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R. H. H. Kröger · H.-J. Wagner

The eye of the blue acara (*Aequidens pulcher*, Cichlidae) grows to compensate for defocus due to chromatic aberration

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Abstract By rearing fish in various monochromatic illuminations we investigated (1) the potential for compensation of refractive error due to chromatic aberration, (2) the contributions of the chromatic channels to emmetropization, and (3) the role of color cues in the control of eye growth. Cichlid fish (*Aequidens pulcher*) were reared for 6 months (12 h light/12 h dark) in monochromatic lights (623.5, 534.1, 485.0 nm; spectral purity 5–10 nm). Light levels were isoirradiant at $1.1 \cdot 10^{12}$ quanta/s/cm^2. Two control groups were reared in white light with down-welling illuminances of 0.2 and 33 lx. Nasotemporal diameters (NTDs) of the eyes were measured in relation to lens size. Due to the oblique axis of highest acuity vision in cichlids, NTD is considered to be a more important dimension than axial length. Variances in NTD were equally small in all rearing groups. NTDs were enlarged with increasing wavelengths of the rearing lights with highly significant values over controls in the red-light group. The wavelength-dependent size of the eyes matched the changes in focal length due to longitudinal chromatic aberration. Complete recovery from eye enlargement was observed after fish reared in red light were exposed to a white light regime for 5 weeks. Small variances in NTD in all groups indicated stringent control of eye growth in the absence of color cues. The reversibility of the increase in NTD in fish reared in red light suggests that the eyes were emmetropized by visually guided mechanisms. Eye size in fish reared in white light was intermediate between the values expected if only blue-sensitive single or the red- and green-sensitive double cones contributed to the control of eye growth. This suggests that all chromatic channels participate in emmetropizing the fish eye.

R. H. H. Kröger (✉) · H.-J. Wagner
Anatomisches Institut, Eberhard-Karls-Universität Tübingen, Österbergstrasse 3, D-72074 Tübingen, Germany
Tel.: + 49-7071/2973022, Fax: + 49-7071/294014

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Introduction

The refractive state of the adult eye depends on visual experience during the development of an animal. Visually guided feedback mechanisms control the growth of the eye, resulting in an optimum of retinal image quality (e.g., Schaeffel and Howland 1988, 1991). Inappropriate stimulation of the eye can lead to severe refractive misdevelopment. For example, deprivation of form vision induces myopia (form deprivation myopia) in animal models, mainly due to excessive growth of the bulbus (e.g., Wiesel and Raviola 1977, 1979; Wallman et al. 1978). If lenses are used to change the apparent refractive state of the eye, the imposed defocus is compensated by emmetropizing changes in eye growth (Schaeffel et al. 1988; Irving et al. 1992; Wildsoet and Wallman 1995). The mechanisms controlling eye growth reside mainly in the retina. Emmetropization continues after sectioning the optic nerve (Troilo et al. 1987; Wildsoet and Wallman 1995) or blockage of accommodation (Schaeffel et al. 1990). Furthermore, local modulation of scleral growth can be induced with partial occluders (Hodos and Kuenzel 1984; Wallman et al. 1987) and by rearing chickens in cages with low ceilings (Miles and Wallman 1990). In spite of intense research, the environmental factors involved in the development of myopia in animals and humans are still incompletely known [See Yinon (1984), Curtin (1985), Holden et al. (1988), Troilo (1992) and Wallman (1993) for detailed reviews, and Schaeffel and Howland (1995) for the current state of myopia research.]

Since fish grow throughout their lives, they are well suited for studying the mechanisms of eye growth control. It has been shown that the development of the fish eye also depends on visual experience. If fish are reared in darkness or scotopic illumination, their eyes become

larger and show more variance in size than after rearing under photopic conditions (Kröger and Fernald 1994). Cone vision is therefore necessary for the regulation of eye growth. It is an open question, though, which chromatic cone type contributes to emmetropizing mechanisms. If several types are involved, the visual system has to take into account differences in focal length due to the longitudinal chromatic aberration of the eye (Rohrer et al. 1992).

In fish, the difference in focal length between the C and F Fraunhofer lines (656 and 486 nm, respectively) is in the range of 2–5% of the focal length of the lens (Scholes 1975; Sroczyński 1976, 1978, 1979; Sivak and Bobier 1978; Otten 1981; Fernald and Wright 1985a; Fernald 1988; Kröger and Campbell 1993, 1996). The contribution of the cornea is negligible since it has very little refractive power in water (Matthiessen 1886; Fernald and Wright 1985a). In the powerful lenses of fish, a change in focal length of 2% is equivalent to a difference in refractive power of 8 D in a lens with a diameter of 2 mm and a focal length of 2.5 mm. The "red" image is therefore considerably blurred when the "blue" image is in focus, and vice versa. The problems originating from longitudinal chromatic aberration could be circumvented if only one chromatic channel were responsible for sensing image quality and controlling the growth of the eye, which would narrow the spectral range used for emmetropizing the eye.

Cichlid fish typically have a very regular cone mosaic of the square type (Wagner 1972; Fernald 1981). Each single cone, sensitive to short wavelengths ("blue" cones), is surrounded by four pairs of double cones consisting of middle- and long-wavelength-sensitive members ("green" and "red" cones, respectively). In a light-adapted retina, all cone types lie in the same focal plane (Fig. 1). The ratio of single to double cones is 1 or 2 in the entire retina, including the area of highest cell density in the temporal region near the margin of the retina (Fernald 1981). All chromatic channels could be involved in emmetropization, with the blue-sensitive system being the least likely candidate since it has only about half the spatial resolution of the green- and red-sensitive systems.

We reared fish in monochromatic and white lights and measured eye sizes to address the following questions.

1. Is the refractive development of the fish eye dependent on the visual environment? In particular, does the eye compensate for longitudinal chromatic aberration by adjusting its size to the focal length of the optics at the wavelengths of the monochromatic rearing lights?
2. What are the contributions of the chromatic cone types to the regulation of eye growth?
3. Are the mechanisms of eye growth control in fish dependent on color cues?

Since rearing in monochromatic light has no influence on the optical properties of the crystalline lens in fish (Kröger et al., in preparation), differences in the focal length due to chromatic aberration persist in chronic experiments.

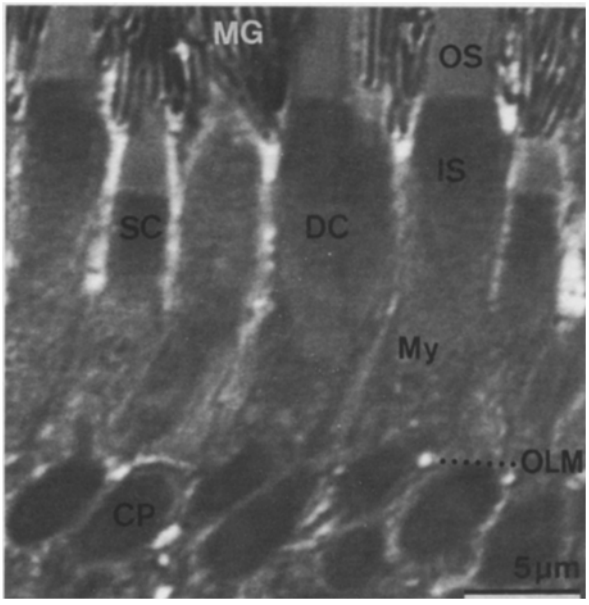

Fig. 1 Radial section through the distal, light-adapted retina of *Aequidens pulcher*. The myoids of single and double cones are fully contracted and there is no difference in the radial positions of the inner segments of both cone types (*SC* single cone, *DC* double cone, *CP* cone perikaryon, *My* myoid, *IS* inner segment, *OS* outer segment, *OLM* outer limiting membrane, *MG* melanin granules in the microvilli of pigment epithelium cells)

The experimental approach of rearing fish in monochromatic lights to study the mechanisms controlling eye growth has also been used by Kröger and Fernald (1994). In that study, statistically significant differences in eye size between the groups reared in white and monochromatic lights were not found. For the present experiments, we had the opportunity to work with a refined method and a different species of fish. Furthermore, the wavelengths used in this study were longer than in that by Kröger and Fernald (1994).

Materials and methods

Rearing conditions and chromatic light regimes

Blue acaras (*Aequidens pulcher*) were bred from a laboratory population, the gene pool of which was occasionally refreshed with animals from other populations to minimize inbreeding. Since *A. pulcher* is a substrate brooder, fry were taken 10–14 days after fertilization as soon as they were swimming freely. Groups of about 100 fish were kept in each of five 150 l tanks. The aquaria were housed in light-tight boxes. The walls of the boxes were covered with a vividly patterned wallpaper to create a complex visual environment. About 10% of the wallpaper surface comprised brightly colored, gray, and black patches and lines on a white background. The remaining interior surfaces of the boxes were painted flat white. The water was conditioned with peat to give a pH of 6–7 at a temperature of 27°C.

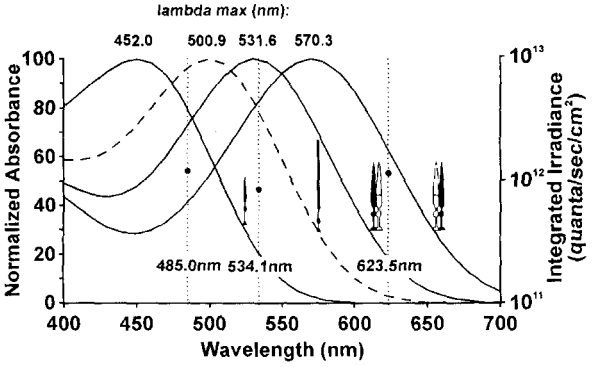

Fig. 2 The absorption spectra of the rods and cones of *A. pulcher* (*left ordinate*) und the integrated irradiances of the monochromatic rearing lights (*right ordinate*). Continuous absorbance curves were calculated from the wavelengths of peak absorption after Stavenga et al. (1993)

All animals were kept in a 12h–12h light-dark cycle for at least 6 months.

Light was delivered from the roofs of the boxes. Reflectors and sheets of white fabric were used to reduce variations in irradiance across the aquaria to less than 30%. The central wavelengths of the monochromatic illumination lights were 623.5 nm ("red group"), 534.1 nm, ("green group"), and 485.0 nm ("blue group") (Fig. 2). Spectral purity of the lights was 5–10 nm. Down-welling irradiances in the centers of the empty aquaria were $1.1 \pm 0.2 \cdot 10^{12}$ quanta/s/cm^2. Two control groups were reared in the white light of Osram Dulux Electronic bulbs. Down-welling illuminances were 33 lx ("bright group") and 0.2 lx ("dim group"), the latter being slightly dimmer to the human eye – and presumably also to the fish eye – than the green light (0.45 lx). Light intensities were measured with an EG&G model 450 photometer/radiometer with appropriate detectors. The two white-light groups were designated to differentiate effects due to light intensity from those brought about by the spectral composition of the light. The light levels used in this study were sufficient to induce fully light adapted retinomoter positions of all cone types in fish reared in white light.

The spectral positions of the illumination lights were chosen according to the information on photoreceptor absorbances in the blue acara published by Levine and MacNichol (1979). When absorption spectra were measured microspectrophotometrically (Bowmaker, unpublished observations), the wavelengths of maximum cone absorption were considerably shorter than previously reported, suggesting that data may have been switched in the table compiled by Levine and MacNichol (1979). The use of longer wavelengths had the disadvantage that the blue-sensitive single cones were not optimally stimulated (Fig. 2). However, the long wavelength of the red light induced significant enlargement of the eye to compensate for longitudinal chromatic aberration and thus was a fortunate choice.

Measuring eye size and shape

Since we used similar methods for measurements and data analysis as Kröger and Fernald (1994), we outline the procedures only briefly and emphasize the modifications. Fish were sacrificed by rapid decapitation, the eyes removed and immediately freeze-embedded in Tissue Tek (Miles). Since rearing and measurements were done in the same building, exposure to white light for up to 3 weeks prior to sacrifice of the fish and enucleation of the eyes (Kröger and Fernald 1994) was avoided. The eyes were sectioned on a cryostat with a video camera directed to the face of the block containing the specimen. Since the lens appeared brilliantly white on the video image, its apparent size changed considerably due to glare depending on how the block was illuminated. Special care was therefore taken to standardize the illumination of the specimen. The video output was directed to an image-capturing and -processing system (Zeiss) and analyzed on a high-resolution monitor (Mitsubishi). Image distortion was measured as less than 1% over the entire field of view.

Eye size was determined in the meridional, nasotemporal plane. Measurements of axial length are biased by distortions of the cornea and the area around the optic nerve due to mechanical deformation during dissection and freeze-embedding (Kröger and Fernald 1994). However, the nasotemporal diameter (NTD) could be measured reliably (see also Kröger and Fernald 1994). NTD is a critical dimension of the cichlid eye, since the most important axis of vision is strongly tilted toward the temporal region of the retina. This is evident by cell densities in the retina (Fernald 1981) and the nasotemporal direction of lens movements during accommodation (Fernald and Wright 1985b). To facilitate comparisons between eyes from different rearing groups, fish of similar body sizes were selected in all groups. Furthermore, all data are expressed in units of the radius of the spherical crystalline lens. This normalization of the data largely removes individual variations in eye size due to differences in body size (Kröger and Fernald 1994).

Kröger and Campbell (1993, 1996) found the following relationship for the longitudinal chromatic aberration of the *Haplochromis burtoni* lens:

$$\Delta f = U + (1\,\mu m/\lambda + V)^W \quad (1)$$

where Δf = difference in focal length as percent of the focal length at 633 nm, λ = wavelength in µm, $U = -(V + 10^3/0.633)^W$ with $V = -1.375$, $W = -0.466$.

From Eq. 1 the NTD expected from the magnitude of chromatic aberration in the cichlid eye can be calculated for any wavelength with

$$NTD(\lambda) = NTD(633\,nm) - NTD(633\,nm)/100 \cdot \Delta f \quad (2)$$

where NTD(633 nm) is the expected NTD of the eyes of fish reared at 633 nm. NTD(633 nm) was obtained by fitting Eq. 2 to the values of focal length measured at 623.5, 534.1 and 485.0 nm.

Strong effects on eye size were induced by rearing fish in monochromatic red light. Animals from the red group were therefore transferred to the bright-white light regime ("red-to-bright" group). After 5 weeks, NTDs were measured in fish of the same age (19 months) from the red-to-bright and bright-white groups to investigate the reversibility of the effects induced by rearing in red light.

Results

NTDs were measured in a total of 70 eyes from 36 fish. The results, after normalization to lens radius, are summarized in Table 1 and Fig. 3. Highly significant differences between the rearing groups were detected by single-factor ANOVA: $P < 5 \cdot 10^{-5}$. The eyes of fish reared in red light were significantly wider than the eyes in all other groups (Student's *t*-tests, Table 1). In the animals reared in monochromatic lights, NTD was positively correlated with the wavelength of the illumination. Fitting Eq. 2 to the dependency of NTD on the wavelengths of the monochromatic rearing lights resulted in good agreement between predicted and measured data (Fig. 4), indicating that the variation in NTD was close to the shift in focal length expected from longitudinal chromatic aberration.

Table 1 The quantitative results and statistical analysis in overview. Fish of similar standard lengths were chosen in all rearing groups to minimize bias in measured nasotemporal diameter (*NTD*) due to differences in individual growth rates. NTDs are expressed in units of lens radius to remove the remaining size-related variation. In fish reared in red light, the eyes were significantly (Student's *t*-test) larger than in all other groups

	Rearing group				
	Bright	Dim	Red	Green	Blue
n (fish/eyes)	7/14	7/14	7/14	8/14	7/14
Fish length ± SD (cm)	4.28 ± 0.50	4.18 ± 0.45	4.33 ± 0.27	4.25 ± 0.41	4.34 ± 0.47
NTD of the eye ± SD	5.28 ± 0.07	5.28 ± 0.08	5.41 ± 0.10	5.31 ± 0.04	5.30 ± 0.07
P (*t*-test vs. Red)	< 0.001	< 0.001	—	< 0.001	< 0.01

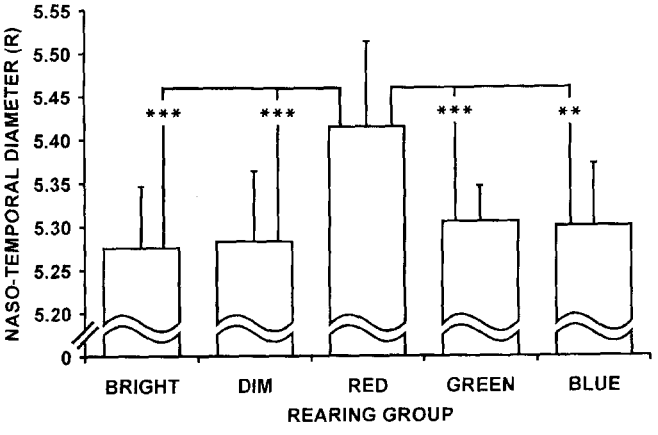

Fig. 3 Nasotemporal diameters (NTDs) in the meridional plane of the eyes of fish reared in white and monochromatic lights for 6 months. The data are expressed in units of lens radius to remove variations in eye size due to differences in body size. The mean NTD in the red-light group was signficantly larger than in all other groups (**$P < 0.01$, ***$P < 0.001$). Note that the relevant region of the ordinate was expanded to facilitate comparisons between the rearing groups. *Error bars* denote standard deviations. White light illumnance: *DIM* 0.2 lx, *BRIGHT* 33 lx; monochromatic light central wavelength: *RED* 623.5 nm, *GREEN* 543.1 nm (0.45 lx), *BLUE* 485.0 nm

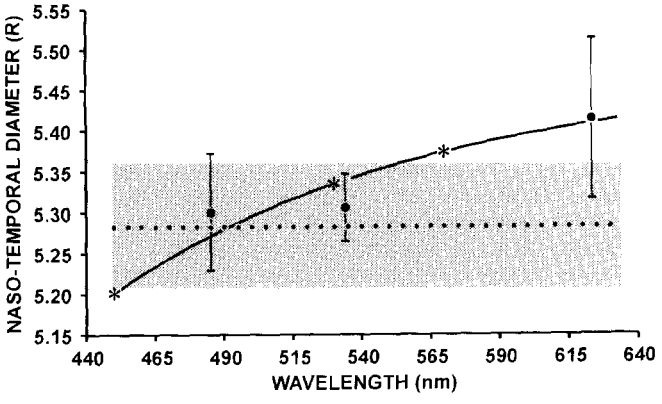

Fig. 4 Mean NTDs in the groups reared in monochromatic lights (*dots*) with standard deviations. The *continuous line* was determined by fitting Eq. 2 to the measured data and illustrates the NTD as a function of wavelength as expected if the longitudinal chromatic aberration of the optics is compensated by adjusting the size of the eye. The *asterisks* mark the NTD predicted at the wavelengths of maximum cone absorbances. The *dotted line* and the *shaded area* show the mean NTD and standard deviation, respectively, found in the dim-white-light group. Note that eye size in the dim group was intermediate between the NTD values expected if eye growth were exclusively controlled by the blue-sensitive single or the red- and green-sensitive double cones

Within each group, eye size showed little variation, indicating that eye growth was visually controlled in all lighting regimes. The eyes of the animals in the bright and dim groups were very similar in size. Regulation of eye growth was thus independent of light intensity.

In the red-to-bright group, complete recovery from eye enlargement was found after 5 weeks of exposure to the bright-white-light regime. NTDs were almost identical to the values found in fish from the bright group of the same age (Table 1, Fig. 5). Differences in NTDs measured at the ages of 6 and 19 months are mainly due to interobserver bias. Those sets of data were acquired by two different people who judged the size of the lens on the video images differently. Within the data sets gathered by each observer, measurements were highly reproducible, as indicated by the small standard deviations in both samples (Table 1; Figs. 3–5).

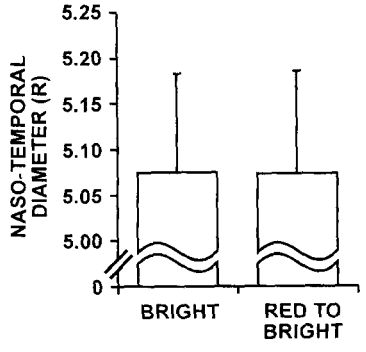

Fig. 5 Mean NTDs of the eyes of fish reared in monochromatic red light for 18 months and thereafter kept in a white-light regime for 5 weeks (red-to-bright group). For comparison, NTDs were also measured in animals of the same age from the bright-white-light group

Discussion

The most obvious results of this study are that the animals reared in red light had enlarged eyes (Fig. 3) and that complete recovery took place within 5 weeks of exposure to a white-light regime. Furthermore, the increase in NTD with increasing wavelength of the rearing light is in good agreement with expectations from longitudinal chromatic aberration (Fig. 4). Those findings indicate that the size of the eye was adjusted to the focal length of the optical elements, mainly the lens, at the wavelength of the rearing light, and that at the age of 18 months, the eyes were emmetropized within 5 weeks after removal of the chromatic defocus.

The importance of color cues

Variances in eye size within the groups reared in monochromatic lights were as small as in the white-light groups. The mechanisms of growth control are thus fully functional in monochromatic light. As was found in chickens (Schaeffel and Howland 1991; Wildsoet and Howland 1991), the mechanisms controlling the growth of the fish eye are independent of color cues. The colored fringes that are present in images of scenes illuminated with white light and that change their color between red and blue depending on the sign of defocus are not the only source of information for the fish eye to properly adjust its size to the focal length of its imaging system.

The contributions of the chromatic cone types

Chromatic aberration of the eye increases rapidly in the blue range (e.g., Sroczyński 1976, 1978, 1979; Mandelman and Sivak 1983). If the eye is emmetropic at middle wavelengths, chromatic defocus most strongly affects the short-wavelength-sensitive system. It was found in chickens that the UV-sensitive cones do not contribute to emmetropization of the eye, at least not under the experimental conditions chosen (Rohrer et al. 1992). The visual system of chickens may thus bypass the problem of differences in focal length due to chromatic aberration by excluding from the control of emmetropization the cones at the short-wavelength end of the spectrum (Rohrer et al. 1992).

In the red-light group, the blue-sensitive single cones were essentially excluded from stimulation (Fig. 2). If they played a crucial role in controlling eye growth, large variations in eye size were to be expected, as are present in fish reared in darkness or scotopic illumination (Kröger and Fernald 1994). The small variance in the red group indicates that eye growth was as stringently controlled as in white light. The blue channel is therefore certainly not only source of information on the image quality.

In both chickens and the blue acara, the short-wavelength-sensitive system has the lowest spatial resolution. For this reason it is least suited to detect image blur. However, in our sample, eye size in the fish reared in white light was smaller than expected if eye growth were controlled exclusively by the red- and/or green-sensitive members in the double cones (Fig. 4). It is therefore likely that both double and blue-sensitive single cones contribute to the regulation of eye growth in spite of the lower spatial resolution of the blue-sensitive system. It cannot be decided whether only one member in the double cones has an input into the control of eye growth, since the difference in eye size expected from chromatic aberration between the wavelengths of maximum absorption is too small to be resolved with our method (Fig. 4).

Eye size was almost identical in the green (534 nm) and blue (485 nm) groups. This observed similarity is most likely due to measurement uncertainty rather than indicating a lack of compensation for chromatic aberration. The crystalline lens of cichlids has considerable longitudinal chromatic aberration between 515, 488, and 457 nm (Kröger and Campbell 1993, 1996). Since eye growth was under equally stringent control in both groups and all cones lie in the same focal plane, one would have to postulate some unknown mechanism to bring green and blue images in focus in the same plane if there were indeed no compensation for chromatic aberration in the middle- to short-wavelength range of the spectrum.

Conclusions

Our results show that (1) the dependency of eye size on the wavelength of the rearing light agrees well with the differences in focal length due to longitudinal chromatic aberration, (2) all chromatic cone types appear to contribute to the control of eye growth, and (3) those mechanisms are independent of color cues.

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