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Cone signals for spectacle-lens compensation: Differential responses to short and long wavelengths

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Abstract

Chick eyes compensate for defocus imposed by spectacle lenses by making compensatory changes in eye length and choroidal thickness, a laboratory model of emmetropization. To investigate the roles of longitudinal chromatic aberration and of chromatic mechanisms in emmetropization, we examined the participation of different cone classes, and we compared the efficacy of lens compensation under monochromatic illumination with that under white light of the same illuminance to the chick eye.

Chicks wore positive or negative 6 D or 8 D lenses on one eye for three days, under either blue (460nm) or red (620nm) light at 0.67 lux or under white light at 0.67 or 0.2 lux (all measures are corrected for chick photopic sensitivity). The illumination conditions were chosen to differentially stimulate either the short-wavelength and ultraviolet cones or the long-wavelength and double cones. Measurements are expressed as the relative change: the inter-ocular difference in the amount of change over the three days of lens wear.

We find that under this low illumination the two components of lens compensation were differentially affected by the monochromatic illumination: in blue light lens compensation was mainly due to changes in eye length, whereas in red light lens compensation was mainly due to changes in choroidal thickness. In general, white light produced better lens compensation than monochromatic illumination.

Negative lenses—Under white light negative lenses caused an increase in eye length (60 μm) together with a decrease in choroidal thickness (-51 μm) relative to the fellow eye. Under blue light, although there was an increase in eye length (32 μm), there was no change in choroidal thickness (5 μm). In contrast, under red light there was a decrease in choroidal thickness (-62 μm) but no increase in eye length (8 μm). Relative ocular elongation was the same in white and monochromatic light.

Positive lenses—Under white light positive lenses caused a decrease in eye length (-142 μm) together with an increase in choroidal thickness (68 μm) relative to the fellow eye. Under blue light, there was a decrease in eye length (-64 μm), but no change in choroidal thickness (2 μm). In contrast, under red light there was an increase (90 μm) in choroidal thickness but less of a decrease (-36 μm) in eye length. Lens compensation by inhibition of ocular elongation was less effective under monochromatic illumination than under white light (white v red: p=0.003; white v blue p=0.014).

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The differential effects of red and blue light on the choroidal and ocular length compensatory responses suggest that they are driven by different proportions of the cone-types, implying that, although chromatic contrast is not essential for lens compensation and presumably for emmetropization as well, the retinal substrates exist for utilizing chromatic contrast in these compensatory responses. The generally better lens compensation in white than monochromatic illumination suggests that longitudinal chromatic aberration may be used in lens compensation.

Keywords

Monochromatic light; longitudinal chromatic aberration; emmetropization; myopia; choroid; sclera; hyperopia; ocular length; choroidal thickness

Introduction

When the eyes of young animals have myopia or hyperopia imposed by positive or negative spectacle lenses, the eyes compensate, returning the eyes to their former near-emmetropic state (Smith, 1998; Wallman & Winawer, 2004; Wildsoet, 1998). This compensation is accomplished in part by a slowing down or speeding up of the increasing eye length (marmosets: Graham & Judge, 1999; macaques: Hung, Crawford & Smith, 1995; chickens: Irving, Sivak & Callender, 1992; Schaeffel, Glasser & Howland, 1988; tree shrews: Siegwart & Norton, 1993; guinea pigs: McFadden, Howlett & Mertz, 2004) and in part by a thickening or thinning of the choroid (chickens: Wallman, Wildsoet, Xu, Gottlieb, Nickla, Marran, Krebs & Christensen, 1995; Wildsoet & Wallman, 1995; guinea pigs: Howlett & McFadden, 2006; marmosets: Troilo, Nickla, Wildsoet, 2000; tree shrews; Shaikh, Siegwart & Norton, 1999; macaque monkeys: Hung, Wallman & Smith, 2000). Two questions concern us about this process: (a) how does the eye discern the sign of defocus from the blurred image? (b) Do the same retinal signals drive both the choroidal changes and the changes in eye length?

With respect to the first question, an attractive possibility is that the eye utilizes a chromatic mechanism that detects the changes in color at edges that occur with defocus as a result of the eye's longitudinal chromatic aberration — the fact that blue light is focused by the eye in front of red light —, as it does in ocular accommodation by comparing cone contrast (Rucker & Kruger, 2004a). Alternatively, any of several monochromatic aberrations of the eye, such as spherical aberration, could also be employed, as could the amount of accommodation, or the amount of blur (Norton & Siegwart, 1995; Wallman & Winawer, 2004; Wildsoet, 1997).

Previous studies of lens-compensation and of recovery from form deprivation by rearing chicks under monochromatic illumination have failed to identify a role for longitudinal chromatic aberration (Rohrer, Schaeffel & Zrenner, 1992; Schaeffel & Howland, 1991; Wildsoet, Howland, Falconer & Dick, 1993). These results demonstrate that longitudinal chromatic aberration is not the only cue used, but they do not rule out the possibility that longitudinal chromatic aberration is employed along with other cues.

As a first step in investigating the chromatic mechanisms in emmetropization, we examined the role of different cone classes in lens-compensation by comparing the efficacy of lens compensation under monochromatic illumination and white light. There are five different cone types in chicks (Bowmaker & Knowles, 1977): long-wavelength-sensitive cones (L-cones), middle-wavelength-sensitive cones (M-cones), short-wavelength-sensitive cones (S-cones), ultra-violet-wavelength sensitive cones (UV-cones), and double cones (D-cones). D-cones have a broad spectral sensitivity that encompasses that of the L- and M-cones and extends into the short-wavelength region. In the present experiment we were able to isolate the two cone populations sensitive to short wavelengths (S- and UV-cones) from the other cone types (D-,

L- and M-cones) by using illuminances close to the lower boundary of lens compensation in white light.

Because the utility of longitudinal chromatic aberration in providing a defocus error signal would be greater if the receptors involved covered a larger wavelength range (a small wavelength range would fall within the depth of focus of the eye), we were especially interested in whether the short-wavelength-sensitive cones participate in lens compensation. Previous studies have demonstrated that S-cones contribute to the reflex accommodation response (Kruger, Rucker, Hu, Rutman, Schmidt & Roditis, 2005; Rucker & Kruger, 2001; Rucker & Kruger, 2004b) suggesting a chromatic component to the reflex accommodation response. With regards to emmetropization, Rohrer, et al. (1992) have shown that the UV-cones do not show a lens compensation response (when +4.00 D lenses were worn on one eye and -4.00 D lenses were worn on the other eye).

With respect to the question of the retinal signals responsible for changes in choroidal thickness and eye length, it would seem most parsimonious that, once the retina determined whether the eye were myopic or hyperopic, the same retinal signal that would direct changes in both the choroidal thickness and eye length. However, there is some evidence of visual manipulations that affect one response more than the other. For example, twice-daily brief episodes of wearing positive lenses cause compensatory changes in eye length but not in choroidal thickness, whereas such episodes of negative lenses do not cause compensatory changes in eye length but do cause compensatory changes in choroidal thickness (Winawer & Wallman, 2002 ; see Discussion for more examples). Such findings do not unequivocally implicate independent retinal control of the two responses because differences in sensitivity might account for the differential effects. Thus, inhibition of ocular elongation by positive lenses might be more sensitive to defocus than choroidal thickening, whereas stimulation of ocular elongation by negative lenses might be less sensitive to defocus than choroidal thinning. In the present study, we find additional evidence for separate signals controlling choroidal thickness and ocular elongation.

Methods

The basic experiment measured the difference in eye growth between the lens-wearing and fellow eye when chicks were kept in a drum environment, and both eyes were exposed to dim monochromatic light, which was chosen to isolate either short-wavelength and UV-wavelength sensitive cones or long-wavelength sensitive and double cones, or to white light. In a second experiment the chick had episodes in the drum environment under monochromatic light, with the fellow eye covered, alternating with episodes in the cage environment under normal illumination, with the lens wearing eye covered.

Animals and measurements

White Leghorn chicks (Cornell K strain; Cornell University, Ithaca, NY) were acquired as eggs. Upon hatching the chicks were raised in a 14 hour light, 10 hour dark cycle, with a continuous supply of food and water. The experiments were performed on chicks that were seven to fourteen days old. A Velcro ring was glued to the feathers around the experimental eye and lenses were attached to these rings using matching Velcro. The lenses were cleaned three times a day. At the start and end of the period of lens wear, chicks had refractive error measured and ultrasound biometry performed under anesthesia. Refractions were measured with a modified Hartinger refractometer (Wallman & Adams, 1987) and ocular dimensions measured with A-scan ultrasonography using separate sound velocities for each component (Nickla, Wildsoet & Wallman, 1998; Wallman & Adams, 1987). All measurements were made between 10 am and 2 pm to avoid the effects of diurnal variation on choroidal thickness (Nickla et al., 1998); within this time period each chick was measured at approximately the same time

of day before and after the experiment. In this experiment eye length was calculated from the anterior cornea to the posterior sclera, and thus was unaffected by changes in choroidal thickness. To present data in a form more comparable to other papers we also present the axial length measured to the anterior retinal surface.

Use of animals in this study was in compliance with the ARVO statement for the Use of Animals in Ophthalmic and Vision Research and was approved by the CCNY Institutional Animal Care and Use Committee.

Chick cone sensitivity functions

The spectral sensitivity of chick cones is a function of the absorption of the visual pigment and transmission of the oil droplets located in front of the outer segment of the cones. In all but the UV-cones these oil droplets contain one or more carotenoid pigments (Bowmaker, Heath, Wilkie & Hunt, 1997; Bowmaker & Knowles, 1977; Goldsmith, Collins & Licht, 1984), which act as short wavelength cut-off filters, thereby narrowing the cone's spectral bandwidth. These pigments include: galloxanthin (S-cones), cis- and trans-zeaxanthin (M-cones), astaxanthin (L-cones), galloxanthin and ε-carotene (D-cones). Because the L-cones and D-cones have the same photopigment, but different carotenoid pigments in the oil droplets, the sensitivity of both cone types is very similar at the long-wavelength side of the peak wavelength sensitivity, but with a sharper short-wavelength cut-off in L-cones.

The spectral sensitivity of the chick (Figure 1) was calculated from microspectrophotometric identification of the peak absorption (λ_{max}) of the individual pigments (Bowmaker et al., 1997), and from avian carotenoid absorption functions (Goldsmith & Butler, 2003). All the pigment sensitivity functions, except the UV pigment function, were plotted using the function described by Lamb (1995). The UV pigment sensitivity function was fitted with an eighth degree polynomial function (Palacios, Goldsmith & Bernard, 1996). The absorption spectra of carotenoids found in avian oil droplets (Goldsmith & Butler, 2003) were used to calculate the screening effect on the pigment spectra using the method of Goldsmith & Butler (2003). The spectral response of a cone is given by:

$$R(\lambda) = 10^{-aD(\lambda)} P(\lambda)$$

Where a is the peak absorbance of the oil droplet, D(λ) is the normalized absorbance spectra of the carotenoid (or mixture of carotenoids) at that wavelength and P(λ) is the spectral absorbance of the cone pigments. Filtering by pre-retinal media was ignored.

Illumination and Color Conditions for Isolating Cones

To study the lens compensation response when only either the UV- and S-cones, or the L- and D-cones were functioning, we calculated the spectral sensitivity of each cone class. To separate the cone types, we made use of the finding that lens compensation in white light occurred at 0.5 "human lux" but not at 0.2 "human lux" for both positive and negative lenses (Roberts, Zhu & Wallman, 2003). Since chicks have different wavelength sensitivities to humans we refer to illuminance corrected for the chick photopic sensitivity function (Chen & Goldsmith, 1984) as "chick lux", which differs from "human lux" as a function of wavelength. There were four conditions: a red, blue and white condition at 0.67 "chick lux" and a white condition at 0.2 "chick lux".

To isolate the response of L-cones and D-cones from the M-, S-, and UV-cones, an illuminance level of 0.67 "chick lux" (0.44 "human lux") was selected for the monochromatic red illumination (620 nm; 10 nm bandwidth) so that M-, S-, and UV-cones were excited less than

in the 0.2 “chick lux” white light condition and should not contribute to lens compensation. We can do this because at 620 nm the response of the S-, M-, and UV- cones is approximately 80 % less than that of the L- or D-cones. We did not attempt to distinguish between responses of the L- and D-cones.

An illuminance level of 0.67 “lux” (0.20 “human lux”) was selected for the monochromatic blue illumination (460 nm;10 nm bandwidth) so that D-cones were excited less than in 0.2 “chick lux” white light and were not expected to contribute to lens compensation. We can do this because the response of D-cones at 460 nm is approximately 60% less than that of the short-wavelength cones. We did not attempt to distinguish between responses of the UV- and S-cones; some evidence exists that the UV-cones alone do not permit lens compensation (Rohrer et al., 1992). Rods do not operate in daylight hours in the chick and Japanese quail retina (Manglapus, Uchiyama, Buelow & Barlow, 1998; Schaeffel, Rohrer, Lemmer & Zrenner, 1991).

We also tested two levels of white light: 0.67 “chick lux” and 0.2 “chick lux”. The use of the 0.67 “chick lux” (0.54 “human lux”) white condition permitted us to compare the degree of lens compensation under our monochromatic illumination (in which longitudinal chromatic aberration did not provide cues for defocus) with the more natural condition of white light. The 0.2 “chick lux” condition was used to verify the results of (Roberts et al., 2003), on which our separation of the cone responses was based.

Illuminance measures

Irradiance measures were multiplied by the chick photopic sensitivity function to high frequency flicker selected to isolate cone function (Chen & Goldsmith, 1984) and converted to illuminance measures (“chick lux”). Average chick spectral sensitivity was based on the reciprocal intensity of the test light required to produce criterion ERG responses to a 25 Hz photopic stimulus (Chen & Goldsmith 1984). Spectral sensitivity functions from other reports are similar (Schaeffel et al., 1991). Irradiance was measured (United Detector Technology 40X Opto-meter) at 25 locations on the bottom of the drum (1 meter from the light source) that housed the chicks with the diffuser lid in place. The illuminance measures were averaged to give the average illuminance at the bottom of the drum. The average illuminances of the red, blue, and white conditions were 0.67 ± 0.03 “chick lux”. All illuminance measures are in “chick lux” unless otherwise noted.

For white light, irradiance of the light was measured at 420 nm and at 20 nm intervals from 460 nm to 620 nm with interference filters (irradiance values were corrected for the transmission of the interference filters). We measured the irradiance of the source for each wavelength over this range. The irradiance values were then extrapolated, using the radiance profile from the bulb manufacturer as a guide, to cover the interval between interference filters and to extend the range to 700 nm. Irradiance for the blue (460 nm) and red (620 nm) conditions were measured with interference filters (460 nm, 10 nm bandwidth; 620 nm, 10 nm bandwidth) and converted to illuminance measures in the same way.

The illuminant had an “equal energy” spectral power distribution (Solux bulb: 4700 K) and illuminance was adjusted using neutral density filters. It should be noted that because the white and monochromatic conditions were equal in “chick lux”, the white illumination condition contained less energy at either the blue or red end of the spectrum than either the blue or red light condition.

Lenses

We used lenses of ± 6-8 D. Chicks wearing these lens powers have demonstrated lens compensation responses in previous experiments in the drum environment (Park, Winawer & Wallman, 2003). Even if an eye had no chromatic mechanisms that would allow it to make use of longitudinal chromatic aberration to infer the sign of defocus, longitudinal chromatic aberration would nonetheless cause blue light to be focused in front of red light, so that imposing the same lens in blue and red light would result in different degrees of defocus.

Although there is no reason to believe that the initial rate of compensation depends on the precise power of the lens worn, we attempted to compensate for this chromatic difference of focus based on the dispersion data of the lens and ocular media (Hughes, 1979) in conjunction with reduced eye parameters of the chick. This defocus was calculated to be about 1.50 D (Mandelman & Sivak, 1983). We had the birds wear -6.00 D lenses in red and white light and -8.00 D lenses in blue light. The red light (620 nm) was close enough to the λ_{max} (580 nm) of the chick's Vλ function (Chen & Goldsmith, 1984) that there is little difference (0.11 D) in the optimal focal plane between red and white conditions. Similarly, + 8.00 D lenses were used in red and white light, and +6.00 D lenses were used in blue. We recognize that this procedure introduces a difference in the inter-ocular difference in defocus between illumination conditions. The inter-ocular difference in the imposed defocus in the blue condition would initially be greater with negative lens defocus and smaller with positive lens defocus by the amount of longitudinal chromatic aberration since the focal plane in the fellow eye is dependent on wavelength. However, we found that the fellow eye rapidly emmetropizes to correct this small imbalance.

Drum conditions

During the experiment, chicks were kept in a 60-cm-diameter drum for three days from 9 am to 5 pm, while wearing either a positive or a negative lens on one eye and nothing on the other eye, and were kept in the dark overnight in a sound- and light-proof chamber (61×81 cm). The walls of the drum and the presence of other birds provided a baseline of hyperopic defocus upon which the effect of the defocusing lenses was added. Therefore, lens compensation for negative lenses may have been reduced by the predominance of hyperopic stimuli for both eyes. The walls of the drum were papered with a black and white high contrast pattern with a broad spatial frequency spectrum (approximately $1/f^2$ power spectrum). The drums and chambers contained food, both in containers and scattered on the floor, in addition to water. Extreme care was taken to avoid exposing the chick to any other illumination other than the experimental illumination, including a double door system to prevent exposure of the chicks to white light.

As an alternative to comparing the lens-wearing eye to the fellow eye, both under dim monochromatic light, we did a separate experiment in which the experimental eye was exposed in the drum and the fellow eye was exposed in a cage environment under room illumination. For one out of every two hours, the lens-wearing eye viewed the drum, while the fellow eye was patched, and then, during the other hour, the chick was in a cage under fluorescent room lighting (300 "human lux") with the fellow eye viewing and the lens-wearing eye patched. At all other times the chicks were kept in the dark in a sound-and light-proof chamber.

Analysis

The difference between the ultrasound and refraction measurements taken before and after the three day exposure period provided a metric of *relative* change in each component: **Relative change** = (Change in experimental eye [X]) ***minus*** (Change in fellow eye [N])

To compare the change in the experimental eye and the fellow eye of the same bird we used paired *t*-tests. To compare the fellow or experimental eyes in different conditions unpaired *t*-tests were used. The relative change (ΔX-ΔN) was compared with a two-way ANOVA testing for the effects of color and sign of defocus and for interactions between color and defocus. If the F value was significant, comparisons between positive and negative defocus were made using Scheffé's *post-hoc* tests (original).

Calculation of the dioptric equivalent of anatomical changes in the vitreous chamber depth

To determine if the anatomical changes measured were sufficient to cause the observed changes in refractive error we followed the method of Troilo & Judge (1993) and Wallman et al. (1995). The optical power of the control eye was calculated using the axial length measured to the retina (using the refractive index of the vitreous and adjusting for different vergence of light in air and in vitreous) and subtracting any refractive error present. Then, substituting only the vitreous length of the experimental eye, we calculated the refractive error that was predicted due to the altered vitreous chamber depth.

Results

Our principal result is that, although there was refractive compensation in both monochromatic red and blue light, the ocular components by which lens compensation occurred differed with the color of the illuminant. In the blue light condition the lens compensation was mainly the result of changes in eye length, whereas in the red light condition the lens compensation was predominantly due to changes in choroidal thickness. In white light both eye length changes and choroidal thickness changes contributed to compensation. The results are summarized in Table 1, and Figure 2.

Refractive change

As in previous experiments, there was good lens compensation for positive and negative lens defocus in white light and in red monochromatic light (Figure 3). Negative lenses in white, blue and red light caused the experimental eye to compensate by -2.71 D, -2.68 D and -5.01 D (paired *t*-test: *all* $p<0.001$) respectively, relative to the fellow eye. Lens compensation in white, blue, and red light was not significantly different to each other (unpaired *t*-test), although the compensation appeared to be greater in red light. Positive lenses in white light and red light caused the experimental eye to compensate +4.31 D (paired *t*-test: $p<0.001$) and 2.48 D (paired *t*-test: $p<0.01$) respectively, relative to the fellow eye, an accurate response if the -3.00 D stimulus arising from the drum walls is taken into consideration. Lens compensation in white and red light were not statistically different, but were both significantly greater than in blue light (-0.55 D; unpaired *t*-test: white v blue: $p=0.0004$; red v blue: $p=0.03$). There was no lens compensation to the myopic defocus in blue light, as if the eye regards mild myopically defocused blue light as indicative of emmetropia, as it does in accommodation (Rucker & Kruger, 2004b;Seidemann & Schaeffel, 2002). Thus, there was no difference in refractive compensation between white and monochromatic red light with positive or negative defocus, while in blue light there was compensation with negative defocus but not with positive defocus.

Positive v negative lens comparisons

A comparison of the refractive compensation to positive and negative defocus indicated there was strong signed lens compensation (ANOVA: $p<0.0001$), which varied with wavelength (ANOVA: $p=0.004$) probably because of the lack of compensation to positive lenses in blue light. The comparison was significant for red and white illumination conditions (Scheffé *post hoc*: $p<0.0001$ for both), but not for blue (Scheffé *post hoc*: $p=0.19$). The finding of equivalent lens compensation in monochromatic light and white light implies that longitudinal chromatic aberration is not essential for lens compensation.

Comparison with dim light condition

We found a lack of a refractive response in the 0.2 “chick lux” white condition (negative lens: - 1.34 ± 1.00 D: positive lens: -0.72 ± 0.76 D). This result validates our rationale for using low illuminance to separate the contribution of the different cone classes.

Choroidal change

Our strongest results were seen in the differential choroidal response to lens-induced defocus of eyes exposed under red and blue monochromatic illumination. In both white and red light, the choroid thickened (white: 68 ± 27 μm [paired *t*-test; $p<0.05$]; red: 90 ± 20 μm [paired *t*-test: $p<0.001$]) in the experimental eye relative to the fellow eye in response to positive lenses, and thinned (white: -51 ± 10 μm; red: -62 ± 14 μm [paired *t*-test: *both* $p<0.001$]) in response to negative lenses (Figure 2 and Figure 4). However, in blue light (460 nm) there was no relative change in choroidal thickness to either positive or negative lenses (2-5 μm) . Because the choroidal compensation for lens-induced defocus was not statistically different in white and red light (unpaired *t*-test: $p>0.05$) these results imply that choroidal compensation does not require longitudinal chromatic aberration. These results also suggest that the S- cones and UV-cones stimulated by the blue light are not sufficient to modulate choroidal thickness.

Positive v negative lens comparisons

When choroidal changes (ΔX-ΔN) for positive defocus were compared with those for negative defocus there was a signed change in choroidal thickness in response to lens-induced defocus (ANOVA; $p<0.0001$) and an interaction between defocus and color (ANOVA; $p<0.0001$), possibly because of the lack of a choroidal response in blue light. Choroidal changes in white and red light were significant while those in blue were not (Scheffé *post hoc*: white: $p<0.0001$; red: $p<0.0001$; blue: $p=0.99$). These results indicate that there was a signed change in choroidal thickness in red monochromatic light and white light but not in blue monochromatic light.

Comparison with dim light condition

We found a lack of a choroidal response (Figure 4) in the 0.2 “chick lux” white condition (negative: -15 ± 16 μm: positive: -10 ± 13 μm). In fact, the choroidal responses to defocus were poor in both the 0.2 “chick lux” white light, and the blue light condition (unpaired *t*-test: negative $p=0.36$; positive: $p=0.47$). Also, since the excitation of the S-, M-, and UV-cones in the red light condition was less than in the 0.2 “chick lux” control condition, it is unlikely that these cone types contributed to the compensatory choroidal changes seen in the red condition.

Eye length change

We also found the opposite wavelength specificity in the ocular elongation component (Figure 5) of the lens-compensation, but to a less dramatic degree than for the choroidal component. The relative change in eye length decreased with positive lens-wear both in white and blue light (white: -142 ± 23 μm; blue: -64 ± 17 μm [paired *t*-test: *both* $p<0.001$]), but not significantly in red light (-36 ± 23 μm). Relative eye length changes increased with negative lens-wear in white light (60 ± 32 μm) and increased less in blue light (32 ± 32 μm) but essentially not at all in red light (8 ± 39 μm). Increases were only significant in white light (paired *t*-test: $p=0.014$). However, when the chick was kept in the cage environment while the fellow eye was exposed (Figure 6 and Table 2) the relative elongation was more pronounced (white: 79 ± 33 μm; blue: 135 ± 49 μm; red light: 154 ± 45 μm) and the changes were significant for all three conditions (blue and white: paired *t*-test: $p<0.05$; red: $p<0.001$).

The difference in ocular elongation between wearing positive and negative lenses in blue light was 47 % of that in white light, whereas in red light it was 22 % of that in white light (both eyes exposed in the drum environment). Compensatory changes with positive defocus in red

light and blue light were significantly smaller than in white light (unpaired *t*-tests: red v white: p=0.003; blue v white: p=0.014). Compensatory changes with negative defocus in red and blue light showed no significant difference to white light. This difference between the compensatory response in white and monochromatic light with positive lenses suggests that longitudinal chromatic aberration may provide a signal for eye length compensation.

Positive v negative comparisons

When eye length changes with positive lens wear were compared with those with negative lens wear, there were the anticipated growth changes in white and blue light, but not in red. Change in eye length with lens-induced defocus varied with sign of defocus (ANOVA: $p<0.0001$), and signed eye length changes were found in blue monochromatic light (Scheffé *post hoc:* p=0.02) and white light ($p<0.0001$), but not in red monochromatic light (Scheffé *post hoc*: p=0.49). Because compensation in eye length was seen in 0.67 “chick lux” white light and blue light, we infer that shortwavelength light and white light of this intensity are sufficient for a lens compensation response.

Comparison with dim light condition

The logic of our choice of illumination levels required that eyes could not compensate for lenses at 0.2 “chick lux”. The measurements made in the control condition (0.2 “chick lux”) confirmed that there were no compensatory changes in eye length at this light level with either positive (-29 ± 30 μm) or negative lenses (+5 ± 17 μm; paired *t*-test: positive: p=0.34; negative: p=0.77). Since the excitation of the D-cones and L-cones in the blue light condition was less than in the 0.2 “chick lux” control condition, it is unlikely that D-cones or L-cones contributed to the compensatory eye length changes seen in the blue condition.

Eye length vs. axial length?

The cone-specific effects we have described were detected because we made separate measurements of the choroidal thickness and eye length. Had we measured only the “axial length” from cornea to retina, the thickening and thinning of the choroid under red light would have been manifested as a relative shortening or lengthening of the “axial length,” respectively (a difference of 190 μm between positive and negative lenses), despite the fact that the actual length of the eye was minimally affected by lens-wear (a difference of 44 μm between positive and negative lenses). As a result, the effect on eye growth of the sign of the lens would have appeared to have been greater under red light, when in fact it was greater under blue light (cf. Fig. 5A and 5B).

For the same reason, the impaired compensation by ocular elongation that we found under red light compared to white light would also not have been observed had we measured the eye-length from cornea to retina.

Do the measured anatomical changes account for the refractive changes?

Calculations of the contribution of the anatomical changes to the observed changes in refractive error showed that there was a linear correlation between the predicted dioptric change in refractive error due to the change in vitreous depth and the measured change in refractive error (Predicted RE= 1.17(Measured RE) + 0.58; R^2=0.83). Across the six conditions tested in this experiment the refractive change was related to the change in vitreous depth with a slope of -25.7 D/mm (R^2=0.98).

Consensual growth effects

In general, the two eyes of chicks show independent responses to visual conditions. For this reason, it is common to show the difference between the lens wearing eye and the fellow eye.

Under the illumination conditions we used, we found several curious interactions in the lens compensation responses between the two eyes in that the fellow eye, which did not wear a lens, was influenced both by the lens worn on the other eye and by the color of the illumination. There were two types of effect on the fellow eye. In red light and white light there was a consensual response (yoking), as previously described (Wildsoet & Wallman, 1995), in which the length of the fellow eye responded in the same direction, but to a lesser degree, as the lens-wearing eye. In addition, in blue and white light, an inverted consensual response (anti-yoking) was seen, in which, although the response of the two eyes was still correlated, the mean length of the fellow eye changed in the opposite direction as that of the lens-wearing eye (Figure 7).

To understand what we mean by a consensual response, consider the left hand panel of Figure 7. Under red light the eye growth of the experimental eye and fellow eye were correlated ([+]: Pearson r = 0.66; [-]: Pearson r = 0.38), though the correlation was weaker for negative lenses. A weak correlation indicates that the eyes were changing independently of each other. In line with a consensual growth response, growth in both eyes was greater when the experimental eye wore a negative lens (X: 259 μm; N: 251 μm) and less when the experimental eye wore a positive lens (X: 164 μm; N: 200 μm). The difference in eye growth between the lens-wearing eyes was 95 μm when the experimental eye was wearing positive and negative lenses, while the difference between fellow eyes was only 51 μm. Thus, despite the consensual lens induced growth there was still a significant difference between the lens wearing eyes.

To understand what we mean by an inverted consensual response, consider the right hand panel of Figure 7. Under white light the eye growth of the experimental eye and fellow eye were still correlated as described above ([+]: Pearson r = 0.64; [-]: Pearson r= 0.79). In addition, the fellow eye grew less when the experimental eye wore a negative lens (X: 210 μm; N:150 μm) and more when the experimental eye wore a positive lens (X:160 μm; N: 302 μm). The difference in eye growth between the fellow eyes was 152 μm when the experimental eye was wearing a positive and negative lens, while the difference between the experimental eyes was only 50 μm. A similar effect was measured in blue light as in white light (Table 1) though the consensual growth was weaker. Thus, despite some consensual lens-induced growth, the mean of the fellow eye changes in the opposite direction from the lens-wearing eye.

Consensual effects were not so obvious in the choroidal responses (Figure 6). Under blue and white light the dim light of the drums caused the choroids to thin a little in general, although in white light there was a positive inter-ocular correlation for positive (White (+); Pearson r = 0.64) and negative lenses (White (-); Pearson r = 0.80) indicating a consensual effect. There was no evidence of inverted consensual effects in blue and white light. Curiously, under red light there was only a small inter-ocular correlation of choroidal changes though inverted consensual effects were evident; choroids of the fellow eyes of eyes wearing positive lenses thinned more than those of eyes wearing negative lenses (mean: (positive lens) -48 μm; (negative lens) -5 μm).

Discussion

Our principal finding is that cones sensitive to short wavelengths (S- and/or UV-cones) can guide lens-compensation by modulating eye length but not choroidal thickness, whereas cones sensitive to long wavelengths (L- and D-cones) can guide lens compensation by modulating choroidal thickness, but with little effect on ocular elongation. There was also some evidence that ocular elongation may be dependent on a chromatic signal from longitudinal chromatic aberration at least with positive defocus; in that significantly greater lens compensation occurred in white light than in monochromatic light.

Our stronger evidence for differential wavelength-sensitivity comes from measurements of choroidal thickness. Choroidal thickness not only differed significantly between positive and negative lenses under red light, but the degree of choroidal thickening to positive lenses was greater under red than blue light, as was the degree of choroidal thinning to negative lenses. The evidence from ocular elongation was weaker in that the difference between positive and negative lenses under blue, but not red light was significant, although the magnitude of the changes was small, so that neither lens had a significantly greater effect in blue than in red light.

We have no way of knowing if the threshold for lens compensation is the same for all cone types. All we know is that for at a certain level of white light (0.2 “human lux”) there is no lens compensation response, while at another level (0.5 “human lux”) there is a lens compensation response. Although the dim light may have impaired the ability of the eye to compensate for lenses, the results indicate surprisingly different responses to red and blue light arguing that we achieved at least a partial separation of cone responses.

In previous experiments (Table 3) it has been found that lens compensation and recovery from form deprivation were not impaired in monochromatic yellow (Schaeffel & Howland, 1991;Wildsoet et al., 1993), green (Wildsoet et al., 1993), or deep red light (Rohrer et al., 1992), but no lens compensation was observed in UV light (Rohrer et al., 1992). The present experiment differs from these experiments in that we demonstrate first, an impairment of the eye length compensation with positive lenses in monochromatic light, and second, under our dim light conditions we demonstrate a separation of the choroidal and ocular elongation lens compensation responses. Neither of these results are evident if one measures only axial length from cornea to retina (Figure 5B).

Of course, even if the eye were indifferent to the wavelength of the illuminant, blue light would focus in front of red light, which would cause the emmetropization mechanism to make the eye more hyperopic in blue than in red light. By comparing the fellow (non-lens-wearing) eyes, we found that those in blue light were about a diopter more hyperopic than those in red light (fellow eyes of positive-lens animals, +1.30 D; those of negative-lens animals, +0.75 D), findings similar to those of Seidemann & Schaeffel (2002). In much the same vein, Kroger & Wagner (1996) found increased eye size in Blue Acaras (*Aequidens pulcher*) when kept in an aquarium illuminated with monochromatic red (623.5 nm) illumination relative to those illuminated with monochromatic blue (485 nm) illumination.

Relationship of choroidal and ocular length changes

We can envision two explanations for this unexpected wavelength specificity of the choroids and ocular elongation responses. It might be that separate cone pathways signal the choroid to thicken and the ocular elongation to be inhibited, but that because most experiments are done under white light, the separateness of the pathways has not been revealed. Alternatively, it might be the case that the two pathways each influence both choroidal and ocular elongation responses, but that the long-wavelength pathway is more effective in modulating choroidal thickness and the short-wavelength pathway is more effective in modulating ocular elongation, so that in the limiting case of our unusual illumination, these asymmetries are accentuated.

It is not unheard of for individual cone types to be used exclusively for particular purposes. For example, chicks are unable to detect texture boundaries if the luminance of the two textures is matched for the D-cones, implying that these cones are specifically used for this task (Jones & Osorio, 2004); because the D-cones have a broad spectral sensitivity they might be particularly suited for detecting small changes in luminance but unsuited to color discrimination. There is also evidence that in humans there are two types of optokinetic nystagmus: one in which S-cones are used, and one in which they are not (von Campenhausen

& Kirschfeld, 1999), while in the zebra fish S-cones are used for phototaxis, but not for optokinetic nystagmus (Orger & Baier, 2005). Furthermore, the primate superior colliculus does not receive retinal inputs from S-cones (Derrington, 2002), and it is asserted that the phenomenon of the saccadic remote distractor effect is blind to visual inputs received by these cones (Sumner, Nachev, Vora, Husain & Kennard, 2004).

Our results are not the first instance of visual conditions differentially affecting choroidal thickness vs. ocular elongation. As mentioned in the Introduction, brief twice-daily episodes of positive lens-wear cause compensatory changes in the rate of ocular elongation but not in choroidal thickness, whereas similar episodes of negative lens-wear cause compensatory changes in choroidal thickness but not in the rate of ocular elongation (Winawer & Wallman, 2002). Furthermore, lightly frosted diffusers largely prevent positive lens-induced changes in choroidal thickness, but enhance the inhibition of ocular elongation (McLean & Wallman, 2003; Park et al., 2003). In addition, disruption of the diurnal rhythms of the choroid and the sclera, by repeated light exposures during the night, attenuated the accelerated ocular elongation, but not the choroidal thinning typically caused by negative lenses (Kee, 1998). Furthermore, choroidal, but not eye length, changes were found when chicks were kept under monochromatic red light with alternating myopic and hyperopic defocus (Winawer, Zhu, Choi & Wallman, 2005). What is added by the present results is that both choroidal thinning and thickening in response to lenses are much weaker in blue than in red light. Thus it is difficult to avoid the conclusion that different pathways are involved.

This conclusion seems at odds with the strong linking of choroidal thinning with ocular elongation and of choroidal thickening with the inhibition of ocular elongation, observed in normal lens compensation. Indeed, Nickla, Wilken, Lytle, Yom & Mertz (2006) and Nickla (2007) have shown that, in several experimental paradigms, inhibition of ocular elongation is always preceded by choroidal thickening, although it may be transient. Therefore, we cannot exclude the possibility that we missed a transient choroidal thickening when positive lenses were worn under blue light, which may have occurred at a different time of day from the thickening under red light. Nonetheless, our finding that red light causes large changes in choroidal thickness without corresponding changes in ocular elongation is not subject to this caveat, because there is no reason to suspect that changes in ocular elongation can appear and disappear in hours.

The explanation for the weaker modulation of ocular elongation may be that the consensual growth effects found under these dim illumination conditions masked the lens compensation responses. Alternatively, perhaps the eyes could not increase as much as usual to negative lenses because they were close to their threshold light intensity for emmetropization.

Consensual or yoking effects

Consensual or yoking effects, where the fellow eye compensates in the same direction as the compensation in experimental eye, have been seen before in both normal and optic nerve sectioned chick eyes (Wildsoet & Wallman, 1995). What is unusual in both this experiment and in another experiment performed in this lab, in which chicks had intermittent lens wear (Zhu & Wallman, 2009), is that inverted consensual effects also have been found. We conjecture that there exists, in addition to the yoking of responses in the two eyes, a tendency for both eyes to grow to reduce the difference between them; if one eye has myopia imposed by positive lenses, and compensates by moving in the hyperopic direction, the fellow eye moves in the myopic direction, by decreasing choroidal thickness or increasing eye growth.

These results add to our understanding of the difference in lens compensation that was found with color. There appeared to be no change in eye length in red light when the experimental eye was wearing either positive or negative lenses because, as a result of the consensual effects,

the experimental eye grew by the same amount as the fellow eye; both eyes grew more with negative lenses and less with positive lenses. In contrast, a significant difference in eye growth was found when wearing both positive and negative lenses in white light, mainly because eye growth of the fellow eye was affected by the inverted consensual response.

Implications of lens compensation in dim monochromatic illumination

We found surprisingly good lens compensation under dim monochromatic illumination, with the refractive compensation being generally comparable to that under white light (except for the positive lens in blue light). However, the inhibition of ocular elongation by positive lenses was substantially and significantly better in white light than in either monochromatic light, suggesting that the eye might be using chromatic cues from longitudinal chromatic aberration to control eye growth under dim white illumination. This finding is especially provocative in that, under our brighter white light condition, S-cones received 21% as much stimulation as under our blue light condition, and the L-cones received 37% as much stimulation as under our red light condition. Such levels of stimulation under monochromatic illumination would probably be below the threshold for lens compensation.

A neural mechanism that operates under conditions of poor image quality would be useful for emmetropization, because it is only when the eye is defocused that emmetropization is required. If a color-sensitive mechanism were available, it might be particularly effective under these circumstances, since chromatic differences at edges are more reliable than luminance differences because they are less affected by shadows, etc. (Barbur, Harlow & Plant, 1994; Hurlbert, 1989; Kingdom, 2003; Li & Lennie, 2001). In addition, the luminance contrast sensitivity of the human eye falls off at low spatial frequencies, whereas chromatic contrast sensitivity does not (review De Valois & De Valois, 1988) and would therefore be relatively more effective on blurred images. As focus improves and higher spatial frequencies increase in luminance contrast and become more salient, the achromatic luminance contrast detecting mechanism may play a more dominant role in detecting defocus, at the expense of chromatic mechanisms.

In this manuscript we have provided evidence that under conditions of dim illumination components of the compensation for defocus imposed by spectacle lenses are driven by S-cones. An S-cone contribution to the compensatory responses potentially increases the magnitude of the signal from longitudinal chromatic aberration by spanning a larger wavelength region. Although we have not directly tested whether longitudinal chromatic aberration is used in lens compensation, our finding that lens compensation was reduced in monochromatic illumination when compared to white light of the same illuminance suggests that longitudinal chromatic aberration may be used in lens compensation. Separation of the choroidal and ocular elongation mechanisms suggests the possibility of at least two types of direction signals for determining the direction of defocus.

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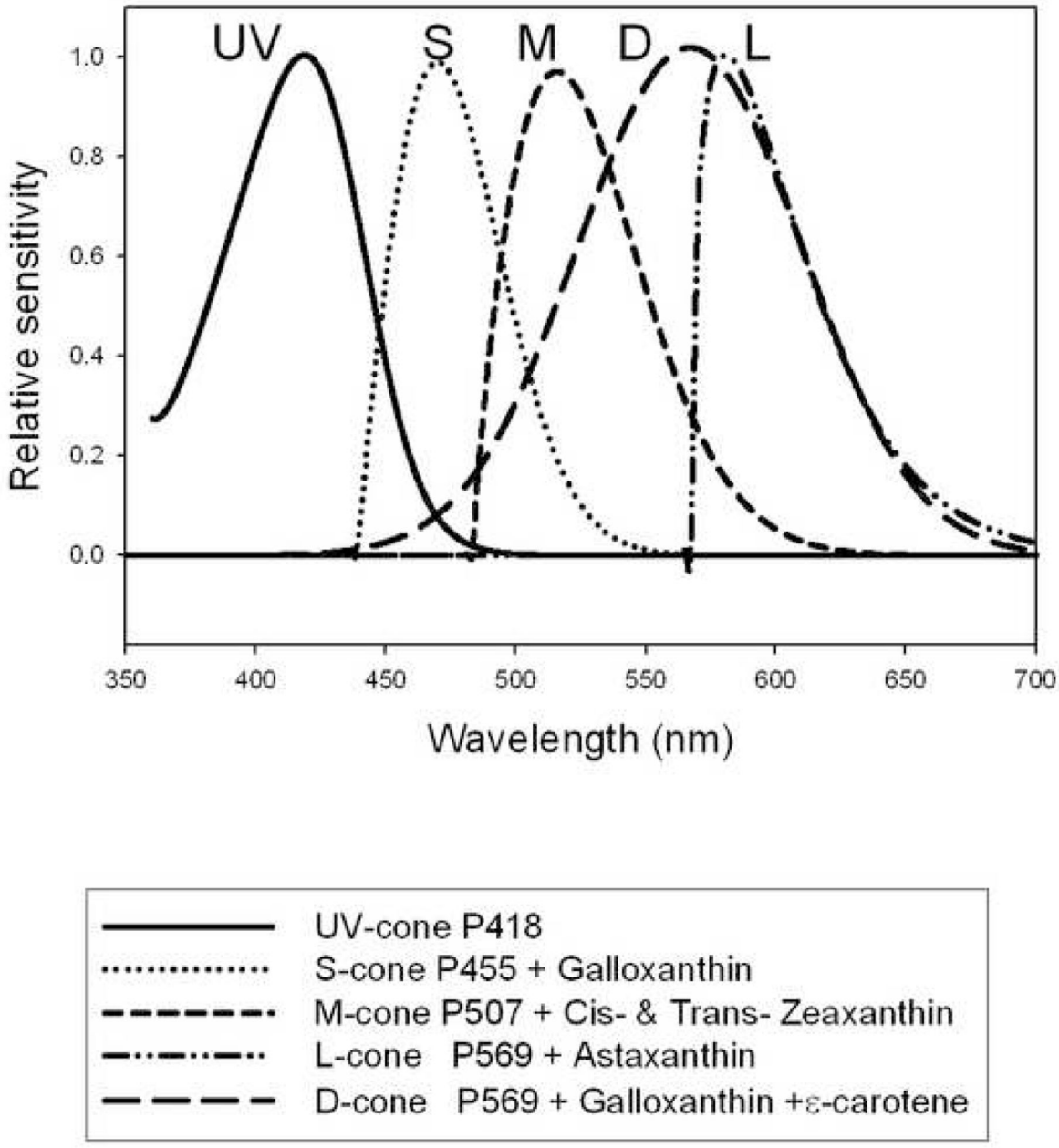

Figure 1.
Relative sensitivity of the ultra-violet (UV), short (S), medium (M), and long (L) wavelength-sensitive cones. The spectrum of the individual cone pigments is normalized to 1 after the relative absorbance spectra for the carotenoid pigments found in each cone type are incorporated.

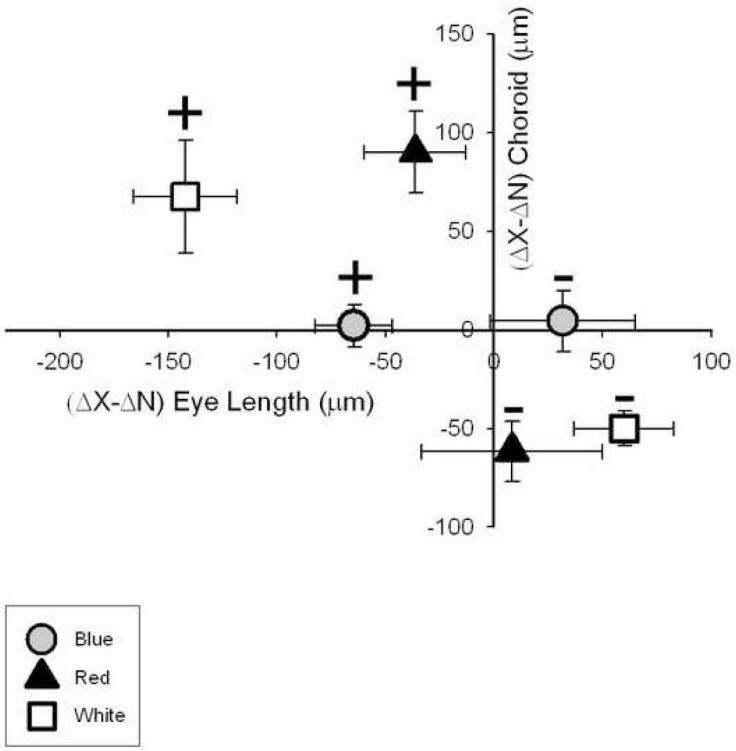

Figure 2.
Choroidal and eye length changes (ΔX-ΔN) to positive lens defocus and negative lens defocus under low intensity illumination (0.67 “chick lux”). Under red monochromatic illumination the choroid thickened in response to positive lenses and thinned in response to negative lenses, but there was little change in eye length. Under blue monochromatic illumination ocular elongation was inhibited in response to positive lenses and increased in response to negative lenses, but there was no change in choroid thickness. The sign of lens defocus is indicated by + and -. Error bars show standard error of the means.

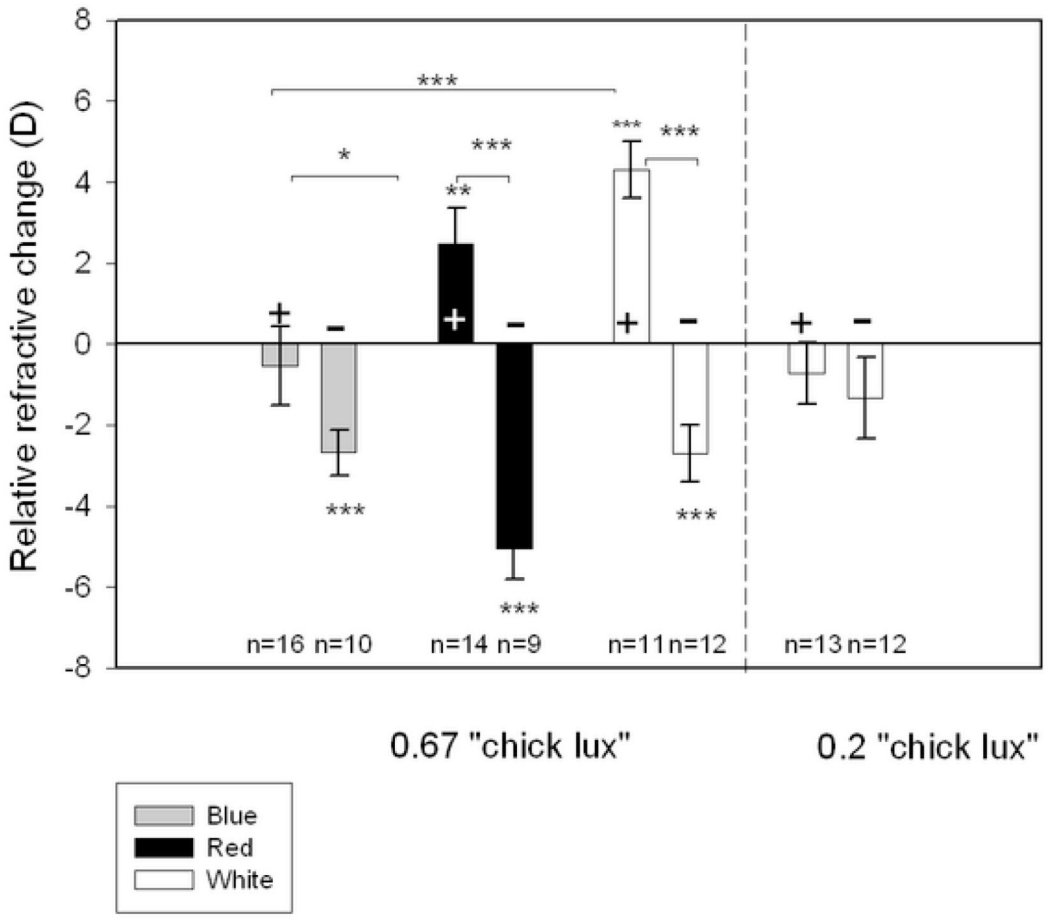

Figure 3.

Change in the relative refractive error (ΔX-ΔN) in response to lens-induced defocus under monochromatic and white light at 0.67 “chick lux”. Eyes compensated for both signs of imposed defocus, except for positive defocus in blue. The sign of defocus is indicated by (+/-). Asterisks on bars indicate paired *t*-tests comparing responses in the experimental eye and control eye. Horizontal lines used to compare positive and negative lens compensation within an illumination condition indicate the results of Scheffé post-hoc tests; those comparing between illumination conditions indicate the results of unpaired *t*-tests. Error bars show standard error of the means. Significance of $p<0.05$, $p<0.01$, $p<0.001$ is indicated by *, **, ***.

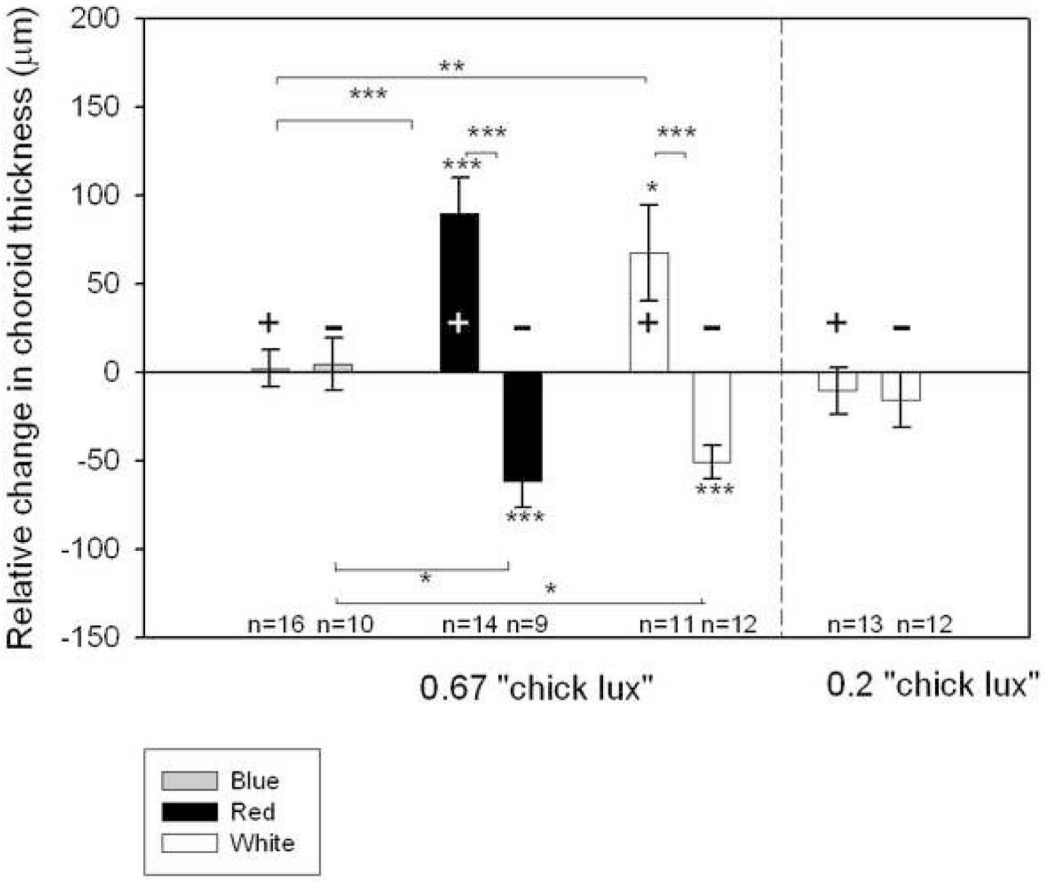

Figure 4.

Relative changes in choroidal thickness (ΔX-ΔN) in response to positive and negative lens defocus at 0.67 “chick lux” and 0.2 “chick lux”. There were signed choroidal changes in white and red light. Choroidal changes in red light were comparable to those in white light for positive and negative defocus. There were no choroidal changes in blue light or in 0.2 “lux” white light. The choroidal changes in white and red light were both significantly greater than those in blue. Symbols are as in Figure 3.

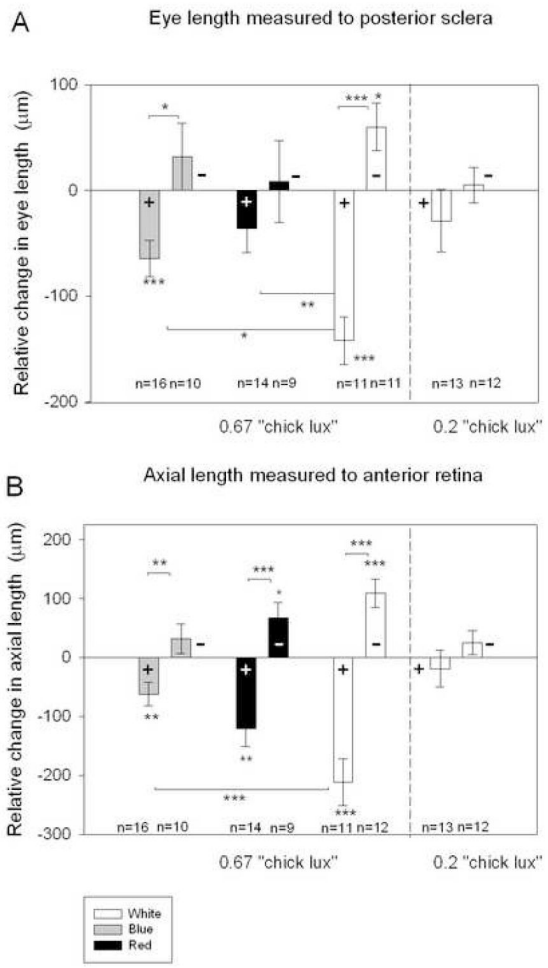

Figure 5.

Relative changes in eye length (ΔX-ΔN) measured to the posterior sclera (Figure 5A) and to the anterior retina (Figure 5B) in response to positive and negative lenses at 0.2 and 0.67 “chick lux”. There was a signed change in eye length in blue monochromatic and white light but not in red monochromatic light or in 0.2 “chick lux” white light. This difference is not evident in red light when measurements are made from the cornea to the retina. The sign of lens defocus is indicated by + and -. Asterisks on bars indicate paired *t*-tests comparing responses in the experimental eye and control eye. Horizontal lines used to compare positive and negative lens compensation within an illumination condition indicate the results of Scheffé post-hoc tests; and those used to make comparisons between illumination conditions indicate the results of unpaired *t*-tests. Significance of $p<0.05$, $p<0.01$, $p<0.001$ is indicated by *, **, *** respectively. Error bars show standard error of the means.

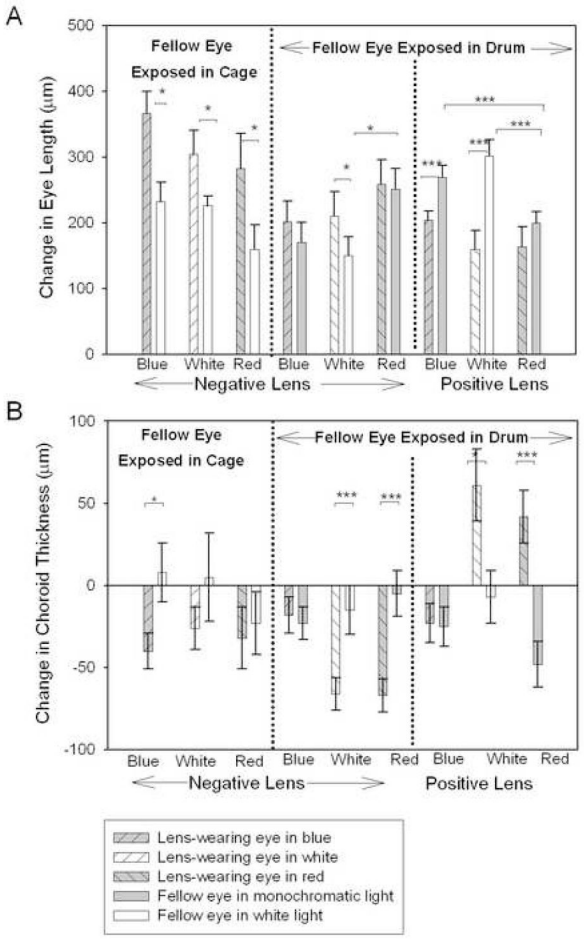

Figure 6.

Changes in eye length (A) and choroidal thickness (B) in response to negative lens defocus at 0.67 “chick lux” when the fellow eye was viewing in either the drum or a cage environment. There was a greater change in eye length when the fellow eye was exposed in the cage environment, but the cage environment disguises the consensual effects seen when the fellow eye is exposed in the drum. Paired *t*-tests were used to compare responses in the experimental eye and control eye. Unpaired *t*-tests were used to compare responses between illumination conditions. Significance of $p<0.05$, $p<0.01$, $p<0.001$ is indicated by *, **, ***, respectively. Error bars show standard error of the means.

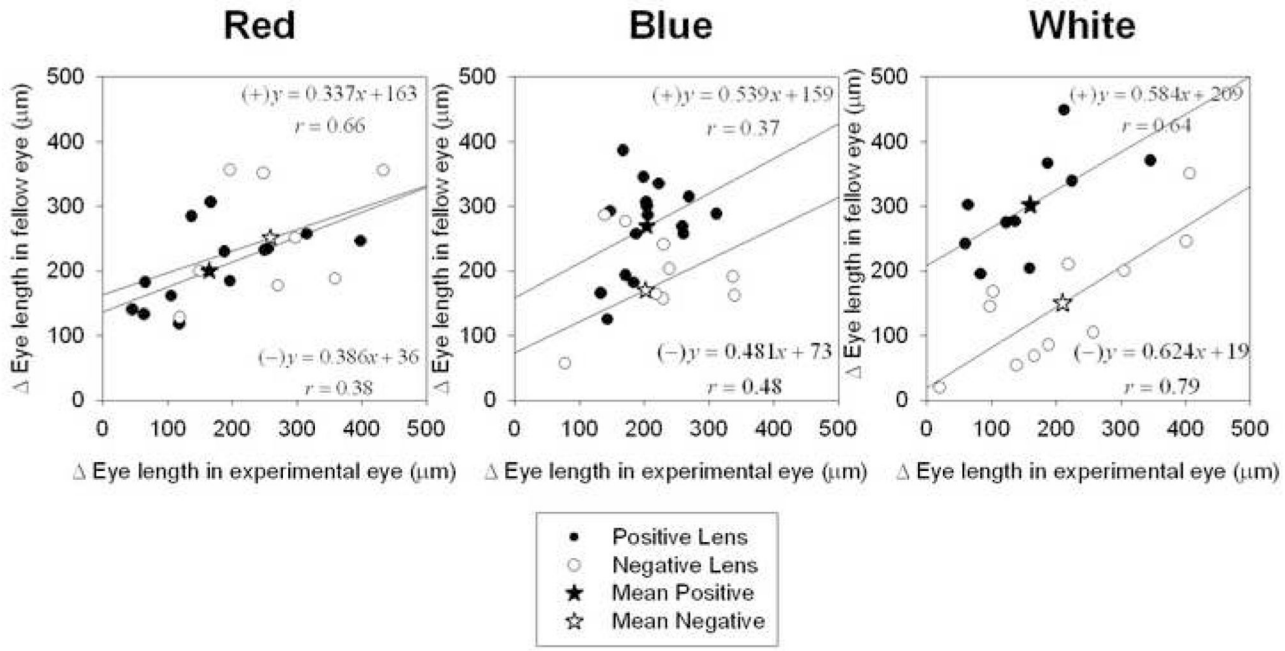

Figure 7.

A comparison of eye length change in experimental and fellow eyes for positive (solid circle) and negative lens wear (open circles). Consensual growth was observed in that there was a positive correlation of eye length change between the two eyes in red and white light. In addition, inverted consensual growth was observed in blue and white illumination in that there was increased growth in the fellow eye when the experimental eye was wearing a positive lens and decreased growth in the fellow eye when the experimental eye was wearing a negative lens. Correlations are indicated by Pearson r values.

Table 1

Summary of Results: Measurement of the relative change (ΔX-ΔN), and change during the experiment in the lens wearing eye (ΔX) and the fellow eye (ΔN) of the anterior chamber depth, lens thickness, vitreous chamber depth, choroid thickness, eye length to posterior sclera, axial length to anterior retina, and refractive error (RX) when exposed to red, blue and white light at 0.67“lux”.

	POSITIVE								NEGATIVE							
Illumination	Blue	Red	White	Blue		Red		White		Blue	Red	White	Blue		Red		White	
(μm)	(ΔX-ΔN)±SE	(ΔX-ΔN)±SE	(ΔX-ΔN)±SE	ΔX	ΔN	ΔX	ΔN	ΔX	ΔN	(ΔX-ΔN)± SE	(ΔX-ΔN)±SE	(ΔX-ΔN)±SE	ΔX	ΔN	ΔX	ΔN	ΔX	ΔN
Anterior Chamber	-1 ±16	30* ±10	1 ±9	16	17	53	23	40	39	-11 ±13	-23* ±8	9 ±16	3	14	13	36	36	27
Lens	-27 ±17	-24 ±13	-1 ±12	55	82	58	82	94	95	3 ±17	22* ±9	-32*** ±9	91	88	100	78	84	116
Vitreous	-34 ±23	-127*** ±29	-212*** ±43	156	190	12	139	-44	168	32* ± 21	69* ±26	136*** ±26	105	73	213	144	158	22
Choroid	2 ±11	90*** ±20	68* ±27	-23	-25	42	-48	61	-7	5 ±15	-62*** ±14	-51*** ±10	-18	-23	-67	-5	-66	-15
Eye Length	-64*** ±17	-36 ±23	-142*** ±23	205	269	164	200	160	302	32 ±32	8 ±39	60* ±32	202	170	259	251	210	150
Axial Length	-62** ±19	-122*** ±31	-212*** ±38	227	289	122	244	90	302	31 ±23	68* ±27	110*** ±25	219	188	286	228	277	167
RE(D)	-0.55 ±0.97	2.48*** ±0.88	4.31*** ±0.70	-1.00	-0.45	1.72	-0.76	3.16	-1.15	-2.68*** ±0.57	-5.01*** ±0.77	-2.71*** ±0.79	-2.89	-0.21	-6.00	-0.99	-3.46	-0.75

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Significance of the change in the experimental eye relative to the fellow eye is indicated by *, **, *** for significance levels of $p<0.05$, $p<0.01$, $p<0.001$.

Table 2

Summary of Results for Control Experiments: Measurement of the relative change (ΔX-ΔN) in the anterior chamber depth, lens thickness, vitreous chamber depth, choroidal thickness, eye length to posterior sclera, axial length to anterior retina, and refractive error (RX). In one control experiment birds were exposed to white light at 0.2 “lux”. In the second control experiment the eye exposure was alternated. The experimental eye of the chicks was exposed to red, blue and white light at 0.67 “lux” and the fellow eye was exposed in the cage environment under fluorescent light.

	Drum 0.2 "lux"		Drum 0.67 "lux" /Cage		
	Positive	Negative		Negative	
Illumination	White		Blue	Red	White
(μm)	(ΔX-ΔN)±SE		(ΔX-ΔN)±SE		
Anterior Chamber	38 ± 8***	4 ± 14	-34 ± 17	-49 ± 23	-60 ± 20*
Lens	-31 ± 13*	-3 ± 6	6 ± 15	-11 ± 27	26 ± 10
Vitreous	-27 ± 29	24 ± 15	20 ± 6*	221 ± 20***	140 ± 45*
Choroid	-10 ± 13	-15 ± 16	-45 ± 15*	-11 ± 31	-27 ± 25
Eye Length	-29 ± 30	5 ± 17	135 ± 49*	154 ± 45*	79 ± 33*
Axial Length	-21 ± 40	25 ± 20	175 ± 53**	160 ± 20***	107 ± 50*
RE(D)	-0.72 ± 0.75	-1.34 ± 1.00			

******Significance of the change in the experimental eye relative to the fellow eye is indicated by *, **, *** for significance levels of $p<0.05$, $p<0.01$, $p<0.001$.

Table 3

Experimental conditions for experiments that have found lens compensation in chicks under monochromatic light. Experiments include those that measured recovery from the effects of lid suture (LS) and from lid suture with ciliary nerve section (CNS).

Author	Wavelength (nm)	Lens power	Irradiance (W/m^2)	Human lux	Chick lux
Schaeffel & Howland 1991	589	+/- 4.00 D	0.3	170	200
Wildsoet et al., 1993 (CNS+LS)	589		0.26	150	179
Wildsoet et al., 1993 (LS)	550		0.049	33	39
Rohrer et al., 1992	665	+/-4.00D	0.048	6	27
Rohrer et al., 1992	383	+/-4.00D	0.066	0.02	5
Rucker & Wallman (present study)	460	+6.00/-8.00D	0.0049	0.2	0.67
Rucker & Wallman (present study)	620	+8.00/-6.00D	0.0018	0.44	0.67