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Multifocal lenses compensate for chromatic defocus in vertebrate eyes

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Abstract The focal length of the vertebrate eye is a function of wavelength, i.e. the eye suffers from longitudinal chromatic aberration. Chromatic defocus is a particularly severe problem in eyes with high light-gathering ability, since depth of field is small due to a pupillary opening that is large in relation to the focal length of the eye. Calculations show that in such eyes only a narrow spectral band of light can be in focus on the retina. For the major part of the visual spectrum, spatial resolution should be limited by the optics of the eye and far lower than the resolving power achievable by the retinal cone photoreceptor mosaic. To solve this problem, fishes with irises unresponsive to light have developed lenses with multiple focal lengths. Well-focused images are created at the wavelengths of maximum absorbance of all spectral cone types. Multifocal lenses also appear to be present in some terrestrial species. In eyes with mobile irises, multifocal lenses are correlated with pupil shapes that allow all zones of the lens, with different refractive powers, to participate in the imaging process, irrespective of the state of pupil constriction.

Key words Color vision · Chromatic aberration · Spherical aberration · Depth of field · Pupil shape

Abbreviations *LCA* longitudinal chromatic aberration · *LSA* longitudinal spherical aberration · *LWS* long-wave-sensitive · *MWS* middle-wave-sensitive · *SWS* short-wave-sensitive

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Introduction

The eyes of many fishes and nocturnal terrestrial vertebrates have small *f*-numbers – short focal length relative to pupil diameter – in order to maximize light-gathering ability. In such eyes, depth of field is much smaller than in the human eye. Since in simple optical systems like animal eyes the focal length is a function of the wavelength of light (longitudinal chromatic aberration, LCA), differences in focal length due to LCA should degrade the image to an extent that the spatial resolution of color vision should be very poor. However, many fish species have excellent color vision with several, spectrally widely spaced visual pigments (Bowmaker 1995). Among nocturnal terrestrial species, geckos, for instance, have three spectral cone types (Loew et al. 1996) and thus face similar problems caused by LCA. We analyzed the optics of the eye of *Haplochromis burtoni*, a cichlid fish from Lake Tanganyika, and present data which indicate that the problem of chromatic defocus is solved by multiple focal lengths in the lens. Furthermore, we examined eyes with small *f*-numbers in other vertebrates and found that multifocal lenses appear to be present in a variety of species.

Since the cornea contributes little to the refractive power of the eye underwater (Matthiessen 1886), the focal length and image quality of the fish eye depend primarily on lens optics. The typical fish lens is spherical in shape, has a radial internal symmetry of refractive index and short focal length. In *H. burtoni*, the difference in refractive power due to LCA between the wavelengths of maximum absorbance (λ_{max}) of the long- (LWS, 562 nm) and middle-wave-sensitive (MWS, 523 nm) cone photoreceptors is 3.3 diopters for a lens with a radius of 1 mm; between the λ_{max} of the MWS and short-wave-sensitive (SWS, 455 nm) cones it is 9.3 diopters. Between 455 and 562 nm, the difference in image position would be 63 μm (Fig. 1a; Kröger and Campbell 1996). In cichlids, different cone lengths cannot compensate for LCA, as has been suggested for

other fish species (Eberle 1968), since all cone inner segments are aligned at the external limiting membrane in the light-adapted cichlid retina (Kröger and Wagner 1996) and the entrance aperture of a cone appears to be at the proximal (vitread) portion of the inner segment (He and MacLeod 1998). If the λ_{max} of the MWS cones (523 nm) is in focus, the diameters of the blur circles for the λ_{max} of the LWS and SWS cones would be about 15 and 40 μm, respectively, assuming that the lens is free of aberrations other than LCA. Spatial resolution of the cone mosaic is significantly greater than the resolution implied by these blur circles for all spectral cone types. Throughout the retina of *H. burtoni*, cones occur in relative numbers of 2:2:1 (LWS, MWS, SWS, respectively; Fernald 1981) with spacings between spectrally identical cones of 4–5 μm (Fernald 1983).

Homogeneous lenses with spherical surfaces focus monochromatic light passing through the periphery of the lens at closer distances than paraxial rays (longitudinal spherical aberration, LSA). In many vertebrate (Matthiessen 1882; Campbell and Hughes 1981; Sivak and Kreuzer 1983; Axelrod et al. 1988; Pierscionek and Chan 1989; Pierscionek and Augusteyn 1991; Kröger et al. 1994; Jagger and Sands 1996) and invertebrate (Sivak 1991; Sivak et al. 1994) eyes, refractive index decreases gradually from the center toward the surface of the lens, which reduces aberrations, most notably spherical aberration. The residual LSA may even be reversed (Campbell and Hughes 1981). In *H. burtoni*, the fine structure of the refractive index profile within the lens leads to a complex shape of the LSA (Fig. 1b; Kröger et al. 1994).

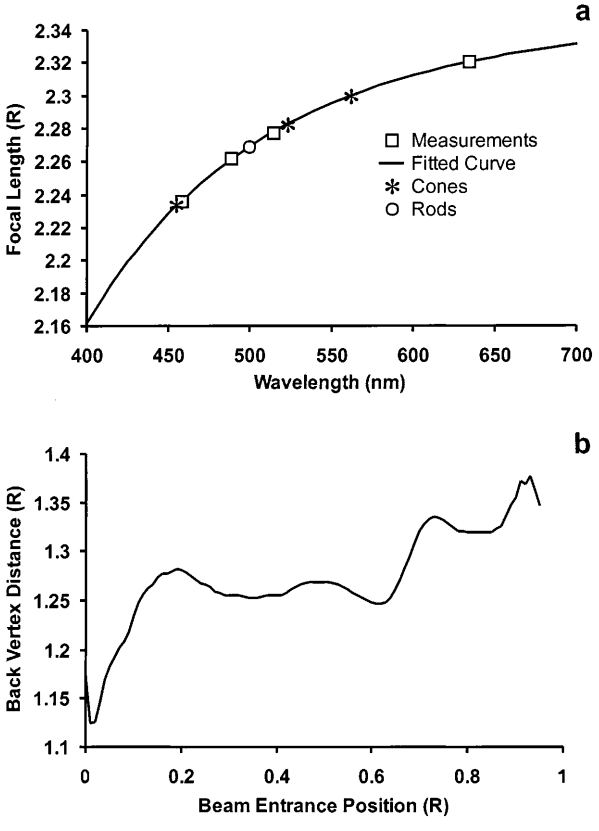

Fig. 1 a The change in the focal length due to longitudinal chromatic aberration (LCA) of the *H. burtoni* crystalline lens. The spectral positions of the λ_{max} of rods and cones are indicated. Data replotted from (Kröger and Campbell 1996). **b** Average longitudinal spherical aberration (LSA) of 21 *H. burtoni* lenses measured at 633 nm. Combined data from Kröger et al. (1994) and Kröger and Campbell (1996)

Ray-tracing was used to determine how the *H. burtoni* lens focuses monochromatic and white light. The results showed that the lens has multiple focal lengths, each creating a well-focused image at the λ_{max} of a distinct spectral cone type. Such tuning of LSA to LCA and cone absorbances was demonstrated directly in isolated lenses of large individuals of *Aequidens pulcher* (blue acara), a cichlid from South and Central American rivers and lakes. Eccentric infra-red photorefractometry (Schaeffel et al. 1987) was used to search for multifocal lenses in a variety of other vertebrate species.

Materials and methods

The proportions of the cichlid eye, which grows throughout life, are constant if expressed in units of lens radius (Kröger and Fernald 1994). We therefore use the relative unit "*R*" throughout this report since our findings on fish eyes are largely independent of absolute eye and lens size.

Ray-tracing model calculations

To determine the three-dimensional imagery of the fish lens from two-dimensional measurements of LSA, 96 incoming rays with equally spaced entrance positions from 0 to 0.95 *R* were traced to the retina. Most of the light incident on the lens beyond 0.95 *R* is reflected and does not contribute to the image (Sroczynski 1976). Except for the axial ray, each incoming ray represented an annulus of light. The contribution of those rays to retinal illumination therefore was weighted for the area of the corresponding annulus. The point of intercept with the retina of each ray was determined by simple geometry since the trajectories of rays were known from the LSA. On the retina, illumination was calculated by summing the contributions of rays per unit retinal area. Bin width on the retina was 0.0015 *R*, which is about the diameter of the perfect disc of diffraction (e.g., Longhurst 1973). The change in focal length due to LCA was calculated from earlier measurement in the *H. burtoni* lens using laser light of four wavelengths ranging from 457 to 633 nm (Kröger and Campbell 1996). Sources of white light were assumed to have the same power at all wavelengths from 400 to 700 nm. For comparison, calculations were performed for an idealized fish lens with the same color-dispersive properties as the *H. burtoni* lens and with perfectly corrected LSA.

Fish lens imagery

An isolated *A. pulcher* lens with a radius of 1.5 mm was placed on an iris diaphragm and immersed in H10 culture medium (Hikida and Iwata 1987). About 95% of the lens aperture was used for imaging, while stray light passing by the lens was blocked from entering the microscope used for observation. The cones of *A. pulcher* have λ_{max} at 453, 530, and 570 nm (Kröger et al. 1999).

Monochromatic illuminations at spectral positions close to those wavelengths (460, 540, and 580 nm) were produced with interference filters (approx. 5-nm half-maximum bandwidths). As a control, we used a filter with a central wavelength of 480 nm. The target was a back-lit copper grid with bars subtending 2 arcmin,