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Optical plasticity in fish lenses

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A B S T R A C T

In a typical fish eye, the crystalline lens is the only refractive element. It is spherical in shape and has high refractive power. Most fish species have elaborate color vision and spectral sensitivity may range from the near-infrared to the near-ultraviolet. Longitudinal chromatic aberration exceeds depth of focus and chromatic blur is compensated for by species-specific multifocality of the lens. The complex optical properties of fish lenses are subject to accurate regulation, including circadian reversible adjustments and irreversible developmental tuning. The mechanisms optimize the transfer of visual information to the retina in diverse and variable environments, and allow for rapid evolutionary changes in color vision. Active optical tuning of the lens is achieved by changes in the refractive index gradient and involves layers of mature, denucleated lens fiber cells. First steps have been taken toward unraveling the signaling systems controlling lens optical plasticity. Multifocal lenses compensating for chromatic blur are common in all major groups of vertebrates, including birds and mammals. Furthermore, the optical quality of a monofocal lens, such as in the human eye, is equally sensitive to the exact shape of the refractive index profile. Optical plasticity in the crystalline lens may thus be present in vertebrates in general.

Contents

1. Introduction

An animal develops from a single cell to a highly complex organism. Developmental plasticity, i.e. regulatory processes involving signaling between cells, tissues, and organs, is a key feature of this self-assembly of the body and the adjustment of its components to each other. In addition, adaptive plasticity allows the organism to optimize its function to the specific conditions it is

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Abbreviations and parameters: BCD, Back center distance; *BEP*, Beam entrance position; DA, Dopamine; 6-OHDA, 6-hydroxy-dopamine; IOS, Inner/outer segment; LSA, Longitudinal spherical aberration; LCA, Longitudinal chromatic aberration; *R*, Lens radius; RI, Refractive index; RIG, Refractive index gradient; UVS, Ultraviolet-sensitive; λ_{max}, Wavelength of maximum photopigment absorbance.

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experiencing. Evolution has brought about highly efficient tuning processes and these mechanisms have played an important role in the evolution of diverse life on Earth. This applies also to the evolution of vision.

The type and amount of information an eye can convey to the central nervous system depends on the performance of the entire organ. The optical system creating images and the retina encoding, processing and transmitting visual information work in concert to provide the animal with vital sensory information. The physical principles of crystalline lens function, i.e. the refraction of light for forming an image on the retina, are well-understood and lens performance can be studied in great detail. Lens optical properties can be measured and retinal images can be reconstructed by computer modeling under a variety of conditions. There are thus effective tools available for studying the role of the lens in the optimization of vision.

Visual function is improved by appropriate adjustments of the eye to changes in natural lighting conditions occurring on various time-scales. Furthermore, the visual needs of an animal may change during life because of growth, change of habitat, sexual maturity and other factors. Functional optimization of the eye during development and in response to external factors is therefore important for visual function. The crystalline lens, however, has long been regarded as a passive element in these processes because of its particular cellular constitution and apparently simple function. This view had to be questioned when it was realized how complex the optical function of the crystalline lens actually is and how intricately it is tuned to the requirements of the retina and the visual needs of the animal. Recent work has shown that the optical properties of the lens are subject to several tuning mechanisms. Despite having been an unlikely candidate, the crystalline lens of the eye has proved to be an excellent model for studies on the power of developmental and adaptive plasticity. Furthermore, the optical plasticity of the lens has to be taken into account for understanding eye development as well as visual function and ecology in vertebrates, and possibly other phylogenetic groups of animals.

2. Typical fish eye

Most of the results on optical plasticity available to date have been obtained by studies on fish lenses and I use “the typical fish eye” to illuminate the need for and the mechanisms involved in optical plasticity of crystalline lenses. A “typical fish” in this context is a teleost, one of about 27000 species of modern ray-finned bony fishes (Pough et al., 2009). Eye design varies considerably in this large group of animals occurring in a wide variety of aquatic habitats. Highly specialized eyes exist mainly in deep-sea species, such as the spookfish (*Dolichopteryx longipes*) (Wagner et al., 2009) and visual specialists, such as the sandlance (*Lymnichthytes fasciatus*) (Pettigrew and Collin, 1995) and the four-eyed fish (*Anableps anableps*) (Sivak, 1976). Despite the great diversity of visual adaptations, the crystalline lenses of fishes share many basic features. Most terrestrial vertebrates have similar needs and solutions, such that the general conclusions drawn from results obtained from typical fish eyes are relevant to the eyes and visual systems of a majority of vertebrates.

Typical fish eyes occur in teleost species living in the upper layers of the water column being reached by sunlight in amounts that make special adaptations to low-light conditions unnecessary. However, light levels are relatively low even in these habitats, if compared to most terrestrial environments. Eyes evolutionary adapted for use at mainly high light levels, such as human and sandlance eyes, are rare in fishes.

The typical fish eye is used in water, a medium of relatively high refractive index (RI: 1.33). Air has an RI of 1.0 and if an eye is used in this medium, the RI of the cornea is considerably higher (about 1.38) (Smith and Atchison, 1997), such that incoming light is refracted at the air–cornea interface. The human cornea, for example, contributes about two thirds of the total refractive power of the eye’s optical system (Smith and Atchison, 1997). If a person dives without goggles, the cornea is in contact with water such that there is little difference in RI and the refractive power of the cornea is lost. In consequence, the underwater scene is severely blurred since the refractive power of the human crystalline lens alone is insufficient to create a well-focused image on the retina.

The contribution of the cornea to refraction is negligible in most fish eyes (Matthiessen, 1886) and this necessitates an optically powerful crystalline lens for clear underwater vision. The high refractive power of a fish lens is achieved by two means: spherical shape and a steep gradient of refractive index (see Section 5). The focal length of a typical fish lens is only about 2.5 times its radius (Matthiessen, 1886; Sroczyński, 1977; Fernald and Wright, 1985a; Kröger et al., 1994). This relative focal length is largely independent of the absolute size of the lens.

The very high protein concentrations in fish lenses make adjustments of refractive power by changes in lens shape at least impractical, if not impossible. Fish lenses are rigid and accommodative changes of focus are achieved by movements of the lens within the eye (Beer, 1894; Fernald and Wright, 1985b). A complex apparatus consisting of several suspensory ligaments and a retractor lentis muscle hold the lens in place within the eye (Khorramshahi et al., 2008) and activation of the muscle moves the lens toward the retina. A fish eye is thus adjusted to near vision in the un-accommodated state, which may be an adaptation to the usually limited visual range underwater.

Many terrestrial vertebrates have pupils constricting quickly when the eye is exposed to high light levels. Looking at, for example, sunlight reflected from a water surface may damage the human retina if the pupil is fully dilated. In contrast, damaging light levels underwater might occur only close to the surface on a sunny day. Pupillary movements occur in fish, but typically the pupil of a fish eye is immobile and fully open at all times. It is so large that the full diameter of the lens can be used to collect light (Fernald and Wright, 1985a). Regulation of light flux to the photoreceptor cells does occur in fishes, but is usually achieved by mechanisms located in the retina (see Section 6.1).

In summary, the crystalline lens of a typical fish eye is a spherical gradient-index lens of short focal length and the only refractive element in the eye. Lens shape is invariable and the entire lens aperture is used under all lighting conditions. These features simplify the analysis of the optical system and allow for realistic and detailed modeling of its performance under various conditions.

3. Cellular structure of the lens

There are two basic functional requirements an eye lens has to fulfill: it has to be transparent and it has to refract light. Lens transparency is dependent on cellular and molecular structure, while RI is directly related to protein concentration. Since vertebrate lenses are gradient-index structures (Pierscionek and Regini, 2012), cytosolic protein concentration varies throughout the lens. Some of the adaptations for maximum transparency and exact control of the refractive index gradient will be presented here since they are of importance to understand the mechanisms behind optical plasticity. However, a comprehensive account of lens cellular and molecular biology is beyond the scope of this review.

A vertebrate crystalline lens is an inverted epithelium (Fig. 1). Its outmost layer is a particularly thick fibrous basement membrane, called the lens capsule. On the inside of the lens capsule there is a monolayer of cells, the so-called lens epithelium, which in a fish