

# Cone contributions to signals for accommodation and the relationship to refractive error

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## Abstract

The accommodation response is sensitive to the chromatic properties of the stimulus, a sensitivity presumed to be related to making use of the longitudinal chromatic aberration of the eye to decode the sign of the defocus. Thus, the relative sensitivity to the long- (L) and middle-wavelength (M) cones may influence accommodation and may also be related to an individual's refractive error. Accommodation was measured continuously while subjects viewed a sine wave grating (2.2 c/d) that had different cone contrast ratios. Seven conditions tested loci that form a circle with equal vector length (0.27) at 0, 22.5, 45, 67.5, 90, 120, 145 deg. An eighth condition produced an empty field stimulus (CIE  $(x,y)$  co-ordinates (0.4554, 0.3835)). Each of the gratings moved at 0.2 Hz sinusoidally between 1.00 D and 3.00 D for 40 s, while the effects of longitudinal chromatic aberration were neutralized with an achromatizing lens. Both the mean level of accommodation and the gain of the accommodative response, to sinusoidal movements of the stimulus, depended on the relative L and M cone sensitivity: Individuals more sensitive to L-cone stimulation showed a higher level of accommodation ( $p=0.01$ ;  $F=12.05$ ; ANOVA) and dynamic gain was higher for gratings with relatively more L-cone contrast. Refractive error showed a similar correlation: More myopic individuals showed a higher mean level of accommodation ( $p<0.01$ ;  $F=11.42$ ; ANOVA) and showed higher gain for gratings with relatively more L-cone than M-cone contrast ( $p=0.01$ ;  $F=10.83$  ANOVA). If luminance contrast is maximized by accommodation, long wavelengths will be imaged behind the photoreceptors. Individuals in whom luminance is dominated by L-cones may maximize luminance contrast both by accommodating more, as shown here, and by increased ocular elongation, resulting in myopia, possibly explaining the correlations reported here among relative L/M-cone sensitivity, refractive error and accommodation.

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## 1. Introduction

Myopia is a significant public health problem that affects 30.5 million Americans aged 40 or older. For many myopes, refractive correction provides clear vision, but in some cases myopia progresses causing myopic retinopathy with associated retinal detachment and blindness. It is therefore essential to understand the etiology of myopia, the signals that mediate eye growth, and physiological differences

between myopes and emmetropes in an effort to find better predictive models for the development of myopia.

Although close work appears to be related to the prevalence of myopia (for reviews, see Goss & Zhai, 1994; Goss & Wickham, 1995; Ong & Ciuffreda, 1997; Rosenfield & Gilmartin, 1998) epidemiological studies that have investigated the relationship between reading hours and myopia have not produced convincing correlations (Zadnik, Satariano, Mutti, Sholtz, & Adams, 1994). Reading induces prolonged periods of accommodation and an association between eye growth and accommodation would be expected to be reflected in the amount of closework. Wallman, Winawer, Zhu, and Park (2000) have suggested that it is not the total time spent reading that is important, but

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something about the pattern of reading that is important. Indeed something about the temporal or focal characteristics of the accommodation response may play an important role in determining the growth rate of the eye.

The accommodation response is sensitive to luminance and chromatic components of the stimulus (Rucker & Kruger, 2004a, 2004b). The luminance and chromatic components produce responses with different temporal characteristics (Rucker & Kruger, 2004a), while the focal characteristics of the response depend on the changes in chromaticity of the retinal image that occur as a result of longitudinal chromatic aberration (Rucker & Kruger, 2004a, 2004b). Chromatic short-wavelength cone contrast biases the response towards near (Kruger, Stark, & Nguyen, 2004; Rucker & Kruger, 2001; Rucker & Kruger, 2004a; Seidemann & Schaeffel, 2002), while greater long-wavelength contrast than middle-wavelength contrast biases the accommodation response towards far. In addition, the time course of the chromatic short-wavelength cone response to a step change in focus, is in the order of three times as slow as the response when luminance contrast is present (Rucker & Kruger, 2004a). Thus an individual's sensitivity to the luminance and chromatic components of the stimuli, which affects the temporal and focal characteristics of the accommodation response, may predispose a person towards the development of myopia.

Sensitivity to the luminance component of the stimulus is thought to be mediated by a negative feedback mechanism. Accurate focus using the even error stimulus from luminance contrast relies on negative feedback as the optical system searches for the point of maximal luminance contrast and smallest blur circle diameter (Bobier, Campbell, & Hinch, 1992; Charman & Tucker, 1978; Heath, 1956; Phillips & Stark, 1977; Stark & Takahashi, 1965; Troelstra, Zuber, Miller, & Stark, 1964; Wolfe & Owens, 1981). For negative feedback to provide an effective signal the accommodation control mechanism must sample the image at two image planes to determine the optimal direction of focus. Hence dynamic sampling is a requirement of a negative feedback control mechanism that attempts to maximize luminance contrast.

The chromatic signal for accommodation is derived from the effects of longitudinal chromatic aberration (LCA) on the retinal image (Aggarwala, Mathews, Kruger, & Kruger, 1995a; Aggarwala, Nowbotsing, & Kruger, 1995b; Campbell & Westheimer, 1959; Fincham, 1951; Kotulak, Morse, & Billock, 1995; Kruger & Pola, 1986; Kruger, Mathews, Aggarwala, & Sanchez, 1993; Kruger, Mathews, Aggarwala, Yager, & Kruger, 1995; Kruger, Mathews, & Aggarwala, 1997a). The signal from LCA arises as a result of the dispersion of white light by the optical medium and provides the sign of defocus when the image is sampled at a single plane of focus. Indeed, image simulations based on a comparison of normalized long (L-) and middle (M-) wavelength cone contrasts, at luminance borders, drive accommodation in the predicted

direction (Kruger et al., 1995; Lee, Stark, Cohen, & Kruger, 1999; Stark, Lee, Kruger, Rucker, & Ying, 2002; Rucker & Kruger, 2004b). Rucker and Kruger (2004b) demonstrated that when M-cone contrast of the retinal image is greater than L-cone contrast, the amplitude of the reflex accommodation response (to near targets) increased, and when L-cone contrast was greater than M-cone contrast the amplitude of the reflex accommodation response decreased. Increased sensitivity to one or other cone type might be expected to enhance this chromatic response, and affect the accuracy of the accommodation response. Indeed Kroger and Binder (2000) found that a reduction in accommodation demand of 0.50 D could be achieved with the use of a short pass filter (SP560). The relative sensitivity of the luminance and chromatic mechanisms to L- and M-cone contrast is described by cone weighting factors.

The cone weightings can be determined by calculation of what is known as the “iso-response” contour in cone-contrast-space (Stromeyer, Kronauer, Ryu, Chaparro, & Eskew, 1995). This contour describes the L- and M-cone contrasts that are required to produce a particular response level, and typically forms a straight line in the luminance quadrant for dynamic accommodation gain (Rucker & Kruger, 2004b). The angle of the iso-response contour for dynamic gain provides information on the relative cone weightings, while the distance of the contour from the origin provides information on the sensitivity to luminance contrast per se (Stromeyer et al., 1995).

This experiment will test the hypothesis that there is a difference in the relative cone sensitivity to the luminance signals for reflex accommodation that is related to refractive error. Recognition of such differences might lead to identification of emmetropic children that are at risk of developing myopia and lead to methods of prevention and treatment.

## 2. Methods

### 2.1. Infrared optometer and Badal stimulus system

An infrared recording optometer (Kruger, 1979) and Badal optical system (Ogle, 1968) were used to measure accommodation responses and present stimuli (2.2 c/d sine waves; 140 Td) that isolated positions in cone contrast space. Seven conditions tested loci that form a circle with equal vector length (0.27) at 0, 22.5, 45, 67.5, 90, 120, 145 deg. An eighth condition produced an empty field stimulus (CIE  $(x, y)$  co-ordinates (0.4554, 0.3835)). Each of the gratings moved at 0.2 Hz sinusoidally between 1.00 D and 3.00 D for 40 s, while the effects of longitudinal chromatic aberration were neutralized with an achromatizing lens. A field stop with blurred edges (5.20 D beyond the emmetropic far point) subtended 7.2 deg at the eye, and an artificial pupil (3 mm) was imaged in the real pupil plane. The apparatus and its calibration have been described in detail previously (Lee et al., 1999; Rucker & Kruger, 2004b).

### 2.2. Stimuli

Stimuli were generated by a video controller (Cambridge Research Systems VSG2/5) and displayed on a color monitor (Sony Trinitron color graphic display GDM-F500R) as described in a previous experiment

(Rucker & Kruger, 2004b). Stimuli were 2.2 c/d sine wave gratings created with different ratios of L- and M-cone contrast, in phase and in counter-phase, thus producing different amounts of luminance and chromatic contrast.

Cone excitation was calculated from the spectral radiation of each phosphor using Smith and Pokorny cone fundamentals (Smith & Pokorny, 1975) based on transformations from Judd (1951) color matching functions. Relative intensity levels for each gun were calculated based on the required Michelson cone contrasts using the formula:  $\text{Contrast} = (E_{\max} - E_{\min}) / (E_{\max} + E_{\min})$ , where  $E_{\max}$  is the maximum cone excitation for the grating and  $E_{\min}$  is the minimum cone excitation for the grating. Stimuli were created with the necessary cone excitations in the peaks and troughs to simulate the retinal image at different levels of defocus in the presence of LCA.

Cone contrasts of the stimuli were maintained in the eye by neutralization of LCA using a specially designed achromatizing lens positioned in the stimulus system (Kruger et al., 1993). This specially designed lens corrected for the eye's natural longitudinal chromatic aberration and light of all visible wavelengths were brought to a focus at a single focal plane. There is a slight under-correction of longitudinal chromatic aberration at short-wavelengths of 0.15 D, but the stimuli used in this experiment contain no S-cone contrast. Correction of the eye's natural chromatic aberration maintains the cone contrast of the image with changes in focus and makes the chromatic stimulus from LCA an open loop stimulus. LCA (between wavelengths of 400 and 700 nm) changes little with change in each diopter of refractive error or accommodation. The small change in LCA amounts to: axial ametropia 0.012 to 0.017 D (0.6 to 0.9%), refractive ametropia 0.05 D (2.2 to 2.4%), and accommodation 0.04 to 0.05 D (2.1 to 2.6%) (Atchison, Smith, & Waterworth, 1993).

The grating stimuli can be represented graphically on orthogonal axes that represent  $\Delta L/L$  and  $\Delta M/M$  cone contrast.  $\Delta L$  and  $\Delta M$  represent the change in cone excitation for the L- and M-cones above the mean excitation level, and L and M represent the mean excitation of L- and M-cones (Fig. 1). Fig. 1 describes the location of the grating stimuli between 0 and 180 deg. The grating stimuli were represented in cone contrast space, in which the origin represents the adapting field.

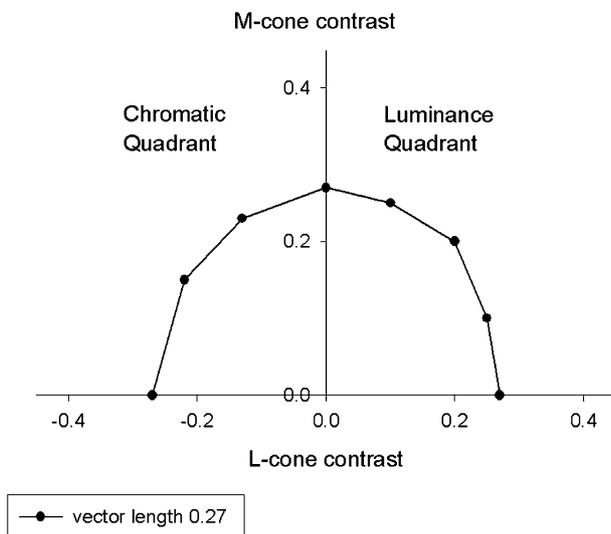


Fig. 1. The stimuli are represented in cone contrast space. The luminance quadrant (from 0 to 90 deg) and the chromatic quadrant (90 to 180 deg) are indicated. The stimuli are equi-distant from the origin with a vector length of 0.27. The stimuli in the luminance quadrant have L- and M-cone contrast in spatial phase ( $\pm 45$  deg), while the stimuli in the chromatic quadrant have L- and M-cone contrast in spatial counter-phase ( $\pm 45$  deg). The stimulus at 90 deg in cone contrast space simulates under-accommodation, while the stimulus at 0 deg simulates over-accommodation.

### 2.3. Stimulus conditions

Seven conditions tested loci that form a circle with equal vector length (0.27) (Fig. 1) at 0, 22.5, 45, 67.5, 90, 120, and 145 deg in cone contrast space. These seven conditions test the effect of different ratios of L- and M-cone contrast on the accommodation response. Stimuli at 0, 22.5, 45, 67.5, and 90 deg represent luminance stimuli; L- and M-cone contrasts are in phase in this quadrant and simulate the presence of LCA at luminance borders. Stimuli at 120 and 145 deg represent chromatic stimuli; L- and M-cone contrasts are in spatial counter-phase in this quadrant. At 120 deg M-cone contrast is greater than L-cone contrast, at 145 deg L-cone contrast is greater than M-cone contrast. This imbalance in L- and M-cone contrasts introduces a small luminance component into the chromatic stimulus and simulates LCA at chromatic borders.

The eighth condition was an empty field stimulus that was also the adapting field (CIE  $(x, y)$  co-ordinates (0.4554, 0.3835)). The adapting field is represented at the origin in cone contrast space and has zero contrast. All the gratings are created by modulating the L- and M-cone excitations around the empty field stimulus, the empty field stimulus represents the mean chromaticity of the gratings.

Each of the eight stimuli moved at 0.195 Hz sinusoidally towards and away from the eye between 1.00 D and 3.00 D (corrected for spectacle lens effectivity using the thin lens formula of Mutti, Jones, Moeschberger, & Zadnik (2000)), while the effects of LCA were neutralized with an achromatizing lens. As the stimulus moved sinusoidally towards and away from the eye, the dynamic stimulus included changes in dioptric vergence and luminance contrast that were the same for all conditions. The dynamic modulations tested for the optimal L/M cone contrast ratio in the stimulus for driving dynamic accommodation in the absence of LCA.

It is important to recognize that the stimuli in this experiment comprised both open loop and closed loop components. First, LCA of the subject's eye was neutralized by an achromatizing lens throughout the experiment, and since LCA from the eye was absent, the stimulus can be considered to be open loop. Second, the chromatic stimulus that was produced by altering the ratio of L/M cone contrast, and that simulated the effect of LCA with defocus, was also open loop (L/M cone contrast ratio did not change with defocus). Finally, the luminance stimulus was a closed loop stimulus (change in focus changes the luminance contrast of the stimulus). In summary, LCA of the eye and chromatic contrast provided an open loop stimulus, while luminance contrast of the target provided a normal closed loop stimulus for accommodation.

### 2.4. Procedure

During preliminary examinations case histories were recorded, and color vision (Nagel anomaloscope), subjective refraction, visual acuity, and amplitude of accommodation were measured. To begin experimental trials, trial lenses were inserted in front of the left eye to correct for ametropia and the right eye was patched. Subjects were positioned on a chin and headrest mounted on a three-way stage. Eye position and pupil diameter was monitored by video and the first Purkinje image was used to align the achromatic axis of the eye (Thibos, Bradley, Still, Zhang, & Howarth, 1990) with the optical axis of the system (Lee et al., 1999). Prior to the main experimental trials, accommodation responses were measured to a maltese cross target (140 Td) that moved sinusoidally toward and away from the eye (1.00–3.00 D; corrected for spectacle lens effectivity) at 0.2 Hz to determine the subject's ability to accommodate in white light and monochromatic light (550 nm; 10 nm bandwidth). Measurement of the accommodation response (gain) to white and monochromatic light provided information on the effects of a closed loop signal from LCA on the reflex accommodation response. There were three trials in both white and in monochromatic light, followed by six trials of each experimental condition (five trials for subject 20 and 21). The conditions were randomized without replacement within a block.

For the experiment trials subjects were dark adapted for 10 min prior to the trials and then adapted to the background field for 2 min prior to measurement, and also between conditions. The subject fixated on the stimulus grating while being re-aligned before the start of each trial. Each

trial lasted 40.96 s with 8 cycles of sinusoidal motion towards and away from the subject (1.00–3.00 D) per trial. The subject was instructed to “Keep the grating clear with as much effort as if you were reading a book” and to “Pay attention to the grating”.

### 2.5. Procedure for Nagel anomaloscope

A measure of each subject’s color vision was made on a Nagel Anomaloscope (Type 1). In the Nagel anomaloscope, an observer views a 2 deg split circular field. One half of the field is illuminated with a mixture of red (670 nm) and green (546 nm), the other half is illuminated with yellow (590 nm). These wavelengths do not appreciably stimulate the short-wavelength sensitive cones. A match between the two hemi-fields can be achieved by adjusting both the red/green ratio and brightness of the yellow field. Subjects are adapted to the internal “adapting light” for two minutes prior to making a match and between measurements to suppress the activity of the rod photoreceptors. The match point was taken as the average of three matches. The Rayleigh match range was found by determining if a given red/green mixture was perceived to match some radiance of the yellow field. In addition to the subjects examined for the main experiment, an additional 32 subjects were examined with the Nagel anomaloscope, to establish if the trends found in this experiment were consistent. Subjects with abnormal color vision were not included in the experiment. The anomaloscope was maintained in a temperature controlled room and kept at a constant voltage (Jägle, Pirzer, & Sharpe, 2005).

The red/green match point in a color normal individual is around a value of 42–46, with a brightness match of around 17. In a deuteranomalous subject the peak sensitivity of the middle-wavelength pigment has shifted slightly towards longer wavelengths compared to normal. As a result the deuteranomalous individual is less sensitive to 546 nm and will require more green to match the test yellow and the value of the red/green match is set around 30. Protanomalous subjects, in whom the peak sensitivity of the long-wavelength pigment is shifted towards shorter wavelengths, are less sensitive than normal to 670 nm. As a result they require more red to match the test yellow, and the value of the red/green match is higher than normal around 50.

The brightness match also changes with color abnormalities. Since the wavelength sensitivity of the long-wavelength pigment is closely matched to the  $V_\lambda$  function, a shift in sensitivity of the long-wavelength pigment reduces the apparent brightness of the red/green mixture field, and the brightness of the yellow field must be reduced to form a match. A color normal subject will match the brightness of the red/green field at a value of around 17, while a protanomalous subject will form a match at lower values. A shift in the spectral sensitivity of the middle-wavelength sensitive pigment has little effect on the perceived brightness of the mixture field. Thus the deuteranomalous individual will set the brightness match at a level similar to those with normal color vision.

### 2.6. Subjects

Subjects were excluded from the study for significant ocular injury or disease, history of amblyopia, defective color vision, excessive blinks, or low gain in monochromatic light. Since subjects demonstrate variability in response to monochromatic targets (Fincham, 1951; Kruger et al., 1993; Kruger et al., 2004, 2005; Lee et al., 1999) subjects with accommodation dynamic gain of less than 0.2 in monochromatic light to a high contrast maltese cross target, were excluded. Hence, only subjects that responded very poorly in monochromatic light were excluded. Sixteen subjects presented, one was excluded for corneal surgery, one for color deficiency, one for excessive blinking, and four for poor gain in monochromatic light. Nine subjects were included in the experiment. Subjects had spherical refractive errors ranging from +2.00 D to –4.75 D. The student subject selection pool was predominantly myopic.

Exclusion of subjects with poor gain in monochromatic light was necessary to distinguish between a weak response in monochromatic light and a lack of response to the stimuli in cone contrast space. A previous experiment (Rucker & Kruger, 2004b) has indicated that with a cut off at this level a chromatic effect can still be measured between conditions, and

luminance sensitive responses can be isolated from noise. Trials with excessive blinks (>20%) or artifacts were excluded.

Subjects gave informed consent, the experiment was approved by the Institutional Review Board of the college, and followed the tenets of the Declaration of Helsinki. Subjects ranged from eighteen to twenty-nine years old and were paid for participation. Refractive errors were corrected either by contact lenses or trial lenses.

### 2.7. Analysis

The effects of blinks were removed from the data using standard signal processing before analysis. Dynamic gain, temporal phase lag, and mean accommodation level were used as measures of the sensitivity of the accommodation system to changes in L/M cone contrast ratios. Dynamic gain and phase lag were calculated after Fourier analysis of the data from each trial, as the ratio of response amplitude to stimulus amplitude at the stimulus frequency (0.195 Hz). Mean gain and phase lag were calculated for each condition using vector averaging. Mean accommodation level was calculated as the mean accommodation response (D) over the duration of the trial.

### 2.8. Iso-response contours

The iso-response contour indicates the amount of L- or M-cone contrast producing a constant response at different locations in cone contrast space (Stromeyer et al., 1995; Tsujimura, Wolffsohn, & Gilmartin, 2001). The advantage of finding an iso-response contour is that the cone contribution to the controlling mechanism can be determined from the gradient of the slope (see Fig. 2). Another way to describe the slope of the contour is with an orthogonal vector (see Fig. 2). The orthogonal vector can be described in terms of the vector angle and the vector length. The vector angle describes the angle between the horizontal axis and the vector, the luminance vector will be in the first quadrant, and the chromatic vector in the second quadrant in cone contrast space. The luminance and chromatic vectors should be orthogonal, since one represents an additive function and the other a subtraction function, but the cone weighting to the respective mechanisms can alter this relationship. Vector angles therefore pro-

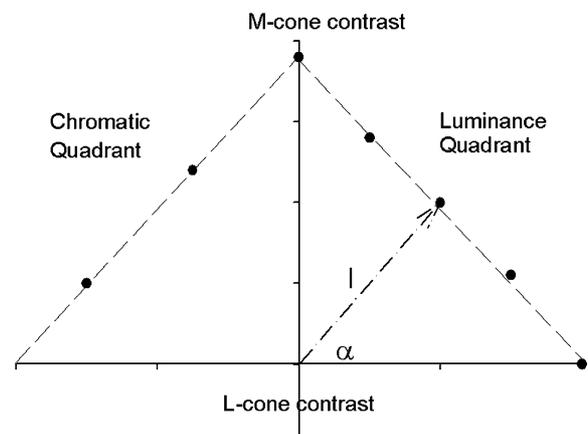


Fig. 2. Diagram shows the iso-response contour (---), vector angle ( $\alpha$ ), and vector length ( $l$ ). The luminance quadrant is shown in the region between 0 and 90 deg. The chromatic quadrant is shown in the region between 90 and 180 deg. The graph represents the amount of L- and M-cone contrast required to produce a fixed reflex accommodation response, the iso-response contour is a line drawn through these points. The controlling mechanism is then found orthogonal to this contour as shown by the vector. The vector angle ( $\alpha$ ) indicates the relative cone weighting of the L- and M-cone signals to the reflex accommodation response. A small angle indicates a greater L-cone weighting. The length of the vector ( $l$ ) is an indicator of the sensitivity of the controlling mechanism, the closer the iso-response contour is to the origin the more sensitive the controlling mechanism.

vide information on the relative sensitivity of the luminance and chromatic controlling mechanisms to long- and middle-wavelength cone contrast.

An additional advantage of describing the contour in terms of an orthogonal vector is that the sensitivity of the detection mechanism can be determined from the length of the vector. The shorter the vector length the less cone contrast is required to produce the response, indicating high sensitivity to cone contrast. The longer the vector length the more contrast is required to produce the same response suggesting that the mechanism is less sensitive to cone contrast. Comparison of the vector length between subjects provides information on the relative sensitivity of the detecting mechanism.

Iso-response calculations assume a linear relationship between gain and the L- and M-cone contrast of the retinal image. A linear relationship for dynamic gain and luminance contrast was confirmed in a previous experiment (Rucker & Kruger, 2004b).

### 3. Results

The results of the preliminary color vision testing suggest that myopes demonstrate a low normal Rayleigh match value. Red/green match values decreased with increasing myopia while brightness matching levels were normal. The match values for myopes ( $\leq -0.50$  D) had a mean value of 39.7 (range 35.5–42), with a mean brightness level of 15.6. The mean match values for emmetropes and hyperopes ( $\geq 0$  D) was 42.9 (range from 37.33 to 46) with a mean brightness level of 15. The width of the “match range” ranged from 1 to 6, with the exception of subject 21 who had a match range of 17 points (low range 27, high range 44). The narrow range and location of the match value indicates that although subjects showed a low normal match value, they were not deuteranomalous per se. The decrease in match value with myopia was confirmed by examining an additional 32 subjects. In Fig. 3 the match value for all 43 subjects is plotted against refractive error. High myopes and low myopes were significantly different to

emmetropes and hyperopes ( $F=6.37$ ,  $p=0.0009$ , ANOVA;  $p=0.03$ ,  $p=0.001$  two tailed  $t$ -test), but not to each other. The results confirm the decrease in the match value with myopia found in the main experiment, and extend the refractive error range up to  $-8.75$  D.

The iso-response contours for gain showed a shift in the vector angle of the iso-gain contour with refractive error. Iso-response contours in the luminance quadrant were drawn for each subject. The vector angles in the luminance quadrant were calculated for each subject (Fig. 4: all graphs are drawn on the same scale to allow comparisons between subjects and respective refractive errors; individual  $r^2$  values are shown). The graphs show a decrease in the vector angle with increasing myopia.

Fig. 5 shows the vector angle plotted as a function of refractive error. There was a significant change in vector angle with refractive error ( $p=0.01$ ;  $F=10.83$ ; ANOVA) with a positive correlation between the vector angle for dynamic gain and refractive error ( $r=0.78$ ;  $r^2=0.61$ ). As myopia increased the vector angle for dynamic gain decreased, indicating an increase in the relative sensitivity to the long-wavelength component of the dynamic luminance signal.

Fig. 6 shows the mean accommodation level for an equichromatic stimulus at 45 deg plotted as a function of refractive error. There was a significant difference in the mean accommodation response to the L/M cone contrast ratio of the image with refractive error ( $p<0.01$ ;  $F=11.42$ ; ANOVA). Mean accommodation level showed a positive correlation with myopia ( $r=0.79$ ;  $r^2=0.62$ ), thus the mean accommodation level increased with myopia.

To examine the relationship between the vector angle for dynamic gain and mean accommodation level, the mean accommodation level was plotted as a function of vector angle (Fig. 7). There was a good correlation between the mean accommodation level and vector angle for dynamic gain (multiple  $r=0.79$ ;  $r^2=0.63$ ). The change in mean accommodation level with vector angle was significant ( $p=0.01$ ;  $F=12.05$ ; ANOVA). Myopic eyes had high mean accommodation levels and small vector angles, while emmetropic and hyperopic eyes had lower mean accommodation levels and an increased vector angle for dynamic gain. Thus the increased sensitivity to L-cone contrast in the luminance component of the grating in myopes was correlated with an increased mean accommodation level.

The iso-response vector provided information on the sensitivity of the luminance mechanism to the stimuli. The luminance vector length for each subject ranged from 0.20 to 0.63, but there is no correlation between luminance vector length and refractive error ( $r=0.17$ ;  $p=0.65$ ;  $F=0.219$ ; ANOVA). Fig. 8 shows vector length plotted as a function of refractive error. Thus there was no clear relationship between the sensitivity to luminance contrast per se and refractive error.

The results indicate that for accommodation the relative sensitivity of the luminance sensitive mechanism to L-cone contrast appears to increase with myopia, and that this

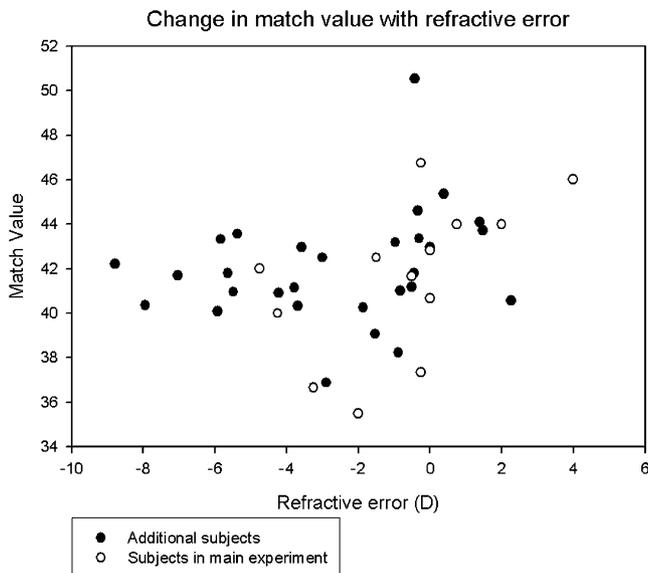


Fig. 3. Nagel anomaloscope match values were plotted as a function of refractive error. The normal match value is considered to be around 42–46, but the match value was lower for subjects with myopia; more green was needed to match the red field. This indicates an increased sensitivity to the red component of the test relative to the green.

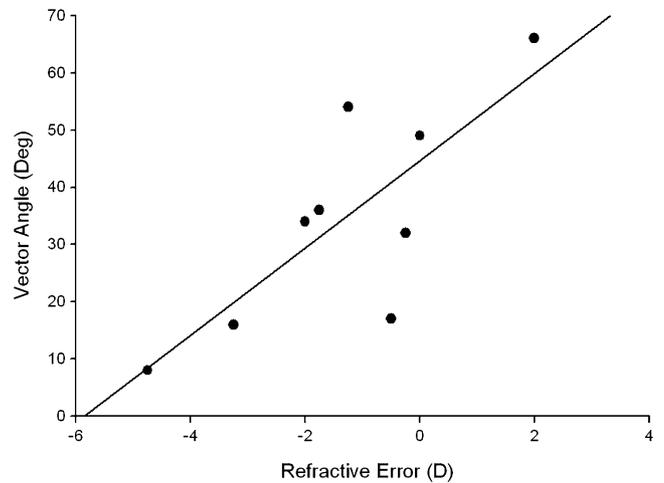
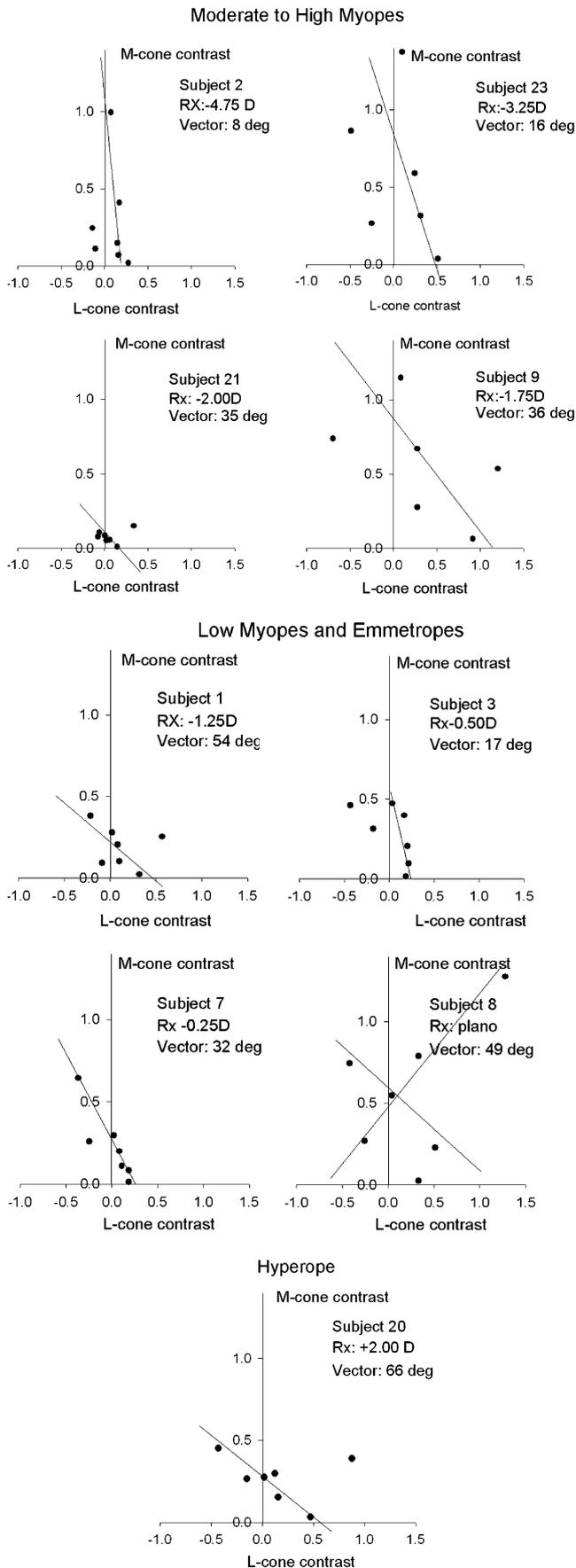


Fig. 5. The vector angle for each subject is plotted as a function of refractive error. Vector angle decreased with increasing myopia. The L-cone weighting to the luminance mechanism for reflex accommodation increased with increasing myopia.

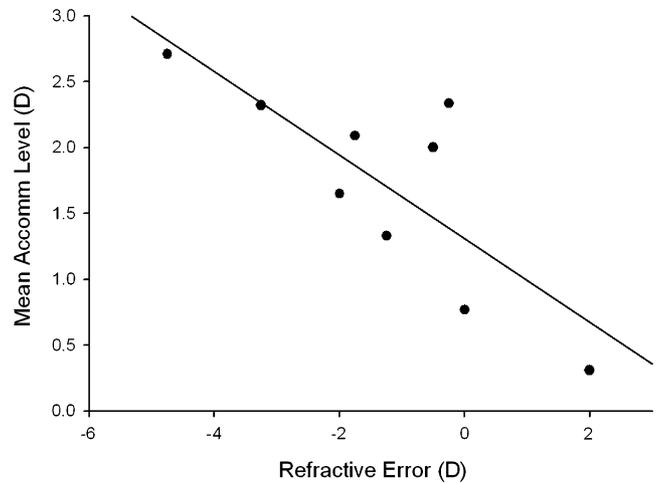


Fig. 6. The mean accommodation level (to the stimulus at 45 deg) is plotted as a function of refractive error. An increase in myopia was correlated with an increase in the mean accommodation level.

increase is correlated with an increase in the mean accommodation level. This relative increase in L-cone weighting to the luminance mechanism does not increase sensitivity of the reflex accommodation system to luminance contrast per se.

#### 4. Discussion

We have shown that the dynamic gain of accommodation depends on both the wavelength composition of the stimulus and the refractive error of the subject: the more myopic a subject is, the more the gain is enhanced by

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Fig. 4. Iso-gain contours for dynamic gain are calculated for each subject and plotted on graphs with identical scales to allow for comparison of the vector angles between subjects. The refractive error and vector angle is indicated on each graph. The vector angle decreases with increasing myopia indicating an increasing L-cone weighting to the luminance signal for reflex accommodation.

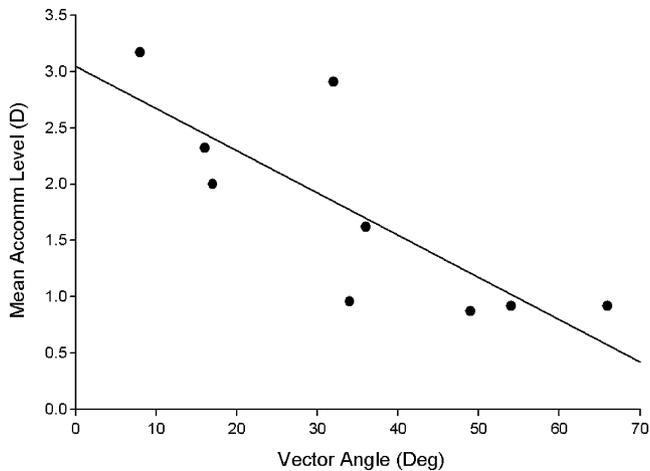


Fig. 7. The mean accommodation level is plotted as a function of the vector angle. Mean accommodation level increased with increased L-cone weighting of the luminance signal for reflex accommodation.

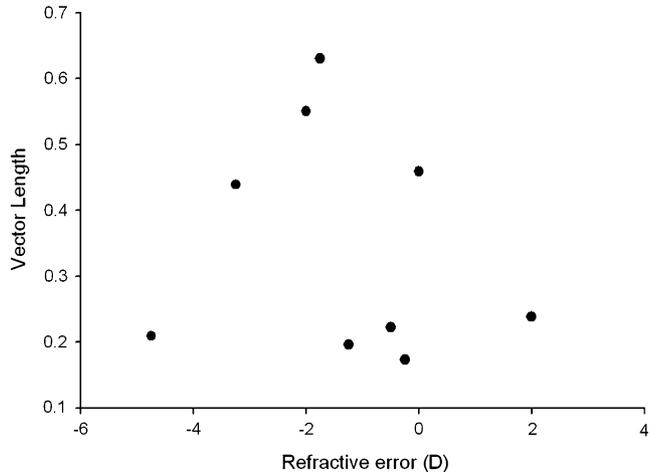


Fig. 8. Vector length is plotted as a function of refractive error. There was no correlation between vector length and refractive error. Sensitivity of the reflex accommodation system to luminance contrast did not change with refractive error.

increased stimulation of L-cones. In this experiment the dynamic response was mediated by a luminance controlled mechanism since the effects of chromatic aberration were neutralized by a specially designed lens. Iso-response contours were evident in the luminance quadrant for all subjects. Although there was no correlation in the overall sensitivity to luminance contrast with refractive error, the relative sensitivity to L- and M-cone contrast showed a good correlation. In this experiment the vector angle for dynamic gain decreased with increasing myopia, indicating an increased sensitivity to L-cone contrast relative to M-cone contrast in the luminance signal for reflex accommodation for myopes.

Increased L-cone sensitivity in myopes may affect the mean accommodation level since the accommodative control mechanism is thought to pursue maximum luminance contrast. In an eye with longitudinal chromatic aberration the location of the in-focus plane, that produces maximum

luminance contrast, changes with the L/M cone sensitivity ratio. Increased sensitivity of long-wavelength cones relative to middle-wavelength cones will bias the point of maximal luminance contrast towards long-wavelengths. Thus, in a subject with a high L/M cone ratio, maximum luminance contrast would be found at a focus plane biased towards longer wavelength light prompting over-accommodation (relative to a 550 nm in focus calibration). In a subject with a low L/M cone ratio maximum luminance contrast would be found at a focus plane biased towards shorter wavelengths. When the ratio is 0 (M-cone only) the peak of the  $V\lambda$  function is 543 nm, and when the ratio is 1 (L-cone only) the peak of the  $V\lambda$  function is 566 nm. The dioptric difference between these two extremes is only 0.12 D, requiring an alternative explanation for the difference in the mean accommodation level.

One alternative would be chromatic signals from longitudinal chromatic aberration which have been found to direct a signed accommodation response (Aggarwala et al., 1995a; Aggarwala et al., 1995b; Campbell & Westheimer, 1959; Fincham, 1951; Kotulak et al., 1995; Kruger & Pola, 1986; Kruger et al., 1993; Kruger et al., 1995; Kruger et al., 1997a). A shift of the spectral sensitivity towards one or other cone type may bias the spectral location of the neutral point for a chromatic mechanism. For example, a bias of the spectral sensitivity of middle-wavelength cones towards long-wavelengths as in deuteranomaly shifts the location of the neutral point towards longer wavelengths increasing the relative sensitivity to red light as opposed to green.

Increased sensitivity to red in myopes may affect the accommodative control mechanism's pursuit of a chromatic neutral point as "unique yellow" is shifted towards longer wavelengths. Although plastic neural mechanisms can correct for this bias the correction is not always complete, and unique yellow can show some variation (Neitz, Carroll, Yamauchi, Neitz, & Williams, 2002). Neitz et al. (2002) found that the neutral point for five deuteranomalous men ranged from  $602.6 \pm 1.5$  to  $613.4 \pm 1.6$  nm compared to the average value of 578 nm. As a result the chromatic control mechanism for a deuteranomalous subject reaches a null at slightly longer-wavelengths than for a color normal subject. To achieve a null at longer wavelengths, accommodation would increase to place longer wavelengths on the retina (in an eye with chromatic aberration). This suggests that myopes with a low normal Rayleigh match value would accommodate more than hyperopes and emmetropes, who have a normal or high normal Rayleigh matches. Correlation of a subject's color vision with refractive error in this experiment (Fig. 3) and in a previous experiment (Wienke, 1960), suggest that color may indeed be a factor that links refractive error with accommodation efficacy of the individual subject.

Factors that affect the Rayleigh color match, include pre-receptoral filtering, differences in photo-pigment optical density or pigment polymorphism (He & Shevell, 1995; Pokorny & Smith, 1976; Sanocki, Teller, & Deeb, 1997).

Pre-receptoral filtering refers to light absorption by inert lens pigmentation and macular pigment, and pigment polymorphism refers to the polymorphism in the amino acid sequence of the opsins in L- and M-cone photo-pigments. Photo-pigment optical density is dependent on the concentration of the photo-pigment molecules and the length of the outer segment of the photoreceptor, factors that affect the probability of photon capture.

Pre-receptoral filters, differences in photo-pigment optical density, and pigment sensitivity also will affect the contrast of the stimuli used in this experiment and the resultant estimate of the L/M cone ratios. Pre-receptoral filters will absorb short-wavelength light and reduce the excitation of L- and S-cones compared to the average observer. The effects of optical density are complicated and depend not only on the optical density of the cones (Pokorny & Smith, 1976), but on the relative optical density of the L- and M-cones (He & Shevell, 1995). The result is that there will be an apparent decrease in the L/M cone ratio when the subject has higher than average amounts of pre-receptoral filters and low optical density, and an increase when the subject has lower than average amounts of pre-receptoral filters and high optical density. It is estimated that the vector angle measured in this experiment would decrease over a range of 8 deg, when the optical density varies from a high value of 0.6 (maximum optical density found in fovea) to a low value of 0.1 (as found in the retinal periphery). This is small compared to the 50 deg range found in this experiment. Also, since accommodation is predominantly a foveal response (Fincham, 1951) the effects of optical density may be limited, but the smaller vector angles found in the hyperopic subject could potentially be partially due to this effect.

A shift in pigment sensitivity compared to the average subject will change the Rayleigh match value, but it will also affect the effective stimulus contrast when the stimuli are created using Smith and Pokorny fundamentals (Smith & Pokorny, 1975). As a result the pigment shift will affect the estimate of the L/M ratio. As the Rayleigh match for an individual shifts towards lower values the subject will get less M-cone contrast from the stimulus than predicted from the Smith and Pokorny fundamentals, and as a result they will appear to be less sensitive to M-cone contrast and relatively more sensitive to L-cone contrast. Consequently, there will be an apparent increase in the estimate of the L/M cone contrast ratio. Indeed in this experiment, when Smith and Pokorny fundamentals are used to predict cone contrast, a 10 nm shift in the peak of the pigment sensitivity curve towards longer wavelengths will cause a 5 deg increase in the angle of the iso-response contour indicating an apparent increase in sensitivity to L-cone contrast relative to M-cone contrast. These calculations suggest that a small shift in pigment sensitivity within the normal range, which affects the Rayleigh match, could contribute to the apparent increase in the L/M cone ratio of myopic subjects, but again the effect is small relative to the measured change in vector angle with refractive error.

A small shift in pigment sensitivity may arise from genetic differences in the spectral sensitivity of the photo-pigments, biasing the weighting for the luminance mechanism towards a particular cone type. The most common polymorphism, the serine/alanine 180 polymorphism, causes a 4–5 nm shift in the sensitivity of the long-wavelength sensitive cone pigment and has been correlated with differences in the Rayleigh color match (Sanocki, Shevell, & Winderickx, 1994). The Rayleigh matches for the subjects in this experiment were in the low normal range and serine–alanine polymorphism could potentially contribute to the lower match point and the increased L-cone sensitivity to the luminance signal for accommodation. A future experiment could examine the genetic differences in the spectral sensitivity of the photo-pigments between refractive groups.

Relative differences in the numbers of L- and M-cones will also affect the weighting for the luminance mechanism towards a particular cone type. Indeed there is a wide variation among subjects in the ratio of L:M cones in the retina (Carroll, McMahon, Neitz, & Neitz, 2000; Hagstrom, Neitz, & Neitz, 1998; Kremers et al., 2000; Roorda & Williams, 1999; Wesner, Pokorny, Shevell, & Smith, 1991). A bias towards increased numbers of L-cones relative to M-cones could weight the sensitivity of the luminance mechanism towards L-cone contrast.

In addition to the above factors, chromatic adaptation can affect the estimate of the L/M ratio (Pokorny, Jin, & Smith, 1993) for light levels above 50 Td. Inequality in the L- and M-cone excitation produced by the stimulus can result in unequal adaptation in the L- and M-cones and produce an apparent change in the L/M cone ratio. In this experiment the retinal illumination was only 140 Td, and the L/M cone sensitivity ratio for the adaptation field in this experiment was in the range of 1.53–1.68:1 (depending on the optical density (0.1–0.6), lens pigment, or deuteranomalous (10 nm) shift in pigment sensitivity). This sensitivity ratio is close to the ratio of 1.24:1, at 570 nm, for which Pokorny et al. (1993) found little change in cone weighting with an increase in retinal illuminance.

Another explanation for the low normal Rayleigh match and the increased L/M cone ratio found in myopes, is that the effects may be by-products of better focus for long-wavelength light. Focus for uncorrected myopes is typically in front of the retina, and since long-wavelength light is refracted less strongly than short-wavelength light as a result of LCA, long-wavelength light will focus closer to the retina than short-wavelength light. This paradigm will result in higher L-cone contrast and reduced M-cone contrast in the retinal image of the uncorrected myope. This could have the effect of increasing sensitivity to red relative to green, and increasing the cone weighting to the luminance mechanism. In addition, it is an effect that would be exacerbated by cone polymorphism or a relative increase in L-cone numerosity.

A final factor that could have affected the results includes the considerable variation in the “dynamic” accommodation response (gain) among subjects. The wide

variation in gain is typical in accommodation experiments of this type, and confirms previous results that show wide variation in dynamic gain to monochromatic stimuli (e.g., Aggarwala et al., 1995a, 1995b; Campbell & Westheimer, 1959; Charman & Tucker, 1978; Fincham, 1951; Kruger et al., 1993, 1997a; Kruger, Mathews, Katz, Aggarwala, & Nowbotsing, 1997b). Gain values ranged from zero to 0.4 in response to the dynamic stimulus. Gain values would have been higher if a higher contrast stimulus had been used (Mathews & Kruger, 1989), but the contrast of the stimulus (27%) was limited by the physical capabilities of the display monitor. Gain also would have been higher with a closed loop stimulus for LCA (Aggarwala et al., 1995a, 1995b), since the gain for a dynamic accommodation response in white light is greater than the gain for a dynamic accommodation response in monochromatic light. Nevertheless, the variability in gain among subjects is a common finding in accommodation experiments.

It is perhaps a different question why increased short wavelength cone contrast can also bias accommodation toward near (Rucker & Kruger, 2004a). The plane of focus for maximum luminance contrast (LM-cones) would have 556 nm imaged on the retina, causing long wavelengths to be focused close behind the retina and short wavelengths to be focused in front of the retina. On the other hand, a blue/yellow (S minus LM cones) color signal will be greatest when short wavelengths are focused on or behind the retina. Thus, if short-wavelengths are focused 2.00 D behind the retina, S-cone contrast would be close to threshold for a 3 c/d grating, while LM-cone contrast would be well below threshold. If accommodation increased, creating the equivalent defocus for short-wavelengths (S-cones) 2.00 D in front of the retina, long wavelengths (LM-cone contrast) would be well above threshold. Thus, under-accommodation (image behind the retina) might be signaled by reduced LM-cone contrast (luminance contrast) and predominance of S-cone contrast (blue color). Whereas, over-accommodation might be signaled by a predominance of LM-cone contrast (luminance contrast) over the detection of S-cone contrast (blue color) contrast. Thus, luminance contrast and color contrast will produce competing luminance and color contrast signals for accommodation.

If over-accommodation results in a myopic image there should not be any myopic progression, unless the eye does not consider the myopically defocused image to be “out of focus”. In myopes the luminance sensitive mechanism may be attempting to maximize luminance contrast by accommodating to place longer wavelengths on the retina. At the same time the chromatic red/green mechanism may be attempting to reach a “neutral point”, (the contrast for blue will be reduced when 555 nm is focused on the retina). The red/green chromatic “neutral point” is typically at 578 nm, at a focal plane that lies 0.14 D distal to the lens than the focal plane for maximal luminance contrast in an average eye. If however, the chromatic null lies closer to 613 nm, as in some deuteranomalous observers, the discrepancy may be as great as 0.30 D when the eye is focused at 555 nm.

Thus, an increase in sensitivity to long-wavelength light may be associated with a chromatic signal for eye growth. A chromatic signal for eye growth has been demonstrated by Rucker, Adeusi, and Wallman (2006).

The increased mean accommodation level for myopes found in this experiment is contrary to the increased lag of accommodation found in other experiments for the 2.00 D stimulus level (McBrien & Millodot, 1986; Gwiazda, Thorn, Bauer, & Held, 1993, 1995; Gwiazda et al., 2004; Abbott et al., 1998; Mutti et al., 2006) and (see Chen, Schmid, & Brown, 2003 for review) at other dioptric levels. Gwiazda et al. (1993, 1995, 2004) found that young progressing myopes have a weaker accommodation response to induced negative defocus, and a slightly greater lag of accommodation to near targets. Child emmetropes accommodated only 1.00 D, to a 2.00 D target, while the child myopes accommodated 0.75 D. The accommodation lag was predominantly found with higher accommodative demand (>3.00 D), and with negative lens induced blur (Abbott, Schmid, & Strang, 1998; Gwiazda et al., 1993, 1995). McBrien and Millodot (1986) also found that myopes accommodated less than emmetropes at the 2.00 D stimulus level, but the difference was very small (0.15 D). It was only at the 4.00 D and 5.00 D stimulus levels that significant differences were found. Mutti et al. (2006) found an accommodative lag in children after the year of onset of myopia, with a 2.00 D Badal stimulus, but not before this period. In these experiments accommodation was measured with a Canon R-1 autorefractor with open field of view and an annular measurement zone of 3.0–3.8 mm diameter or with a Grand Seiko WR 5100-K. In contrast, our measurements were made with a Badal optometer with a restricted field of view, with a 3 mm artificial pupil diameter that minimizes monochromatic aberrations.

The results of the current experiment agree with other studies that have found a greater, or equal accommodation response in myopes (Abbott et al., 1998; Schaeffel, Weiss, & Seidel, 1999; Strang, Gray, Mallen, & Seidel, 2004). Abbott et al. (1998) using a Canon Autorefractor and distance induced blur, found that while progressing myopes accommodated accurately to a 2.00 D stimulus level, adult emmetropes and stable myopes over-accommodated by about 0.25 D. Schaeffel et al. (1999) found that at a stimulus distance of 30 cm, both myopes and emmetropes under-accommodated equally, and at 1 m emmetropes accommodated less than myopes. These measurements were made with a photorefractor, which unlike the Canon Autorefractor uses the entire pupil area to derive the measurement. The conflicting results may be attributed to many factors: the accommodation stimulus level, the correction for spectacle lens effectivity, the amount of spherical aberration, the grouping of subjects into progressive and stable myopes, the size of the stimuli, and the presence of multiple accommodation cues.

Spectacle lens effectivity is the change in the accommodation stimulus at the entrance pupil (or cornea depending on the point of reference) with the distance of the spectacle correcting lens from the eye. The effects of spectacle lens

effectivity may explain some of the apparent accommodation lag in myopes (see Buehren & Collins, 2006). Higher myopic corrections reduce the effective accommodation stimulus and produce an apparent lag in the response. For example using Mutti et al.'s (2000) thin lens formula, for a 33 cm (3.00 D) stimulus the effective accommodation stimulus is only 2.64 D when wearing a  $-3.00$  D spectacle lens (back vertex distance 15 mm), and for  $-6.00$  D spectacle lens the stimulus is reduced to 2.42 D, producing an apparent lag of 0.58 D. For a stimulus at 20 cm the accommodation stimulus is reduced to 4.25 D when a  $-6.00$  D spectacle correcting lens is placed 15 mm in front of the entrance pupil, producing an apparent 0.75 D lag. As the accommodation stimulus increases, the error from spectacle lens effectivity also increases. As a result the apparent accommodation lag increases for myopes at higher stimulus levels and with larger refractions.

Spherical aberration and pupil size also affect the apparent accuracy of the accommodation response (Collins, Buehren, & Iskander, 2006; Hazel, Cox, & Strang, 2003). The Canon R1, which does not adjust for changes in pupil size or spherical aberration, is significantly affected by the effects of spherical aberration (Collins, 2001). The apparent accommodation error due to spherical aberration is highly correlated with a measured lead or lag in accommodation when the pupil size is greater than 3 mm (Buehren & Collins, 2006). However, for a 3 mm pupil that was used in the current experiment there is no correlation between these factors (Buehren & Collins, 2006). Thus the difference in the results between this experiment and those that have shown a lag of accommodation may be largely explained by the difference in the amount of spherical aberration present and by the stimulus error induced by spectacle lens effectivity.

To summarize, sensitivity to the long-wavelength component of the luminance signal and to the color signal appeared to increase with myopia, and was correlated with an increased mean accommodation level. The apparent change in sensitivity to the long-wavelength, luminance, and chromatic component of the accommodation signal may be due to the effects of LCA with myopic defocus, or at least partially to a shift (within the normal range) in the cone pigment sensitivity of myopic subjects possibly as a result of pigment polymorphism. In addition, differences in the relative numbers of L- and M-cones may have contributed to the increased L-cone weighting to the luminance component of the accommodation signal.

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