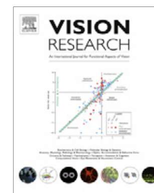
Vision Research 51 (2011) 1099–1108

Contents lists available at ScienceDirect

Vision Research

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



A comparative study on the visual adaptations of four species of moray eel

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ARTICLE INFO

Article history:
Received 18 November 2010
Received in revised form 22 February 2011
Available online 6 March 2011

Keywords:
Moray eel
Microspectrophotometry (MSP)
λ_{max}
Visual characteristics
Opsin gene

ABSTRACT

The goal of this study was to investigate how the eyes of different species of moray eel evolved to cope with limitations to vision imposed on them by the photic environments in which they reside. The comparative retinal histological structures and visual pigment characteristics including opsin gene sequences, of four species of moray eel inhabiting diverse habitats (i.e., shallow-water species, *Rhinomuraena quaesita* and *Gymnothorax favagineus*, and deep-sea species, *Gymnothorax reticularis* and *Strophidon sathete*) were examined. The histological sections showed that retinal layer structures of *R. quaestia* are significantly different from those of the other three species which likely reflects the effects of distribution depth on the structures. The maximal absorbance wavelength (λ_{max}) of photoreceptor cells, as measured by microspectrophotometry (MSP), showed a close correlation between the λ_{max} and the intensity/spectral quality of the light environment where each species lives. The spectra-shift, between shallow and deep-sea species, observed in the rods cells results from amino acid substitution in Rh1 gene, while that in cones most likely results from differential expression of multiple Rh2 genes.

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1. Introduction

The solar irradiance measured at depth in natural waters is influenced by the absorptive characteristics of the water as well as the time of the day, suspended particle, nutrient load, phytoplankton and zooplankton concentrations. Due to these factors, the photic environment of aquatic organisms exhibits a great diversity of irradiant and optical conditions. In order to adapt to the wide extent of specific photic environments, such as those found in estuaries, coastal, shallow, deep-sea, rivers and lakes, fishes have evolved various visual system characteristics allowing them to operate under different types of photic conditions (Loew & McFarland, 1990). As solar radiation penetrates clear blue oceanic water, the shorter wavelengths (i.e., blue light; *ca.* 400–500 nm) are absorbed less than longer wavelengths resulting in a narrowing of the visible spectrum at depth with the peak of the downwelling light being in the region of 435 nm (Kirk, 1983). In coastal and fresh water the increase in dissolved organics, i.e., the so-called "Gelbstoff" and scattering particulates shifts the transmission maximum to longer wavelengths (Jerlov, 1968). Therefore, in clear water, the photic environment exists as a blue–green color, while the spectrum of the ambient light in coastal and lake waters would be more in the green to orange wavelength range (McFarland, 1986; Morel, 1980).

Vision begins when photons are absorbed by photoreceptors in the retina. Two types of photoreceptors are found in most vertebrate retinas – rods and cones. Rods mediate scotopic vision and generally have long, cylindrical outer segments. Cones mediate photopic, high acuity vision, and usually have shorter, more conical outer segments. They can exist as single cells or into coupled groups as doubles or even triples (Sandström, 1999). Both types of photoreceptors contain visual pigments, which are composed of an opsin protein and a chromophoric group, either 11-*cis*-retinal (based on vitamin A_1) or 11-cis-3-dehydroretinal (based on vitamin A_2). In vertebrates, there are five opsin gene families giving rise to the visual pigments (Yokoyama, 1994, 1995, 1997; see Bowmaker & Loew, 2008). Rh1 is expressed in the rods and yields vitamin A_1-based visual pigments having λ_{max} from 460 to 530 nm (Yokoyama, 1997). The vitamin A_1-based visual pigments found in cones formed by the other four expressed opsin genes are a long- to middle-wave class (LWS) maximally sensitive in the red–green spectral region from about 490–570 nm, a middle-wave class (RH2) sensitive in the green from about 480–535 nm, a short-wave class (SWS2) sensitive in the blue–violet from about 410–490 nm and a second short-wave class (SWS1) sensitive in the violet–ultraviolet from about 355–440 nm (Bowmaker, 2008; Bowmaker & Loew, 2008; Bowmaker, Semo, Hunt, & Jeffery, 2008; Ebrey & Koutalos, 2001; Yokoyama, 2000; Yokoyama & Yokoyama, 1996).

A number of visual system adaptations allow fish to cope with the constraints imposed by a habitat's specific photic environment. First, variations in eye and retinal structure allow some fishes to exploit different habitats and niches more effectively (Bowmaker,

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0042-6989/$ - see front matter © 2011 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2011.02.025

1990, 1995; Collin, 1997). For example, fishes that live in deep-sea environments have adaptations that address the problems of low light intensity such as larger eyes or a tapetum which reflects light back (Nicol & Somiya, 1989; Warrant & Locket, 2004). There may also be longer outer segments that increase the probability of photon capture or banked retinas (see McFarland, 1991). The problems of the spectral shifts in background space light due to depth and changes in water quality have been addressed by altering the absorptive properties of the visual pigments either by amino acid alterations of visual pigment opsins that create visual pigments more appropriately 'tuned' to the visual tasks present, or by altering the expression pattern of the opsin genes, or both (Bowmaker et al., 2008; Carleton & Kocher, 2001; Cottrill et al., 2009; Parry et al., 2005; Shand, Hart, Thomas, & Partridge, 2002; Shand et al., 2008). There is also the possibility of switching chromophore class (vitamin A_1- to vitamin A_2-based) or employing some kind of photosensitizer as has been found for some deep-sea species (see Bowmaker & Loew, 2008).

Numerous studies have documented the changes associated with the retinas and visual pigments of fishes inhabiting different photic environments. For visual pigments, the findings have been interpreted in the context of two hypotheses. The Sensitivity Hypothesis states that for maximizing the brightness contrast of a target against its background a single photoreceptor visual pigment λ_{max} should be located close to the maximum of the downwelling space light to maximize quantum catch. Thus, the λ_{max} of rod visual pigments shifts to shorter wavelengths as habitat depth increases (see Bowmaker, 2008). The Contrast Hypothesis states that two visual pigments are necessary for maximizing chromatic (i.e., color) contrast – one with its absorbance matched to the background space light and the other offset from the background so as to maximize the difference in the background and target chromaticities (see Bowmaker, 2008).

Numerous fish groups from different habitats have been examined for their visual pigment complement and their retinal structure. However, few have been conducted on members of eel families, including freshwater eels and the conger eels. To adapt to the deep-sea environments, freshwater eels (*Anguilla* spp.) and conger eels (*Conger* spp.) possess photoreceptors with a blue-shifted λ_{max} (Archer & Hirano, 1996; Denton & Walker, 1958; Shapley & Gordon, 1980). Moreover, freshwater eels can alter their spectral sensitivities during their migration from the freshwater to the deep-sea environment either by switching chromophore type, or by expressing different opsin genes to cope with the changing light environments (Bowmaker et al., 2008; Cottrill et al., 2009).

Moray eels are generally recognized as nocturnal predators because of their relatively smaller eyes and well-developed olfactory sense and sensory pores, all of which could enhance their foraging ability during the night (Bardach & Loewenthal, 1961; Bardach, Winn, & Menzel, 1959; Hess, Melzer, & Smola, 1998; Winn & Bardach, 1959; Young & Win, 2003). However, some moray eel species have been reported to forage during the day relying on their eyes (Böhlke & Randall, 2000; Chave & Randall, 1971; Hobson, 1975). This contradictory information seems to imply that moray eel species may have different visual perceptual abilities in terms of responses to light, i.e., color perception.

Four species of moray eels in the subfamily Muraeninae were selected to conduct a comparative study on their retinal structure and their visual pigment/opsin gene complement. In terms of the depth of environments where they reside, these four species can be divided into two groups: (1) The shallow-water group, consisting of the ribbon eel, *Rhinomuraena quaesita* (depth range: 1–57 m) and the laced moray, *Gymnothorax favagineus* (depth range: 1–45 m). These two species are crevice-dwelling predators inhabiting coral reefs in shallow seas (Böhlke & Randall, 2000; King & Fraser, 2002); (2) the deep-water group, consisting of the dusky-banded moray, *Gymnothorax reticularis* (depth range: 30–200 m) and the slender giant moray, *Strophidon sathete* (depth range: 1–300 m), which live in sand–muddy sediment (Randall, Allen, & Steene, 1990; Smith & Bohlke, 1997). Since the habitats of these two groups of moray eels differ so much in their respective photic environments, comparisons of the differences between these two groups could provide useful information to delineate how moray eels evolved to cope with the environmental constraints in terms of light conditions.

In this study, histological methods were used to measure the thickness of each retinal layer with the expectation that increases in photoreceptor and outer nuclear layer thicknesses would be associated with the dim light condition. Second, the absorption spectra of the photoreceptor cells were obtained by microspectrophotometry (MSP). Finally, the opsin genes from these four moray eel species were cloned and sequenced. The combination of these data allow us to speculate on how moray eels have adapted to their photic environments.

2. Materials and methods

2.1. Samples collection

The moray eel species used in this study were obtained in a variety of ways. Specimens of *R. quaesita* (ribbon eel) were imported from Southeast Asian waters via a vendor in Singapore. *G. favagineus* (laced moray) were bought in Bi-Sha Fishing Harbor, Keelung, Taiwan, where they were caught with plastic tubing traps at a depth of approximately 30 m around Peng-Hu Archipelagos, in the middle of Taiwan Strait. *G. reticularis* (dusky-banded moray) and *S. sathete* (slender giant moray) were caught by bottom trawlers from depths of 50–800 m and landed in Da-Si Fishery Harbor, I-Lan, Taiwan. All specimens were kept in a tank with running seawater (temperature of 25–28 °C) under natural light cycle at the Marine Research Station, Institute of Cellular and Organismic Biology, Academia Sinica, Taiwan. They were fed with fish meat *ad libitum* three times a week until use. The animal use protocols used in this study were approved by Academia Sinica Institutional Animal Care and Use Committee (No. RFiZOOYH2007012).

2.2. Histology and samples preparation

All specimens were dark-adapted overnight (at least 6 h) inside a darkroom prior to use. Under infrared light illumination, with the aid of a pairs of night vision goggle (Bushnell-Night Eye M220) and a dissecting stereomicroscope, the fishes were first anesthetized with MS-222 (50 ppm), and then the eyes were enucleated. The cornea, lens and vitreous humour were removed from both eyes of each fish. The retina of one eyecup, intended for MSP measurement, was separated from the pigment epithelium and immediately immersed in chilled phosphate buffered saline (Sigma, USA; pH 6.5); the other eyecup, used for histological study, was fixed in Bouin's solution (Ricca Chemical Company, No. 1120-32).

For histological analysis, retina preparations were then dehydrated through a series of ethanol solutions, embedded in paraffin, sectioned at 5 μm, and stained with hematoxylin and eosin (H&E). Radial sections of the retina were examined under a light microscope. In order to compare the differences of overall structures of the retinae among the four species, retinal preparations from two adult individuals of each studied species were used. The thicknesses of four distinct layers, including pigment epithelium (PE) layer, photoreceptors layer (PL, layer of rod and cone cells), outer nuclear layer (ONL, layer of nuclei of photoreceptors), and inner nuclear layer (INL, layer of cell body of interneurons) were

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