

## ORIGINAL PAPER

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**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 isoirradian at  $1.1 \cdot 10^{12}$  quanta/s/cm<sup>2</sup>. 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.

**Key words** Eye growth · Emmetropization · Monochromatic light · Fish · Chromatic aberration

**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

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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).

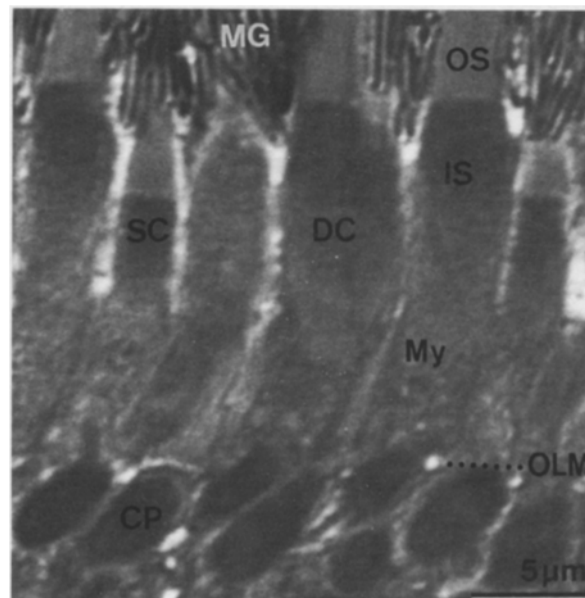
In fish, the difference in focal length between the C and F Fraunhofer lines (656 and 486 nm, respectively) is in the range of 2–5% of the focal length of the lens (Scholes 1975; Sroczyński 1976, 1978, 1979; Sivak and Bobier 1978; Otten 1981; Fernald and Wright 1985a; Fernald 1988; Kröger and Campbell 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



**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)

fish (Kröger et al., in preparation), differences in the focal length due to chromatic aberration persist in chronic experiments.

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.