Vision Research 49 (2009) 1775–1783

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Chick eyes compensate for chromatic simulations of hyperopic and myopic defocus: Evidence that the eye uses longitudinal chromatic aberration to guide eye-growth

Frances J. Rucker [*,1], Josh Wallman [1]

Department of Biology, City College of New York, 138th and Convent Ave, NY 10031, United States

A R T I C L E I N F O

Article history:
Received 3 March 2009
Received in revised form 9 April 2009

Keywords:
Emmetropization
Myopia
Choroid
Sclera
Hyperopia
Ocular length
Choroidal thickness
Chromatic
Color

A B S T R A C T

Longitudinal chromatic aberration (LCA) causes short wavelengths to be focused in front of long wavelengths. This chromatic signal is evidently used to guide ocular accommodation. We asked whether chick eyes exposed to static gratings simulating the chromatic effects of myopic or hyperopic defocus would "compensate" for the simulated defocus.

We alternately exposed one eye of each chick to a sine-wave grating (5 or 2 cycle/deg) simulating myopic defocus ("MY defocus": image focused in front of retina; hence, red contrast higher than blue) and the other eye to a grating of the same spatial frequency simulating hyperopic defocus ("HY defocus": blue contrast higher than red). The chicks were placed in a drum with one eye covered with one grating, and then switched to another drum with the other grating with the other eye covered. To minimize the effects of altered eye-growth on image contrast, we studied only the earliest responses: first, we measured changes in choroidal thickness 45 min to 1 h after one 15-min episode in the drum, then we measured glycosaminoglycans (GAG) synthesis in sclera and choroid (by the incorporation of labeled sulfate in tissue culture) after a day of four 30-min episodes in the drum.

The eyes compensated in the appropriate directions: The choroids of the eyes exposed to the HY simulation showed significantly more thinning (less thickening) over the course of the experiment than the choroids of the eyes exposed to the MY simulation (all groups mean: -17 μm; 5 c/d groups: -24 μm; paired *t*-test (one-tailed): $p = 0.0006$). The rate of scleral GAG synthesis in the eye exposed to the HY simulation was significantly greater than in the eye exposed to the MY simulation (HY/MY ratio = 1.20; one sample *t*-test (one-tailed): $p = 0.015$). There was no significant interaction between the sign of the simulated defocus and either the spatial frequency or the presence of a +3 D lens used to compensate for the 33 cm distance of the drum.

Although previous work has shown that chromatic cues to defocus are not essential for lens-compensation, in that chicks can compensate in monochromatic light, our evidence implies that the eye may be able to infer whether the eye is myopic or hyperopic from the different chromatic contrasts that result from different signs of defocus.

1. Introduction

Emmetropization is an active process that uses visual cues to match the eye length with the focal length of the eye's optics. How the eye discerns the sign of defocus has been a question that has resisted resolution for many years. One possibility is that a color signal from longitudinal chromatic aberration (LCA) could be used to help detect the sign of defocus of the eye (Fincham, 1951; Flitcroft, 1990), as it does in accommodation (Kruger, Mathews, Aggarwala, & Sanchez, 1993; Kruger, Mathews, Aggarwala, Yager, & Kruger, 1995). However, eyes can compensate for spectacle lenses in monochromatic light (Rohrer, Schaeffel, & Zrenner, 1992; Rucker & Wallman, 2008; Schaeffel & Howland, 1991; Wildsoet, Howland, Falconer, & Dick, 1993). This shows that LCA is not necessary for lens compensation; we now test whether it is sufficient.

LCA affects the contrast transmitted by the different cone types. As a result of LCA, the shorter wavelengths of the incident light are refracted more than the longer wavelengths by the cornea and lens, producing an image in which the shorter wavelengths (blue) are focused closer to the lens than the longer wavelengths (red). This difference in refraction with wavelength affects the contrast of the retinal image differentially for the different cone types (Marimont & Wandell, 1994; Rucker & Osorio, 2008). In a well

---

[*] Corresponding author.
E-mail address: rucker@sci.ccny.cuny.edu (F.J. Rucker).

[1] Supported by NIH Grants EY-02727 and RR-03060.

0042-6989/$ - see front matter Published by Elsevier Ltd.
doi:10.1016/j.visres.2009.04.014

focused image the focal plane lies between the optima for the middle-wavelength-sensitive cones (M-cones) and the long-wavelength-sensitive cones (L-cones). The short-wavelength light which stimulates the short-wavelength-sensitive cones (S-cones) tends to be somewhat out of focus; with myopic defocus (focal plane in front of the photoreceptors) this defocus of short-wavelengths is exaggerated. Conversely, if the retinal image is focused hyperopically (focal plane behind the photoreceptors) then short wavelengths will be more in focus than long wavelengths, and so the short-wavelength component of the retinal image will have higher contrast than the long-wavelength component.

1.1. Criteria for an emmetropization signal from LCA

The first criterion for the existence of an emmetropization signal from LCA is that the eye can detect the effects of LCA. Several investigators have demonstrated changes in eye length that correspond to changes in focus caused by illumination with different wavelengths. In fish (blue acara) eyes, the naso-temporal diameter was larger when they were exposed to red light compared to when they were exposed to blue light (Kröger & Wagner, 1996). In birds, chicks kept in red (615 nm) or blue (430 nm) monochromatic illumination for two days developed a relative myopic or hyperopic shift, respectively (Seidemann & Schaeffel, 2002); similar results were found by Rucker and Wallman (2008). Clearly the eye can detect the effects of LCA.

A second criterion for the existence of an emmetropization signal from LCA is that several different cone types must contribute to the response because a chromatic response from LCA requires comparing the responses of two or more cone types. Early experiments (Kröger & Wagner, 1996; Rohrer et al., 1992) suggested that long-wavelength sensitive cones (L-cones) or double cones (D-cones) contribute to lens compensation, but ultra-violet sensitive cones (UV-cones) do not (Rohrer et al., 1992). Rucker and Wallman (2008) subsequently showed that in addition to an L- or D-cone contribution, short-wavelength sensitive (S-cones) can also contribute to the emmetropization response. At low illumination levels the form of the emmetropization response in chicks depends on cone type. If these short-wavelength sensitive cones were stimulated, defocus was compensated mostly by adjusting the rate of ocular elongation, whereas if L-cones or D-cones were stimulated it was the choroidal thickness that changed (Rucker & Wallman, 2008). These experiments confirm that more than one cone type participates in detecting the effects of LCA and compensating for lens-induced defocus.

1.2. Effect of LCA on the retinal image of a black/white grating

The effects of LCA on the image of a black and white square-wave grating pattern are shown in Fig. 1. With hyperopic defocus (Fig. 1: top row) the red and green components of the image are focused further behind the retina than the blue components, and hence the image of these components will be more blurred. Therefore, if the eye views a black/white edge, then the red and green components of the edge will be blurred relative to the blue (Fig. 1A). If the pattern is repetitive as in a square wave, the blurred wavelengths will reach neither the maximum nor the minimum brightness of the focused wavelengths, resulting in lower modulation or contrast (Fig. 1B). Thus, there will be a lower amplitude of red in the bright bars and a higher amplitude of red in the dark bars. In a sine-wave grating the effect of defocus is only to reduce contrast (Fig. 1C). Therefore, if the image is defocused hyperopically (behind the photoreceptors) the amplitude of the blue component will be higher than the green or red component. The reverse is true with myopic defocus (Fig. 1D).

In this experiment we have simulated the effects of defocus caused by LCA with sine-wave gratings to determine if a chromatic signal from LCA can drive an emmetropization response. Image simulations of this sort have been shown to drive reflex accommodation in the predicted direction (Kruger et al., 1995; Lee, Stark, Cohen & Kruger, 1999; Stark, Lee, Kruger, Rucker, & Ying, 2002; Rucker & Kruger, 2004). Some of this work has been presented previously at ARVO 2007.

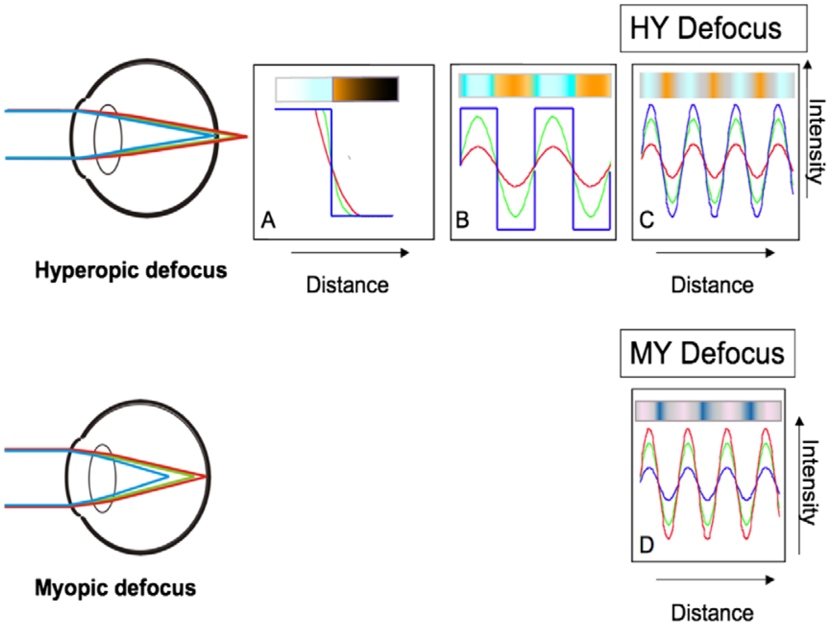

Fig. 1. Effect of LCA on defocus and contrast. Top row: If the eye is focused on short wavelengths, longer wavelengths would be focused behind the retina and would produce a blurred retinal image. (A) a black/white edge will therefore be better defined by the short wavelengths, (B) if the pattern is a square-wave, then the longer wavelengths may never reach maximum or minimum intensity, (C) if the pattern is a sine-wave, in which the only change with defocus is a change in contrast, with hyperopic defocus the short-wavelength component will have a higher contrast than the longer-wavelength components (HY defocus). Bottom row: The reverse is true for myopic defocus (MY defocus).