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Opsin genes: research perspectives with Neotropical cichlids (Perciformes: Cichlidae) and their relevance in floodplain studies

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ABSTRACT. Vision not only plays an important role in the behavior and exploration capacity of new ecology niches but also influences the evolution of species exposed to the heterogeneity of light. Floodplain environments have high habitat heterogeneity and, thus, different light gradients. Cichlids are a group of vertebrates that has stirred interest in evolutionary studies due to their morphological and behavioral diversity and their widely used vision. The molecular basis of vertebrates' vision occurs through the interaction of opsin proteins and retinal chromophores. Proteins are expressed by opsin genes where each is responsible for absorbing certain light wavelengths. Current review analyzes the main characteristics of opsin genes family and the possibility of using them in floodplain and Neotropical cichlids studies. Opsins may have different levels of expression and molecular polymorphisms according to the dispersion of the species. They are also related to such behavior as sexual selection, nourishment and exploration of new habitats. Floodplains are natural experiments and dynamic environments that provide a wide range of habitats. In fact, the integration of studies in floodplains and the opsin genes in Neotropical cichlids seems to be a promising and still unexplored area in Neotropical regions.

Keywords: ecology, evolution, visual pigments, visual system.

Genes opsins: perspectivas para pesquisas com ciclídeos Neotropicais (Perciformes: Cichlidae) e sua relevância para estudos em planícies de inundação

RESUMO. A visão desempenha um importante papel no comportamento e capacidade de explorar novos nichos, e também influencia o processo evolutivo de espécies que estão sujeitas à heterogeneidade de luz. Ambientes de planície de inundação têm alta heterogeneidade de habitats, exibindo diferentes gradientes de luminosidade. Um grupo de vertebrados que desperta interesse para estudos evolutivos são os ciclídeos, pela sua diversidade morfológica e comportamental, além de usarem amplamente a visão. A base molecular da visão dos vertebrados ocorre pela interação de proteínas opsinas e cromóforos retinais. Essas proteínas são expressas pelos genes opsins, cada uma responsável por absorver determinado comprimento de onda de luz. Esta revisão aborda as principais características destes genes e a possibilidade de sua utilização em estudos de planície de inundação e ciclídeos neotropicais. Os opsins podem apresentar diferentes níveis de expressão e polimorfismos de acordo com a dispersão das espécies estudadas. São relacionados com comportamentos de seleção sexual, forrageamento, e capacidade de explorar novos habitats. As planícies de inundação representam experimentos naturais, sendo ambientes dinâmicos e que apresentam vários tipos de habitats. Assim, a integração de estudos de planície de inundação e genes opsins em ciclídeos parece ser uma área promissora e ainda inexplorada em regiões neotropicais.

Palavras-chave: ecologia, evolução, pigmentos visuais, sistema visual.

Introduction

The perception of visual signals that animals use, related to behavioral aspects, is a function of their visual system. For instance, the perceived color of specimens of their own species usually involved in important processes, such as reproduction mechanisms, is a well-known case. Since the environment in which these signals are transmitted is highly important (Boughman, 2002), vision may interfere in many species by limiting conditions, habitat choice, foraging, predation, escape ability and even sexual selection (Bowmaker, 1995; Hofmann et al., 2012).

Due to the lightness gradient caused by the environment characteristics, water is an environment requiring the adaptation of the visual system (Terai et al., 2006). Since lotic and lentic environments are dynamic, floodplain environments present great habitat heterogeneity (Thomaz, Bini, & Bozelli, 2006). Thus, aquatic vertebrates that inhabit these sites are great models for vision studies since they are exposed to different light wave spectra in relatively closed habitats.

Different classes of vertebrates have distinct vision capabilities. Some aquatic vertebrates, for example, have the ability to see a wide spectrum of colors, varying between ultraviolet and red (Yokoyama, 2008). These spectra may vary if the surroundings are exposed to a greater light heterogeneity due to their physicochemical characteristics.

The molecular mechanism that differentiates wavelengths related to color perception in the visual system depends on the presence of specific proteins that form the visual pigments (Trezise & Collin, 2005). These pigments are formed by the interaction of opsin proteins related to retinal chromophores (11-cis-retinal), which are vitamin A aldehyde of two types, A1 (aldehyde A) or A2 (3,4-didehydroretinal). Aquatic vertebrates may have only one or a mixture of the two retinal chromophores, forming a mosaic on the retina (Schwanzara, 1967). Visual pigments may have two different types of photoreceptors, cones or rods cells in the animal's retina (Terakita, 2005).

Opsin proteins are encoded by genes from the subfamily opsin that are part of the transmembrane G protein-coupled family (Bowmaker, 1995), constituted by cone opsin and rhodopsin genes (Carleton, 2009). Each gene is responsible for expressing a type of opsin protein that is involved in the perception of different light wavelengths.

Opsin genes, categorized according to the peak of light spectra that the opsin protein absorbs when it interacts with the chromophore, are responsible for color vision by absorbing short-wavelengths *SWS1*, *SWS2A*, *SWS2B*, medium-wavelength *RH2A* and *RH2B*, and long-wavelength *LWS* (Terakita, 2005; Carleton, 2009). The rhodopsin is responsible for scotopic vision or black and white - *RH1* (Nagai et al., 2011). Modifications in DNA sequences of these genes, occurring in the binding chromophore regions, may lead to minor changes in the wavelength absorbed by each pigment. Even a difference of a few nanometers in relation to a specific absorption of a wavelength would be capable of generating an impact in relation of the animal's behavior (Carleton, 2009; Spady et al., 2005).

The African cichlids are currently getting significant evolutionary biological attention when compared to other fish (Seehausen, Mayhew, & Alphien, 1999). The Cichlidae family, highly common as aquarium fish and in game fishing and fish farming (Nelson, 2006; Maan & Sefc, 2013), features a wide variety of colors, morphology and behavior, and uses the visual system in various situations.

Current review analyzes the ecological aspects related to opsin genes. Possible implications for Neotropical cichlids and ecology of floodplains are also investigated, taking into account the dynamics and importance of this ecosystem to maintain biodiversity.

Opsin genes expression

Molecular polymorphisms may modify the wavelength absorbed by each opsin protein. Differences in the expression level of these genes are another type of modification related to wavelength absorption (Carleton, 2009). Despite the quantity of opsin genes classes, only a portion is expressed in cichlids, according to the species ontogeny and the plasticity of expression (Hofmann, O'Quin, Smith, & Carleton, 2010a). In fact, the animal has distinct visual pigments in the course of its development (Spady et al., 2006).

The expression of these genes in natural populations of African cichlids is affected by genetic and environmental mechanisms in which populations of the same species may differ in expression even within small spatial scales (Smith et al., 2011). The gene sets appear to be genetically limited and the retinal sensitivity may be affected by the site in which the fish grows. Plasticity seems to vary according to genus and species (Hofmann et al., 2010a). For example, only three or four out of the set of cone opsin genes in the African cichlids are expressed, usually according to environment characteristics (O'Quin, Hofmann, Hofmann, & Carleton, 2010).

Absorbed light spectrum varies according to the opsin protein in the organism's retina (Smith, Ma, Soares, & Carleton, 2012b), environment, diet, and lens transmittance. According to the species, the lens allows UV light input towards the retina, increasing the *SWS1* opsin gene expression, although its reverse is not necessarily true. Some species get UV light on the retina, but do not have the *SWS1* gene expressed (Hofmann, O'Quin, Marshall, & Carleton, 2010b).

Changes in the environment's lightness may also modify the behavior of aquatic organisms, affecting retinal development and gene expression. Further, the responsiveness to different gradients of lightness seems to be influenced by the environment in which the animal develops (Fuller & Noa, 2010a).

Differences in habitats may increase the plasticity of the population level in highly dispersed species. Clear water, for example, enables higher levels of opsin genes *SWS1* and *SWS2B* expression, whereas fish that develop in dark water have high *RH2* and *LWS* levels (Fuller, Carleton, Fadool, Spady, & Travis, 2005b). In the case of these genes, *SWS1* and *SWS2B* are responsible for absorbing short-wavelength, *RH2* for absorbing medium-wavelength and *LWS* for absorbing long-wavelength.

Another important aspect related to the cichlids' opsin genes, particularly rhodopsin *RH1* responsible for low light conditions vision, is the ability to exploit new niches and its evolutionary significance (Sugawara et al., 2005; Schott, Refvik, Hauser, López-Fernández, & Chang, 2014).

Sexual selection

Sexual selection models deal with the manner females change preferences and how males have sexual characteristics selected to attract females. This has been a debated subject since the publication of *On the Origin of Species* by Charles Darwin, who defined it as the struggle of specimens of the same sex for the opposite sex, resulting in an increase or decrease in the number of offspring (Darwin, 1875).

Another aspect intrinsically related to sexual selection, important for reproduction in vertebrates, is sexual recognition during mating where several stimuli (such as vision) are related (Orr, 1986). Therefore, opsin genes, as part of the cichlid's sensory mechanism, focusing on color diversity, are very relevant.

Several models explain sexual selection among which the sensory drive (Endler, 1992) and the Fisherian model may be mentioned (Fisher, 1930). In the case of Neotropical cichlids sexual selection, the opsin genes must interfere somehow. They also interfere on the habitat in which the specimen lives due to the wide use of vision by fish from this family.

In the sexual selection model based on the sensorial drive, natural selection would act on the issue, transmission and perception of the signs, considering the influence of environmental characteristics on the sensory system and communication (Endler & Basolo, 1998; Smith, Van Staaden, & Carleton, 2012a), or rather, changing the habitat would generate new selective pressures on the female preference.

The Fisherian model (Fisher Runaway) initially comprises the male sexual characteristics and small arbitrary genetic variations for the outbreak of female preference, by genetic drift or gene flow (Fuller, Houle, & Travis, 2005a). Later, sexual selection would act on female preference for the male sexual characteristic, favoring those who possess and increase them.

Regardless of sexual selection models, opsin genes (consequently, the vision) must play an important role in cichlid mating, especially when its colors are taken into account (Carleton, 2009). Color marks seem to be also important with regard to the pre-zygotic isolation when aquatic organisms are involved (Miyagi et al., 2012).

When related to the partners' choice for mating, color patterns are important especially for species that have diverged recently. Evidence exists that females generally prefer males of their own species or, in their absence, those of other species that have similar color patterns, which may cause hybridization (Couldridge & Alexander, 2002).

Through sexual selection experiments performed in the laboratory, Seehausen et al. (2008) discovered that the genotype of opsin genes interacting with light and natural environment, determined stronger mating preferences than merely laboratory light conditions. Since the females' preference for certain color patterns during mating is related to their ability to perceive and distinguish these patterns, differences in the characteristics of the visual system in different species and even among populations may be expected (Smith et al., 2011).

Females' sexual preference cannot be limited to a single characteristic, but to a number of interacting factors related to this aspect. Furthermore, different environments in which females develop lead to different mating preferences that influenced by light through various mechanisms such as genetic variation and development plasticity. Related to the males' colors, those with greater color contrast vis-à-vis the environment are preferred by females (Fuller & Noa, 2010a).

Perspectives for neotropical cichlids research

A survey conducted in the Pubmed database on the main markers used for the phylogeny of cichlids showed an increase in the use of opsin genes for this purpose, coupled to their relationship with the fish's ecological and behavioral aspects (Fabrin, Simone, Gasques, Prioli, & Prioli, 2014).

Research on opsin genes in Neotropical cichlids is still fledging. In fact, few studies have been published, including an article on *Crenicichla frenata* opsin genes (Weadick, Loew, Rodd, & Chang, 2012), two on Neotropical cichlids *RH1* opsin gene (Schott et al., 2014; Torres-Dowdall, Henning, Elmer, & Meyer, 2015) and one on the use of the *LWS* opsin gene for the phylogenetic studies of Neotropical cichlids (Fabrin, Gasques, Prioli, & Prioli, 2015). It has been noted that the polymorphic regions of this specific gene do not appear to overlap the same gene in African cichlids. Further, there are differences among the types of selective pressures that the two groups undergo.

Another important aspect on gene research involves their relationship to anthropogenic impacts on aquatic systems and the corresponding alterations of limnological parameters, such as those related to light. The construction of dams represents a major impact on aquatic systems by changing several limnological characteristics (Agostinho, Vazzoler, & Thomaz, 1995).

Due to the plasticity of these genes, it is interesting to study this feature in Neotropical cichlids since it would be a manner to analyze the species's potential of adaptation to new environments (Hofmann et al., 2012). Even variations in the preference of foraging may occur according to the environment where the animal develops (Fuller, Noa, & Strellner, 2010b). Consequently, there is a complex connection between the ratio of expression of these genes and the visual system development. Further, studies could also contribute towards the investigation on the success of biological invasions.

Perspectives for floodplains research

Floodplains are characterized by dry and flood systems and by different environments connected to their main channel, according to the time of year, such as marginal and temporary ponds that occur during the floods. In fact, floodplain environments have high habitat heterogeneity and biodiversity (Junk, Bayley, & Sparks, 1989; Thomaz et al., 2006).

Since they are periodically exposed to different hydrological regimes, the limnological variables related to water transparency change over time. Differences in connectivity among the environments due to the frequency of the hydrological regimes also contribute to changes (Rocha & Thomaz, 2004). Thus, the increase of similarity or dissimilarity among habitats according to the hydrological regime may still occur. Consequently, the homogenization of the characteristics of wetland systems occurs during floods, which appears to be standard for this type of environment (Thomaz et al., 2006).

These differences would change the opsin genes expression since they depend on changes in limnological variables (Fuller et al., 2010b) and also on environmental characteristics. Thus, animals that depend largely on the visual ability may have this capacity affected. Therefore, floodplains are interesting places to carry out research specifically involving the opsin genes expression, due to the dynamics of these environments and plasticity of the family genes.

Starting with the interruption of the fluvial environment gradient, the limnological variables may also be modified (Vannote, Minshall, Cummins, Sedell, & Cushing, 1980). For instance, the upper Paraná river basin has several sections separated by dams, enhancing a cascade effect (Agostinho et al., 1995).

Several environments may also be subject to anthropogenic influences such as sewage discharges without treatment. Thus, eutrophication may also be associated to changes in aquatic environments light gradient by modifying the way the species coexist (Seehausen et al., 2008). For example, if eutrophication increases in turbidity with greater transmission of long wavelengths (Smith et al., 2012a), it will favor the *LWS* opsin gene expression causing the spectrum absorption of red wavelengths.

Conclusion

Floodplains environments could represent natural experiments in studies involving opsin genes. These aspects provide conditions for time and space-scale studies. Neotropical cichlids have a wide distribution at these sites, allowing the analysis of polymorphisms fixing in geographically distant populations and the comparison of expression levels of these genes in close populations that live in different environments. It may also be related to human impacts.

Integrated studies of these areas seem to be promising and should be encouraged since it is an unexplored field in Neotropical regions. They would help understand evolutionary and behavioral aspects of Neotropical cichlids.

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