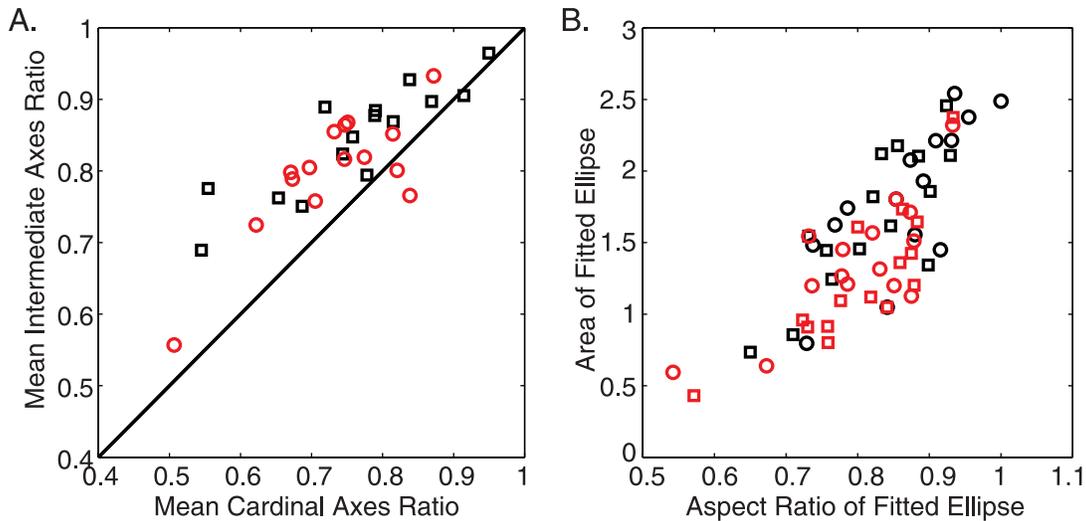


Figure 6. Black and red symbols denote younger and older observers, respectively. (a) The mean cardinal axes aspect ratio vs. the mean intermediate axes ratios for each individual observer. The solid black line is a line of unity. (b) The aspect ratio of the fitted ellipse vs. the area of the fitted ellipse for each individual observer for the 45–225° (squares) and 135–315° (circles) axes.

ellipses fitted to the mean data in Figure 4 (which are consistently smaller for the older age group).

In Figure 9, aspect ratios for the two cardinal axes (top panel) and the two intermediate axes (bottom panel) are plotted against each other. The preceding analysis predicts that older observers should have shown more selectivity than younger observers for the noncardinal adapting directions because they showed greater adaptation. An overall effect of age on the fitted aspect ratios did not reach significance ( $F_{(1,28)} = 1.24$ , NS). Yet mean aspect ratios were slightly lower for the older (mean = 0.80) than the younger (mean = 0.84) group, a difference that reached significance ( $t_{(58)} = 1.92$ ,  $p_{(\text{one-tailed})} = 0.03$ ) when the prediction of greater selectivity for the older age group was taken into account. There was also a trend for younger observers to be more selective for the 90–270° axis and older observers to be more selective for the 0–180° axis. This difference is consistent with a greater age-related reduction in contrast and larger hue shifts for the LvsM axis and was significant ( $p < 0.01$ , two-way interaction of 0–180 vs. 90–270° × age group). Note again that this is unlikely to be the result of contrast sensitivity differences to the two axes because these differences were not evident in the observer’s contrast matches, and such differences when they were actually introduced do not lead to corresponding biases in the pattern of aftereffects (as discussed above in the control experiments).

To summarize, older observers showed stronger adaptation. And perhaps because of this, as a group they also showed slightly more selectivity for the noncardinal adapting axes. These patterns were next confirmed in a further analysis based on modeling the set of putative channels underlying the adaptation effects.

#### Adaptation effects based on modeled channel distributions

While the fitted ellipses provided a convenient characterization of the adaptation effects, they were not tied to a specific model of color mechanisms and thus were silent about the characteristics of these mechanisms such as their selectivity or number. To explore these factors, each observer’s settings were also fit with a multiple-channel model of the color contrast adaptation similar to one developed by Webster and Mollon (1994). Details of the model are presented in their paper. Briefly, the model assumes adaptation in a population of chromatic channels whose preferred directions form two Gaussian distributions centered on the LvsM and SvsLM axes. The predicted contrast and hue correspond to the vector sum of the channel responses. The predicted responses are thus given by:

$$D(\Theta) = \left\{ \exp \left[ -1/2 \left( \frac{\Theta}{\sigma} \right)^2 \right] + \exp \left[ -1/2 \left( \frac{90 - \Theta}{\sigma} \right)^2 \right] \right\} \times \left[ (1 - m) \left( |\cos(\Theta - \varphi)|^\alpha \right) \right]$$

where the first two terms defined the distribution of channels as a function of angle in the chromatic plane ( $\Theta$ ), and the third term gives the adaptation within each mechanism as a function of its preferred chromatic axis ( $\varphi$ ) and the adapting axis ( $\Theta$ ). The model of Webster and Mollon thus had two free parameters:  $m$ , the sensitivity loss along the axis of adaptation assuming a

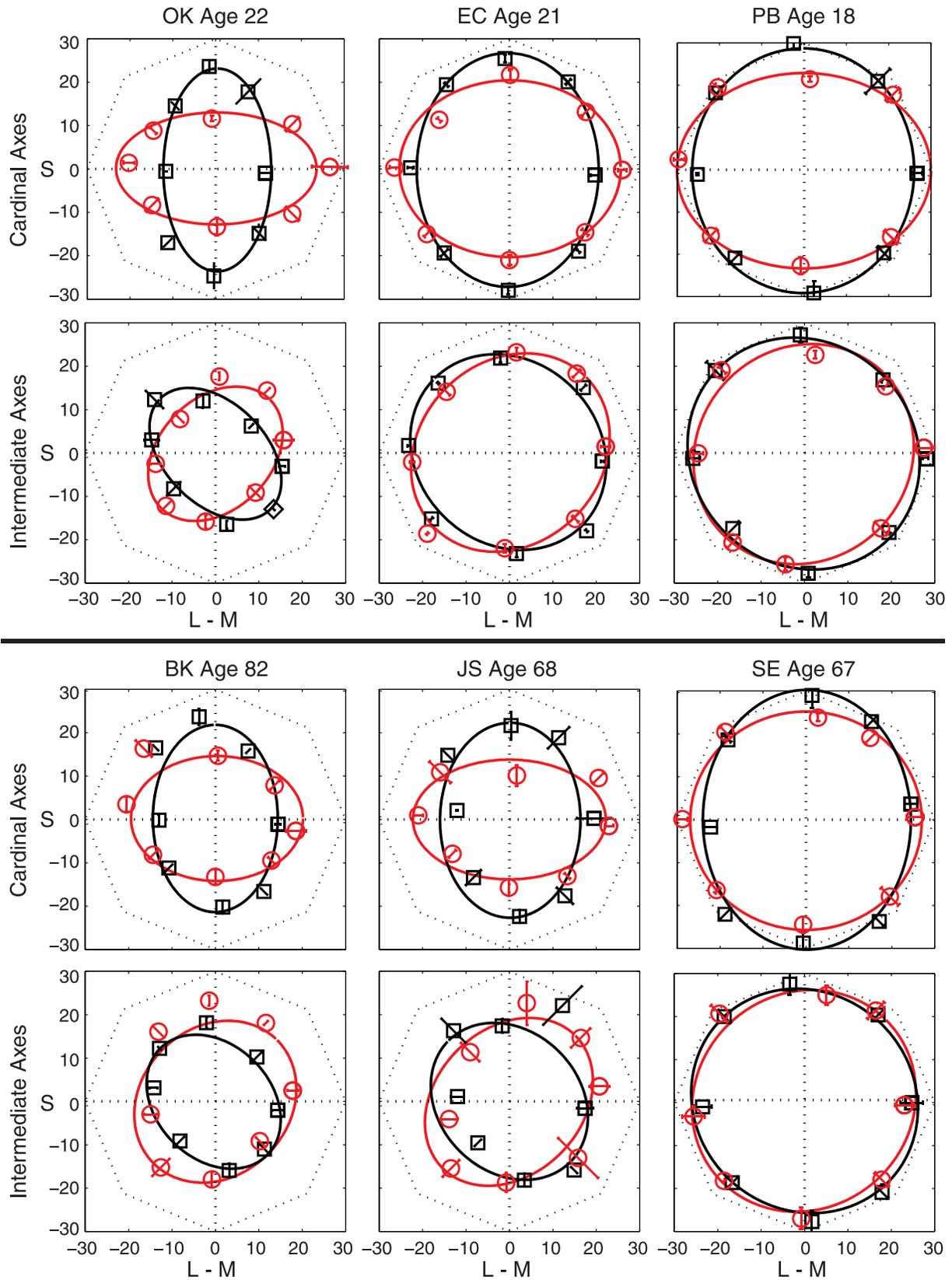


Figure 7. Color changes within the equiluminant plane for three younger (top panel) and three older (bottom panel) observers. The top row in each panel illustrates changes following adaptation to the LvsM (0–180°, black symbols) and SvsLM (90–270°, red symbols) axes. The bottom panel illustrates changes following adaptation to the 45–225° (black symbols) and 135–315° axes (red symbols). Solid lines denote the ellipse fit to each adaptation condition. The black dotted lines illustrate the cardinal axes and the contrast and hue angles of the eight test stimuli. Error bars are  $\pm 1$  SEM for contrast matches, only. Standard errors for hue matches are shown in [Figure 8](#).

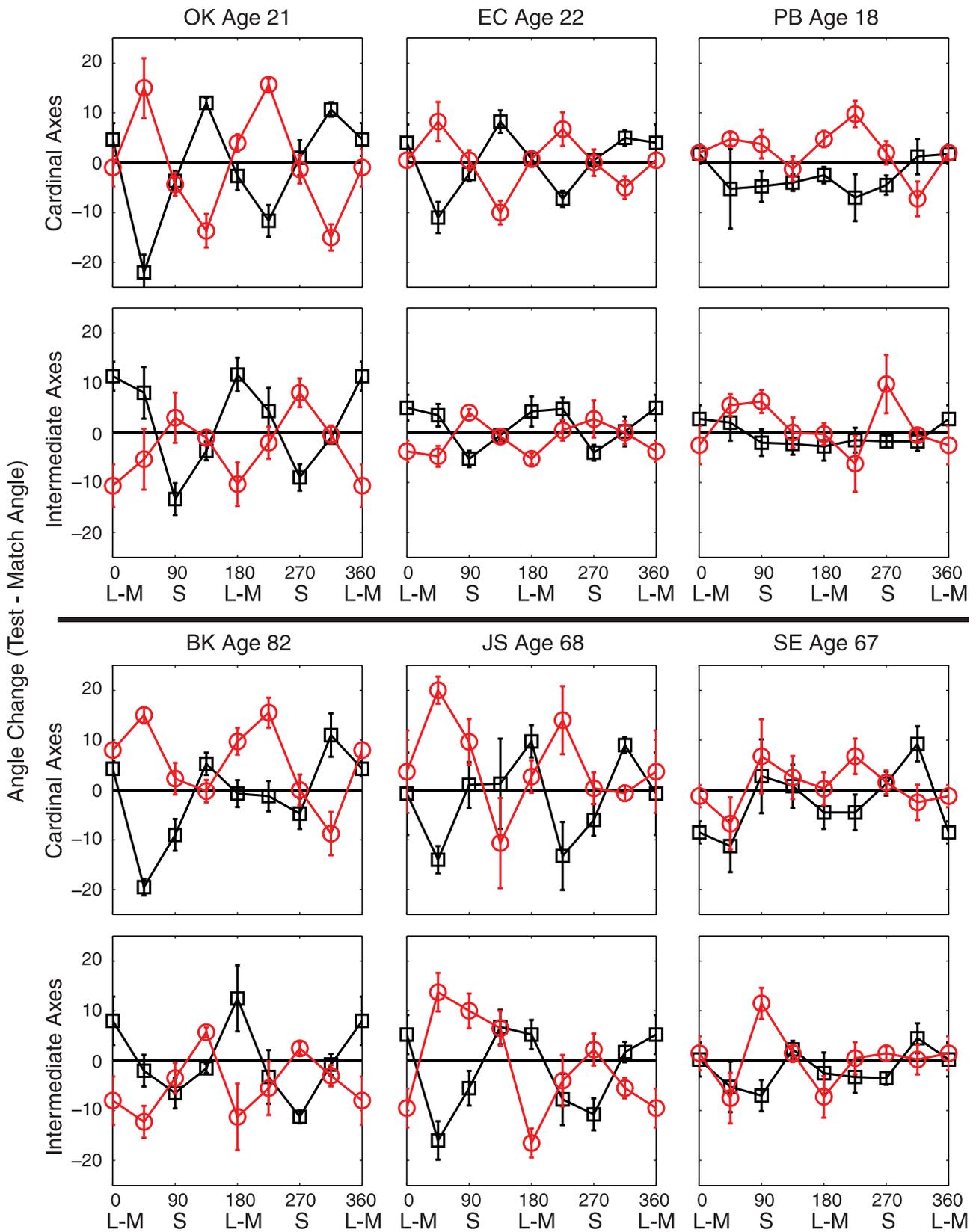


Figure 8. Shifts in perceived hue (test hue angle – matched hue angle) measured for the six sample observers in Figure 7. Panels and symbols are the same as Figure 7. The horizontal black line indicates a perfect hue angle match. Error bars are  $\pm 1$  SEM for the matched hue angle.

Observer (age)	Aspect ratio of fitted ellipse				Fitted value of minor axis			
	0	45	90	135	0	45	90	135
OK (21 years)	0.54	0.65	0.55	0.73	0.42	0.39	0.43	0.43
EC (22 years)	0.78	0.90	0.80	0.85	0.70	0.73	0.68	0.70
PB (18 years)	0.90	0.92	0.77	0.93	0.87	0.85	0.77	0.81
Younger group mean	0.78	0.82	0.76	0.87	0.69	0.65	0.65	0.70
$\pm 1$ SEM	0.03	0.02	0.03	0.02	0.04	0.03	0.03	0.03
BK (82 years)	0.67	0.76	0.73	0.85	0.48	0.44	0.48	0.57
JS (68 years)	0.72	0.82	0.62	0.78	0.54	0.54	0.46	0.56
SE (67 years)	0.80	0.93	0.94	0.93	0.80	0.84	0.84	0.83
Older group mean	0.70	0.80	0.76	0.80	0.55	0.56	0.58	0.58
$\pm 1$ SEM	0.02	0.02	0.03	0.03	0.03	0.03	0.03	0.03

Table 2. Aspect ratios and minor axis values of fitted ellipses for sample observers (in Figure 7) and the corresponding age group means.

multiplicative sensitivity change (which instead is represented as  $(1 - m)$  to correspond to the channel sensitivity after adapting), and  $\sigma$ , the standard deviation of preferred directions along the LvsM and SvsLM axes. If  $\sigma$  is small, the data can be accounted for by a small number of channels, as few as two (one sensitive to LvsM signals, the other to SvsLM signals). As  $\sigma$  increases, the channels approach a more uniform distribution, with a similar density in any chromatic direction. In the present study, a third parameter was added to vary the bandwidth or selectivity of the chromatic channels. In the case examined by Webster and Mollon, the spectral sensitivity of each channel was assumed to depend on a linear combination of the cone signals, and thus had a sensitivity that varied as the cosine of the channel's preferred color angle. (This was further assumed to be half-wave rectified, so that each channel signaled only positive responses to stimuli within  $+90^\circ$  of the preferred angle). To test for narrower or broader channels, the cosine tuning function was raised to a power greater or less than 1.0, respectively. The value of the exponent,  $\alpha$ , was thus varied as a third free parameter.

The model was first fit with  $\alpha$  fixed at 1.0, to replicate the conditions Webster and Mollon examined for linear chromatic channels. For each observer, the values for  $\sigma$  and  $m$  were varied to minimize the sum of squared deviations between the observed and predicted values for all four adapting axes simultaneously. The model provided a good approximation to the observed color changes for all adapting and test directions for each observer (and predicted fits were similar to the ellipse fits shown in Figure 4). As expected from the pronounced individual differences in the matches, the predicted standard deviations ( $\sigma$ ) of the Gaussian distributions and relative sensitivity  $(1 - m)$  changes varied widely across observers, ranging from 1 to  $20^\circ$  and 0.38 to 0.90, respectively. This is illustrated in Table 3, which lists the individual values for the

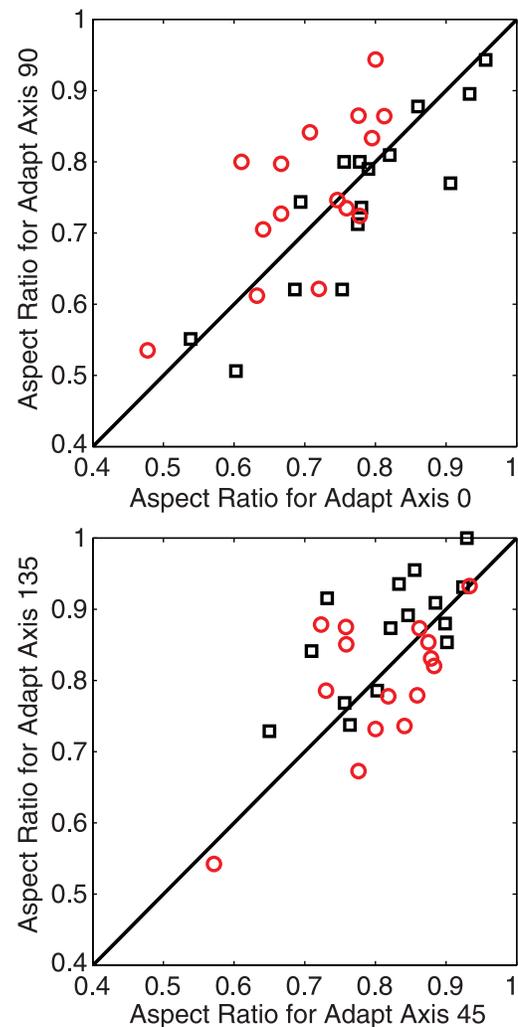


Figure 9. Black and red symbols denote younger and older observers, respectively. The top and bottom panel illustrate differences in aspect ratios for the two cardinal axes and the two intermediate axes, respectively. The solid black line is a line of unity.

example observers in [Figure 7](#) as well as the age group means.

With this model, a clear age difference was found in the predicted standard deviations of the distributions, which were almost doubled for the older observers ( $F_{(1, 28)} = 15.71, p < 0.001$ ). Alternatively, in this case age differences in the magnitude of adaptation did not reach significance ( $F_{(1, 28)} = 2.27, \text{NS}$ ). However, for both age groups, a broader channel distribution—predicting greater noncardinal selectivity—was strongly correlated with a greater magnitude of adaptation ( $r = 0.58$  and  $0.66$  for the young and older age group, respectively,  $p < 0.01$ ). Importantly, this effect was not simply a tendency for the matching contours themselves to become more elliptical with increasing adaptation, which is predicted even with a fixed distribution of mechanisms. Rather, the distribution itself had to be broadened to account for the matches. Thus, this analysis again confirmed a clear tendency for higher-order mechanisms to be more prevalent in observers who showed stronger adaptation.

Finally, as noted, the model was extended to explore the spectral tuning of the channels by allowing the exponent of the cosine tuning function to vary. For two older observers, this resulted in aberrant estimates with poorly defined minima in which the channels were very narrow ( $\alpha > 2.0$ ) and the distribution was very broad ( $\sigma \sim 100$ ). These observers were therefore excluded from the mean estimates of the older age group in [Table 3](#). For the remaining 28 observers, the best-fitting exponent remained close to a value of 1.0 and adding this parameter improved the overall fits by only 1.2%. Moreover, the estimates of the channel distribution and the adaptation magnitude remained very similar to the values based on the linear model. This can be seen in

[Table 3](#), where the values in parentheses are the estimates when the exponent was included in the model. For both age groups, the mean exponents (1.02 for young and 1.06 for old) did not significantly differ from 1.0 or from each other. Thus based on this analysis there is little evidence for a difference in channel selectivity between the two age groups, and for both, the adaptation effects are best described by sensitivity changes in chromatic mechanisms with approximately linear tuning functions.

## Discussion

The aim of the current study was to explore both characteristic and variable aspects of chromatic contrast adaptation and to assess whether normal variations in the pattern of these aftereffects reflect age-related changes in adaptation or color coding. Briefly, it was found that the two age groups were very similar in the basic form of the aftereffects and that for both, the adaptation was consistent with sensitivity changes in mechanisms with linear spectral sensitivities tuned to both the cardinal and intermediate axes. The extent to which an individual's matches revealed mechanisms tuned to these intermediate axes depended largely on how strong the adaptation was for that individual. There was no evidence for a loss of spectral tuning or of higher-order chromatic mechanisms with aging. The effects of aging were instead revealed as a tendency to show stronger adaptation. The general implications of the aftereffects are discussed first and then the individual and age-related differences in them.

Observer (age)	Sigma ( $\sigma$ )	Adapted sensitivity ( $1 - m$ )	Spectral tuning ( $\alpha$ )
OK (21 years)	13 (14)	0.47 (0.47)	(1.12)
EC (22 years)	7 (7)	0.77 (0.77)	(1.00)
PB (18 years)	1 (1)	0.83 (0.83)	(1.02)
Young group mean	$7.53 \pm 3.58$ ( $7.73 + 1.00$ )	$0.74 \pm 0.13$ ( $0.74 + 0.034$ )	( $1.02 + 0.025$ )
BK (82 years)	19 (20)	0.62 (0.61)	(1.10)
JS (68 years)	15 (14)	0.64 (0.64)	(0.91)
SE (67 years)	3 (4)	0.86 (0.88)	(0.89)
Old group mean	$14.07 \pm 1.36$ ( $14.23 + 1.82$ )	$0.67 \pm 0.030$ ( $0.71 + 0.023$ )	( $1.06 + 0.046$ )

Table 3. Fits of the channel distribution model for the sample observers shown in [Figure 7](#) and mean values with standard errors for each age group. Sigma indicates the spread of the distribution, magnitude is the adaptation strength in terms of the postadaptation sensitivity (so that smaller values correspond to stronger adaptation), and spectral tuning denotes the bandwidth of each channel as varied by raising the cosine tuning by the exponent indicated. Values not in parentheses were based on fitting the model with the tuning exponent fixed at 1.0 so that the channels had linear spectral sensitivities. Values in parentheses show the estimates when the channel tuning was also allowed to vary. In this latter case values for two older observers have been excluded from the mean values because the model generated aberrant fits (see text).

## Chromatic contrast adaptation and cortical color coding

While they have been implicated in a wide variety of tasks, the nature and prevalence of higher-order chromatic mechanisms remain uncertain (Eskew, 2009), as does their potential function in the visual representation of color. All of the observers tested here showed selective aftereffects for adapting directions that were intermediate to the cardinal axes, though observers differed widely in both the magnitude and degree of this selectivity. This is consistent with previous research (Krauskopf et al., 1982; Krauskopf et al., 1986; Webster & Mollon, 1991, 1994) and suggests higher-order chromatic dimensions are a ubiquitous feature of cortical color coding across the lifespan, at least as measured by contrast adaptation. Moreover, as in these earlier studies, aftereffects were more selective for the cardinal axes for all observers, an asymmetry that could arise if the cardinal axes are disproportionately weighted within the neural mechanisms that are affected by the adaptation. Notably these patterns were also evident in the interobserver variability in the matches under neutral adaptation, again confirming the features of intraobserver variance in color contrast discrimination observed in previous reports (Krauskopf & Gegenfurtner, 1992).

A weighting biased toward the cardinal axes could be expected because these axes represent the geniculate inputs to the cortex (Derrington et al., 1984), and could arise if adaptation in part takes place early in the cortex (Tailby et al., 2008). Downstream mechanisms would presumably inherit these sensitivity changes (Kohn & Movshon, 2003) and thus could continue to show a cardinal axis bias even if the color tuning of the mechanisms at subsequent stages were more uniformly distributed. Thus while the adaptation reveals the presence of higher-order mechanisms, it does not necessarily reflect how prominent they might be—or in other words what the actual distribution of chromatic preferences is—at different levels of cortical color coding.

A second point which has plagued interpretations of color coding is that color contributes to many visual functions beyond color appearance, such as spatial judgments (Shevell & Kingdom, 2008). Thus the color organization revealed by a particular task may not bear on the specific mechanisms underlying a different task, just as characterizing the chromatic tuning of a single cell leaves unanswered the role that cell may play in color perception (Lennie & Movshon, 2005). In this regard, the current task directly measured color appearance and the adaptation necessarily altered the responses of mechanisms that contribute to perceived color. These appearance changes were selective for multiple directions in the chromatic plane for nearly all observers and adapting directions, and this confirms that color appearance itself

normally depends at some level on mechanisms that are higher-order, or again are an elaboration of the independent signals carried by the cardinal axes.

The basic changes in color appearance following chromatic contrast adaptation replicate the results of Webster and Mollon (1994). They showed that the aftereffects could be well described by sensitivity changes in multiple chromatic mechanisms that were each assumed to have linear spectral sensitivities. In the present study we extended their model to explicitly test for nonlinearities in the spectral tuning of the adapted channels. The spectral sensitivities of color-opponent cells in the geniculate are generally well described by linear combinations of the cone signals (Derrington et al., 1984). Cortical cells show progressively narrower tuning for color in higher visual areas which may reflect the emergence of substantial nonlinearities (Conway et al., 2010; Gegenfurtner, 2003; Horwitz & Hass, 2012). Residual adaptation effects consistent with narrower tuning can be found for stimuli that should form silent substitutions for linear mechanisms (Mizokami, Paras, & Webster, 2004). However, for almost all of our younger and older observers, the selectivity of the aftereffects were best fit by assuming adaptation within mechanisms with spectral sensitivities that were close to linear, and the average tuning for both age groups remained close to linear. This might itself point to an early cortical locus of the adaptation, but again one which also includes a substantial contribution of higher-order color mechanisms.

A second difference in the present study is that the analysis of ellipse fits revealed a consistent asymmetry in the effects for the two intermediate chromatic axes (an effect which was not explored in the small sample of observers tested by Webster and Mollon, 1994). Again these have the same component contrasts along the cardinal axes but combine them in opposite phases. Yet the change in perceived contrast with adaptation was significantly weaker for the 135–315° axis compared to the 45–225° axis. Absolute hue shifts were also weakest along the 135–315° axis, although this difference was not significant compared to the 45–225° axis. Finally, under neutral adaptation it was found that the variance in the matches for hue (though not contrast) was significantly greater along for the 45 and 225° test stimuli compared to stimuli at 135 and 315°. Thus observers were more consistent in judging the red-green changes in the blue and yellow tests than vice versa. As noted, these asymmetries have been found in other studies of chromatic discrimination (Boynton et al., 1986; Danilova & Mollon, *in press*; Krauskopf & Gegenfurtner, 1992; McDermott et al., 2010) as well as in a variety of other tasks (Goddard, Mannion, McDonald, Solomon, & Clifford, 2010; Juricevic, Land, Wilkins, & Webster, 2010; McDermott et al., 2010; Webster & Leonard, 2008; Werner & Scheffrin,

1993). McDermott and Webster (2012) recently showed that they are also built into the structure of common perceptually uniform color spaces and systems. One possible account of the reduced sensitivity to blue-yellow is that both natural illumination (Lee, 1990; Mollon, 2006; Shepard, 1992) and the distribution of color in the natural world (Webster, Mizokami, & Webster, 2007; Webster & Mollon, 1997) vary primarily along bluish-yellowish axes. Observers may thus be naturally adapted to this variation (Juricevic & Webster, 2009).

## Individual differences

There have been few systematic studies of individual differences in adaptation, though observers can reliably differ in the pattern and strength of aftereffects (e.g., Vera-Diaz, Woods, and Peli, 2010). This study found large differences in both the strength and selectivity of the adaptation, and importantly, these were strongly related. Specifically, observers who showed stronger adaptation also tended to show more selectivity for both cardinal and intermediate directions. It remains possible that this is simply a trivial consequence of the fact that selective aftereffects may become more selective the stronger the adaptation. This is precisely the pattern predicted for adaptation confined to either cardinal axis, but adaptation effects should be nonselective for adapting directions midway between the cardinal axes under the extreme assumption of only two chromatic channels, and thus the tuning of the aftereffects will be independent of adapting strength. Moreover, at least for the restricted model considered, the changes in selectivity were not tied to adaptation strength alone as they also predicted broader channel distributions. Whether this correctly captures the actual pattern of response changes, the results suggest that higher-order mechanisms are more clearly uncovered when the adaptation digs deeper to reveal them. Given these results, the most parsimonious account of the individual differences in selectivity observed here is that to a large extent observers have a similar channel structure but differ in the magnitude of adaptation and thus in the ways in which this structure is manifest. In particular, it seems more plausible to assume that old and young observers differ in the strength of adaptation than that the older observers actually have a stronger representation of higher-order mechanisms.

This account can also explain the large quantitative differences between the modeled results in the present study and in Webster and Mollon (1994). The estimated channel distributions in the current study were much narrower than those they reported, but the magnitude of the adaptation was also much weaker (e.g., compare Figures 7 and 8 to Figures 4 and 7 in Webster & Mollon).

In fact, many observers in the present study exhibited narrower channel distributions than predicted for cells in the parvocellular layers of the LGN [8–10° standard deviations, based on estimates from Derrington et al., 1984 (Webster & Mollon, 1994)]. These differences are likely the result of differences in the stimuli and procedures. The current study used higher adapting (80 vs. 48× threshold units) and test (30 vs. 17× threshold units) contrasts. Aftereffects of contrast adaptation may be more pronounced when the test contrast is low (Georgeson, 1985; Webster & Mollon, 1994). The two studies also used very different adapting durations. Webster and Mollon tested only a single adapting axis in daily sessions that lasted up to three hours, compared to the much briefer adaptation to all axes (neutral and four chromatic axes of adaptation) within a single session in the present study. The briefer testing sequence was adopted here to accommodate the time constraints, attention span, and fatigue for observers of varying ages. However, the difference in results between the two studies reinforces the possibility that the salience of higher-order selectivity in the adaptation may increase with adapting magnitude and/or the adapting duration. Please note, it is also possible that the actual pattern changes with longer adapting times. For example, a recent study found that the functional form of luminance contrast adaptation changed at short and long durations (Kwon, Legge, Fang, Cheong, & He, 2009).

## Age-related differences

The current study was motivated to test older observers in order to explore whether chromatic coding, and how it is affected by adaptation, might change with normal aging. Again, higher-order color mechanisms are built within the cortex and thus could be potentially more susceptible to age-related changes in neural integrity. Moreover, as noted in the [Introduction](#), a number of studies have pointed to senescent changes in neural selectivity. Thus perhaps the most striking feature of the current results is how little the basic pattern of adaptation appeared impacted by aging. Specifically, there was no evidence that selectivity of the adaptation for color directions intermediate to the cardinal axes was reduced or that the selectivity of individual mechanisms was increased, in the older group. In fact if anything the results trended in the opposite direction.

The finding that mechanism bandwidths for color did not increase is not necessarily incompatible with tuning changes that have been documented for other stimuli (Leventhal et al., 2003; Wilson et al., 2011); these bandwidths are already broad for linear mechanisms, and this linearity may be the upper limit of chromatic bandwidths in mechanisms that mediate color appear-

ance. The contrast adaptation may not sufficiently engage stages where chromatic selectivity narrows, again potentially because its effects may be dominated by response changes at early cortical levels. It is notable that in the task of matching itself, poorer hue discrimination in the older observers was observed, an effect which could result from weaker selectivity. It thus remains possible that this task taps a different level or substrate where chromatic tuning does vary with age.

The one clear difference in adaptation across the two age groups was in the magnitude of the adaptation. Both an increase or decrease in adaptation strength could potentially have occurred. For example, stronger aftereffects could reflect greater *fatigue* of the neural response (Carandini, 2000; Ibbotson, 2005), whereas weaker aftereffects might arise from a reduction in the efficiency for mechanisms to recalibrate neural sensitivity. For instance, if the aftereffects depended on inhibition, then older observers could exhibit weaker aftereffects due to a decrease in Gamma-aminobutyric acid (GABA) mediated inhibition in the older brain (Leventhal et al., 2003). The actual neural mechanisms underlying cortical contrast adaptation are not fully understood, though current evidence points to intracellular rather than presynaptic mechanisms (Kohn, 2007). Finally, a third null prediction is that there would be no effect of age on the adaptation. In fact, this result was recently reported following adaptation to image blur, which may have a cortical locus similar to the color contrast adaptation and which was similar in strength for young and old adults (Elliott, Hardy, Webster, & Werner, 2007).

In contrast to the results for blur, however, the present study instead found that the older observers showed significantly stronger levels of adaptation to chromatic contrast, an effect which was consistent across all four adapting axes. While this could be consistent with greater fatigue, it might also be related to previous findings of age-related increases in neural noise (Betts, Sekular, & Bennett, 2007) and shifts in contrast gain functions (Elliott & Werner, 2010) that may also be explained by an increase in noise (see Pokorný, 2011). Regardless of its basis, the results suggest that differences in adaptability may be the primary difference in the older observers, and that the underlying channel structure remains robust.

## Conclusion

Selectivity for both cardinal and noncardinal chromatic directions is a prevalent and general feature of color contrast adaptation that remains robust with aging. Individual differences in the degree of selectivity for higher-order mechanisms may depend primarily on

the how adaptable the observer is rather than on how uniformly their color channels tile color space. Older observers showed significantly stronger adaptation but no evidence for weakened chromatic coding either in terms of the selectivity or distribution of chromatic channels. Thus to a large extent, both the processes and consequences of the adaptation, and the cortical mechanisms of color coding that they reveal, appear largely stable across the lifespan. This robustness is striking given the pronounced neural declines accompanying healthy aging, and could reflect the importance of these processes for maintaining color perception. As noted at the outset, adaptation may be critical for compensating for neural losses in order to maintain perceptual constancy, and thus may be an essential mechanism to preserve. The current results suggest that whatever the functional role of color contrast adaptation, it may continue largely intact through the life span.

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Corresponding author: Sarah L. Elliott.

Email: slelliott@uchicago.edu.

Address: Institute for Mind & Biology, University of Chicago, Chicago, IL, USA.

## References

- Anstis, S., & Cavanagh, P. (1983). A minimum motion technique for judging equiluminance. In J. D. Mollon & L. T. Sharpe (Eds.), *Color vision*. (pp. 155–166). London: Academic.
- Baker, C. L., & Mareschal, I. (2001). Processing of second-order stimuli in the visual cortex. *Progressive Brain Research*, *134*, 171–191.
- Belmore, S. C., & Shevell, S. K. (2008). Very-long-term chromatic adaptation: Test of gain theory and a new method. *Visual Neuroscience*, *25*(3), 411–414.
- Betts, L. R., Sekular, A. B., & Bennett, P. J. (2007). The effects of aging on orientation discrimination. *Vision Research*, *47*, 1769–1780.
- Billino, J., Bremmer, F., & Gegenfurtner, K. R. (2008). Differential aging of motion processing mecha-

- nisms: Evidence against general perceptual decline. *Vision Research*, *48*, 1254–1261.
- Boynton, R. M., Nagy, A. L., & Eskew, R. T., Jr. (1986). Similarity of normalized discrimination ellipses in the constant-luminance chromaticity plane. *Perception*, *15*(6), 755–763.
- Carandini, M. (2000). Visual cortex: Fatigue and adaptation. *Current Biology*, *10*, 605–607.
- Cavanagh, P., & Mather, G. (1989). Motion: The long and short of it. *Spatial Vision*, *4*, 103–129.
- Chubb, C., & Sperling, G. (1988). Drift-balanced random stimuli: A general basis for studying non-Fourier motion perception. *Journal of the Optical Society of America A*, *5*, 1986–2007.
- Conway, B. R., Chatterjee, S., Field, G. D., Horwitz, G. D., Johnson, E. N., Koida, K. et al. (2010). Advances in color science: From retina to behavior. *The Journal of Neuroscience*, *30*(45), 14955–14963.
- Conway, B. R., & Livingstone, M. S. (2006). Spatial and temporal properties of cone signals in alert macaque primary visual cortex. *The Journal of Neuroscience*, *26*(42), 10826–10846.
- Daniilova, M. V., & Mollon, J. D. (in press). The cardinal axes are not independent in color discrimination. *Journal of the Optical Society of America A*.
- Delahunt, P. B., Hardy, J. L., Okajima, K., & Werner, J. S. (2005). Senescence of spatial chromatic contrast sensitivity. II. Matching under natural viewing conditions. *Journal of the Optical Society of America A*, *22*, 60–67.
- Delahunt, P. B., Webster, M. A., Ma, L., & Werner, J. S. (2004). Long-term renormalization of chromatic mechanisms following cataract surgery. *Visual Neuroscience*, *21*, 301–307.
- Derrington, A. M., Krauskopf, J., & Lennie, P. (1984). Chromatic mechanisms in lateral geniculate nucleus of macaque. *Journal of Physiology*, *357*, 241–265.
- Elliott, S. L., Hardy, J. L., Webster, M. A., & Werner, J. S. (2007). Aging and blur adaptation. *Journal of Vision*, *7*(6):8, 1–9, <http://www.journalofvision.org/content/7/6/8>, doi:10.1167/7.6.8. [PubMed] [Article]
- Elliott, S. L., & Werner, J. S. (2010). Age-related changes in contrast gain related to the M and P pathways. *Journal of Vision*, *10*(4):4, 1–15, <http://www.journalofvision.org/content/10/4/4>, doi:10.1167/10.4.4. [PubMed] [Article]
- Engel, S. A., & Furmanski, C. S. (2001). Selective adaptation to color contrast in human primary visual cortex. *The Journal of Neuroscience*, *21*(11), 3949–3954.
- Eskew, R. T., Jr. (2009). Higher order mechanisms: A critical review. *Vision Research*, *49*(22), 2686–2704.
- Fairchild, M. D., & Lennie, P. (1992). Chromatic adaptation to natural and incandescent illuminants. *Vision Research*, *32*(11), 2077–2085.
- Gegenfurtner, K. R. (2003). Cortical mechanisms of colour vision. *Nature Reviews Neuroscience*, *4*(7), 563–572.
- Georgeson, M. A. (1985). The effect of spatial adaptation on perceived contrast. *Spatial Vision*, *1*(2), 103–112.
- Georgeson, M. A., & Sullivan, G. D. (1975). Contrast constancy: Deblurring in human vision by spatial frequency channels. *Journal of Physiology*, *252*(3), 627–656.
- Goddard, E., Mannion, D. J., McDonald, J. S., Solomon, S. G., & Clifford, C. W. (2010). Combination of subcortical color channels in human visual cortex. *Journal of Vision*, *10*(5):25, 1–17, <http://www.journalofvision.org/content/10/5/25>, doi:10.1167/10.5.25.
- Goh, J. O., Suzuki, A., & Park, D. C. (2010). Reduced neural selectivity increases fMRI adaptation with age during face discrimination. *Neuroimage*, *51*, 336–344.
- Habak, C., & Faubert, J. (2000). Larger effects of aging on the perception of higher-order stimuli. *Vision Research*, *40*, 943–950.
- Habak, C., Wilkinson, F., & Wilson, H. R. (2009). Preservation of shape discrimination in aging. *Journal of Vision*, *9*(12):18, 1–8, <http://www.journalofvision.org/content/9/12/18>, doi:10.1167/9.12.18.
- Hardy, J. L., Delahunt, P. B., Okajima, K., & Werner, J. S. (2005). Senescence of spatial chromatic contrast sensitivity. I. Detection under conditions controlling for optical factors. *Journal of the Optical Society of America A*, *22*, 49–59.
- Herbert, A. M., Overbury, O., Singh, J., & Faubert, J. (2002). Aging and bilateral symmetry detection. *Journal of Gerontology B*, *57*, P241–245.
- Horwitz, G. D., Chichilnisky, E. J., & Albright, T. D. (2007). Cone inputs to simple and complex cells in V1 of awake macaque. *Journal of Neurophysiology*, *97*(4), 3070–3081.
- Horwitz, G. D., & Hass, C. A. (2012). Nonlinear analysis of macaque V1 color tuning reveals cardinal directions for cortical color processing. *Nature Neuroscience*, *15*, 913–921.
- Ibbotson, M. R. (2005). Physiological mechanisms of adaptation in the visual system. In C. W. G. Clifford & G. Rhodes (Eds.), *Fitting the mind to the*

- world: *Adaptation and after-effects in high level vision*. (pp. 15–45). Oxford: Oxford University Press.
- Johnson, E. N., Hawken, M. J., & Shapley, R. (2001). The spatial transformation of color in the primary visual cortex of the macaque monkey. *Nature Neuroscience*, 4(4), 409–416.
- Juricevic, I., Land, L., Wilkins, A., & Webster, M. A. (2010). Visual discomfort and natural image statistics. *Perception*, 39(7), 884–899.
- Juricevic, I., & Webster, M. A. (2009). Variations in normal color vision. V. Simulations of adaptation to natural color environments. *Visual Neuroscience*, 26(1), 133–145.
- Knoblauch, K., Vital-Durand, F., & Barbur, J. L. (2001). Variation of chromatic sensitivity across the life span. *Vision Research*, 41, 23–36.
- Kohn, A. (2007). Visual adaptation: Physiology, mechanisms, and functional benefits. *Journal of Neurophysiology*, 97(5), 3155–3164.
- Kohn, A., & Movshon, J. A. (2003). Neuronal adaptation to visual motion in area MT of the macaque. *Neuron*, 39(4), 681–691.
- Krauskopf, J. (1999). Higher order color mechanisms. In Gegenfurtner, K. & Sharpe, L. T. (Eds.), *Color vision: From genes to perception*. (pp. 303–316). Cambridge: Cambridge University Press.
- Krauskopf, J., & Gegenfurtner, K. (1992). Color discrimination and adaptation. *Vision Research*, 32(11), 2165–2175.
- Krauskopf, J., Williams, D. R., & Heeley, D. W. (1982). Cardinal directions of color space. *Vision Research*, 22(9), 1123–1131.
- Krauskopf, J., Williams, D. R., Mandler, M. B., & Brown, A. M. (1986). Higher order color mechanisms. *Vision Research*, 26(1), 23–32.
- Kwon, M., Legge, G. E., Fang, F., Cheong, A. M., & He, S. (2009). Adaptive changes in visual cortex following prolonged contrast reduction. *Journal of Vision*, 9(2):20, 1–16, <http://www.journalofvision.org/content/9/2/20>, doi:10.1167/9.2.20. [PubMed] [Article]
- Laframboise, S., De Guise, D., & Faubert, J. (2006). Effect of aging on stereoscopic interocular correlation. *Optometry and Vision Science*, 83, 589–593.
- Lee, H.-C. (1990). A computational model for opponent color encoding. *Advanced Printing of Conference Summaries, SPSE's 43rd Annual Conference (Rochester, NY, May 1990)*, 178–181.
- Lennie, P., Krauskopf, J., & Sclar, G. (1990). Chromatic mechanisms in striate cortex of macaque. *Journal of Neuroscience*, 10(2), 649–669.
- Lennie, P., & Movshon, J. A. (2005). Coding of color and form in the geniculostriate visual pathway. *Journal of the Optical Society of America A*, 22(10), 2013–2033.
- Leventhal, A. G., Wang, Y., Pu, M., Zhou, Y., & Ma, Y. (2003). GABA and its agonists improved visual cortical function in senescent monkeys. *Science*, 300, 812–815.
- Liang, Z., Yang, Y., Li, G., Zhang, J., Wang, Y., Zhou, Y. et al. (2010). Aging affects the direction selectivity of MT cells in rhesus monkeys. *Neurobiology of Aging*, 31, 863–873.
- MacLeod, D. A. I., & Boynton, R. M. (1979). Chromaticity diagram showing cone excitation by stimuli of equal luminance. *Journal of the Optical Society of America*, 69, 1183–1186.
- McDermott, K. C., Malkoc, G., Mulligan, J. B., & Webster, M. A. (2010). Adaptation and visual salience. *Journal of Vision*, 10(13):17, 1–32, <http://www.journalofvision.org/content/10/13/17>, doi:10.1167/10.13.17.
- McDermott, K. C., & Webster, M. A. (2012). Uniform color spaces and natural image statistics. *Journal of the Optical Society of America A*, 29, A182–A187. [PubMed] [Article]
- Mizokami, Y., Paras, C., & Webster, M. A. (2004). Chromatic and contrast selectivity in color contrast adaptation. *Visual Neuroscience*, 21(3), 359–363.
- Mollon, J. D. (2006). Monge (The verriest lecture). *Visual Neuroscience*, 23, 297–309.
- Neitz, J., Carroll, J., Yamouchi, Y., Neitz, M., & Williams, D. R. (2002). Color perception is mediated by a plastic neural mechanism that is adjustable in adults. *Neuron*, 35, 783–792.
- Pokorny, J. (2011). Review: Steady and pulsed pedestals, the how and why of post-receptoral pathway separation. *Journal of Vision*, 11(5):1–23, <http://www.journalofvision.org/content/11/5/7>, doi:10.1167/11.5.7. [PubMed] [Article]
- Pokorny, J., Smith, V. C., & Lutze, M. (1987). Aging of the human lens. *Applied Optics*, 26, 1437–1440.
- Rinner, O., & Gegenfurtner, K. R. (2000). Time course of chromatic adaptation for color appearance and discrimination. *Vision Research*, 40(14), 1813–1826.
- Schefrin, B. E., Shinomori, K., & Werner, J. S. (1995). Contributions of neural pathways to age-related losses in chromatic discrimination. *Journal of the Optical Society of America A, Optics, Image Science, and Vision*, 12, 1233–1241.

- Scheffrin, B. E., & Werner, J. S. (1990). Loci of spectral unique hues throughout the life span. *Journal of the Optical Society of America A*, 7, 305–311.
- Scheffrin, B. E., & Werner, J. S. (1993). Age-related changes in the color appearance of broadband surfaces. *Color Research and Application*, 18, 380–389.
- Schmoleky, M. T., Wang, Y., Pu, M., & Leventhal, A. G. (2000). Degradation of stimulus selectivity of visual cortical cells in senescent rhesus monkeys. *Nature Neuroscience*, 3, 384–390, doi:10.1167/11.5.7.
- Shepard, R. N. (1992). The perceptual organization of colors: An adaptation to regularities of the terrestrial world?. In H. Jerome, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture*. (pp. 495–532). New York: Oxford University Press.
- Shevell, S. K., & Kingdom, F. A. (2008). Color in complex scenes. *Annual Review of Psychology*, 59, 143–166.
- Shinomori, K., Scheffrin, B. E., & Werner, J. S. (2001). Age-related changes in wavelength discrimination. *Journal of the Optical Society of America A*, 18, 310–318.
- Smith, V. C., & Pokorny, J. (1975). Spectral sensitivity of the foveal cone photopigments between 400 and 500 nm. *Vision Research*, 15(2), 161–171.
- Smithson, H. E., Sumner, P., & Mollon, J. D. (2003). How to find a tritan line. In J. D. Mollon, J. Pokorny, & K. Knoblauch (Eds.), *Normal and defective colour vision*. (pp. 279–287). Oxford: Oxford University Press.
- Solomon, S. G., Peirce, J. W., Dhruv, N. T., & Lennie, P. (2004). Profound contrast adaptation early in the visual pathway. *Neuron*, 42(1), 155–162.
- Switkes, E., & Crognale, M. A. (1999). Comparison of color and luminance contrast: Apples versus oranges? *Vision Research*, 39, 1923–1831.
- Tailby, C., Solomon, S. G., Dhruv, N. T., & Lennie, P. (2008). Habituation reveals fundamental chromatic mechanisms in striate cortex of macaque. *The Journal of Neuroscience*, 28(5), 1131–1139.
- Vera-Diaz, F. A., Woods, R. L., & Peli, E. (2010). Shape and individual variability in the blur adaptation curve. *Vision Research*, 50, 1452–1461.
- Wachtler, T., Sejnowski, T. J., & Albright, T. D. (2003). Representation of color stimuli in awake macaque primary visual cortex. *Neuron*, 37(4), 681–691.
- Weale, R. A. (1988). Age and the transmittance of the human crystalline lens. *The Journal of Physiology*, 395, 577–587.
- Webster, M. A. (1996). Human colour perception and its adaptation. *Network: Computation in Neural Systems*, 7, 587–634.
- Webster, M. A., & Leonard, D. (2008). Adaptation and perceptual norms in color vision. *Journal of the Optical Society of America A*, 25(11), 2817–2825.
- Webster, M. A., Miyahara, E., Malkoc, G., & Raker, V. E. (2000). Variations in normal color vision. I. Cone-opponent axes. *Journal of the Optical Society of America A, Optics, Image Science, and Vision*, 17(9), 1535–1544.
- Webster, M. A., Mizokami, Y., & Webster, S. M. (2007). Seasonal variations in the color statistics of natural images. *Network*, 18(3), 213–233.
- Webster, M. A., & Mollon, J. D. (1991). Changes in colour appearance following post-receptoral adaptation. *Nature*, 349(6306), 235–238.
- Webster, M. A., & Mollon, J. D. (1994). The influence of contrast adaptation on color appearance. *Vision Research*, 34(15), 1993–2020.
- Webster, M. A., & Mollon, J. D. (1995). Color constancy influenced by contrast adaptation. *Nature*, 373, 694–698.
- Webster, M. A., & Mollon, J. D. (1997). Adaptation and the color statistics of natural images. *Vision Research*, 37(23), 3283–3298.
- Webster, M. A., & Wilson, J. A. (2000). Interactions between chromatic adaptation and contrast adaptation in color appearance. *Vision Research*, 40(28), 3801–3816.
- Werner, J. S. (1982). Development of scotopic sensitivity and the absorption spectrum of the human ocular media. *Journal of the Optical Society of America*, 72, 247–258.
- Werner, J. S., Bieber, M. L., & Scheffrin, B. E. (2000). Senescence of foveal and parafoveal cone sensitivities and their relations to macular pigment density. *Journal of the Optical Society of America A*, 17, 1918–1932.
- Werner, J. S., & Scheffrin, B. E. (1993). Loci of achromatic points throughout the life span. *Journal of the Optical Society of America A*, 10, 1509–1516.
- Werner, J. S., & Steele, V. G. (1988). Sensitivity of human foveal color mechanisms throughout the life span. *Journal of the Optical Society of America A, Optics and Image Science*, 5, 2122–2130.
- Wilson, H. R., Mei, M., Habak, C., & Wilkinson, F. (2011). Visual bandwidths for face orientation increase during healthy aging. *Vision Research*, 51(1), 160–164.

Winn, B., Whitaker, D., Elliott, D. B., & Phillips, N. J. (1994). Factors affecting light-adapted pupil size in normal human subjects. *Investigative Ophthalmology & Visual Science*, *35*, 1132–1137.

Wuerger, S., Xiao, K., Fu, C., & Karatzas, D. (2010). Colour-opponent mechanisms are not affected by age-related sensitivity changes. *Ophthalmic and Physiological Optics*, *30*, 653–659.