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Evolution of vertebrate visual pigments

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ABSTRACT

The visual pigments of vertebrates evolved about 500 million years ago, before the major evolutionary step of the development of jaws. Four spectrally distinct classes of cone opsin evolved through gene duplication, followed by the rod opsin class that arose from the duplication of the middle-wave-sensitive cone opsin. All four cone classes are present in many extant teleost fish, reptiles and birds, but one or more classes have been lost in primitive fish, amphibians and mammals. Gene duplication within the cone classes, especially in teleosts, has resulted in multiple opsins being available, both temporally and spatially, during development.

1. Introduction

Vision provides an animal with the ability to detect, almost instantaneously, the environment around it. There is a tendency for humans to have an anthropocentric view of vision in assuming that we have evolved the 'best' visual system, especially in terms of colour discrimination. However, the human retina with rods and just three spectral classes of single cone looks relatively simple when compared to that of say a diurnal bird or turtle, where the retina contains not only rods, but four spectral classes of single cone with an additional class of double cone. These cones are also more complex in possessing in their inner segments an array of colour filters in the form of oil droplets containing high concentrations of carotenoids. What is the evolutionary history behind these differences? In this review, I shall concentrate on the evolution of visual pigments and photoreceptors within vertebrates, but the parallel evolution of the neural complexity of the retina and higher visual centres required to analyse the input signals from the receptors should not be forgotten.

The earliest vertebrates, the jawless fish (agnaths) of the Cambrian and Ordovician periods (about 450–550 million years ago, MYA) lived in shallow lagoons probably feeding by sifting food from the muddy substrate where vision would be of little importance. Their visual sense would be primarily directed at identifying the approach of predators simply by detecting the movement of a sudden shadow or an abrupt change in illumination. Superficially, this could be achieved by a single class of photoreceptor. However, such a detection task in shallow waters, where surface ripples and waves, as well as reflections from the substrate, cause continuously flickering and variable luminance, is not straightforward (McFarland & Loew, 1983; Snyder & Dera, 1970). It would be difficult for a fish to distinguish between relatively intense slow-frequency flickering and potential predators or to detect objects against a background solely on luminance differences, if the brightness of either the object or the background were highly variable. Flicker, on the other hand, will change the luminance, but will not change chromaticity, so that an opponent process between two spectrally different receptors can filter out the flicker, but will have the added advantage of leaving a 'colour' signal enabling the easier detection of objects against the background (Maximov, 2000). Similarly, potential confusion from highly variable luminance can also be overcome by an opponent process providing the ability to detect differences in the spectral composition of the environment, where spectral reflectance (colours) will be independent of luminance.

Although the minimum requirement for colour vision is two spectrally distinct classes of photoreceptors combined with a nervous system that can compare the quantum catch of one class of receptor with the quantum catch of another, this may not give maximum information about wavelength discrimination and colour vision throughout the full 'visible' daylight spectrum, from the near-UV around 300–350 nm to the far-red above 700–750 nm. An effective colour vision system has to contend with the broad spectral sensitivity functions of opsin-based photosensitive pigments, the high energy demands of the receptors and the complexity of the neural mechanisms required for colour perception. Given these constraints, the most efficient number of spectral classes of photoreceptor appears to be four, and adding a fifth spectral class probably provides little or no advantage (Barlow, 1982; Osorio & Vorobyev, 2005). Vertebrate photopic vision is generally mediated by more than one spectral class of cone with dichromacy, trichromacy and tetrachromacy common amongst most lower

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vertebrate groups. It should be emphasised that although there is a considerable database on the number of spectral cone classes possessed by a wide range of species, there is really very little data on the dimensionality of their colour vision. For example, the presence of four cone classes may strongly infer tetrachromacy, but only behavioural studies can establish this, and these data are often sadly lacking.

Rods and cones contain visual pigments that are composed of a protein moiety, opsin, linked to a chromophore, retinal, the aldehyde of Vitamin A. Opsins are members of an extensive family of G-protein-linked membrane receptors that are composed of about 350 amino acids that form a palisade of seven α-helical transmembrane regions enclosing a ligand-binding pocket (Fig. 1). Retinal is bound into the pocket through a Schiff base linkage to a lysine residue in the seventh helix. Since all vertebrate visual pigments contain retinal (either retinal or 3-dehydroretinal), their spectral sensitivity is determined primarily by the structure of the opsin, predominantly by interactions of the chromophore with specific amino acids lining the ligand-binding pocket (Fig. 1).

Comparative studies across all of the major vertebrates groups have established that in addition to the rod class of pigment, there are four spectrally distinct classes of cone pigments encoded by distinct opsin gene families (Fig. 2): 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 (for a review, see Yokoyama, 2000). This is a somewhat unhelpful and cumbersome classification of opsin classes, but has become firmly established in the literature. The LWS (sometimes L/M) and SWS notation is intuitive, but the RH2

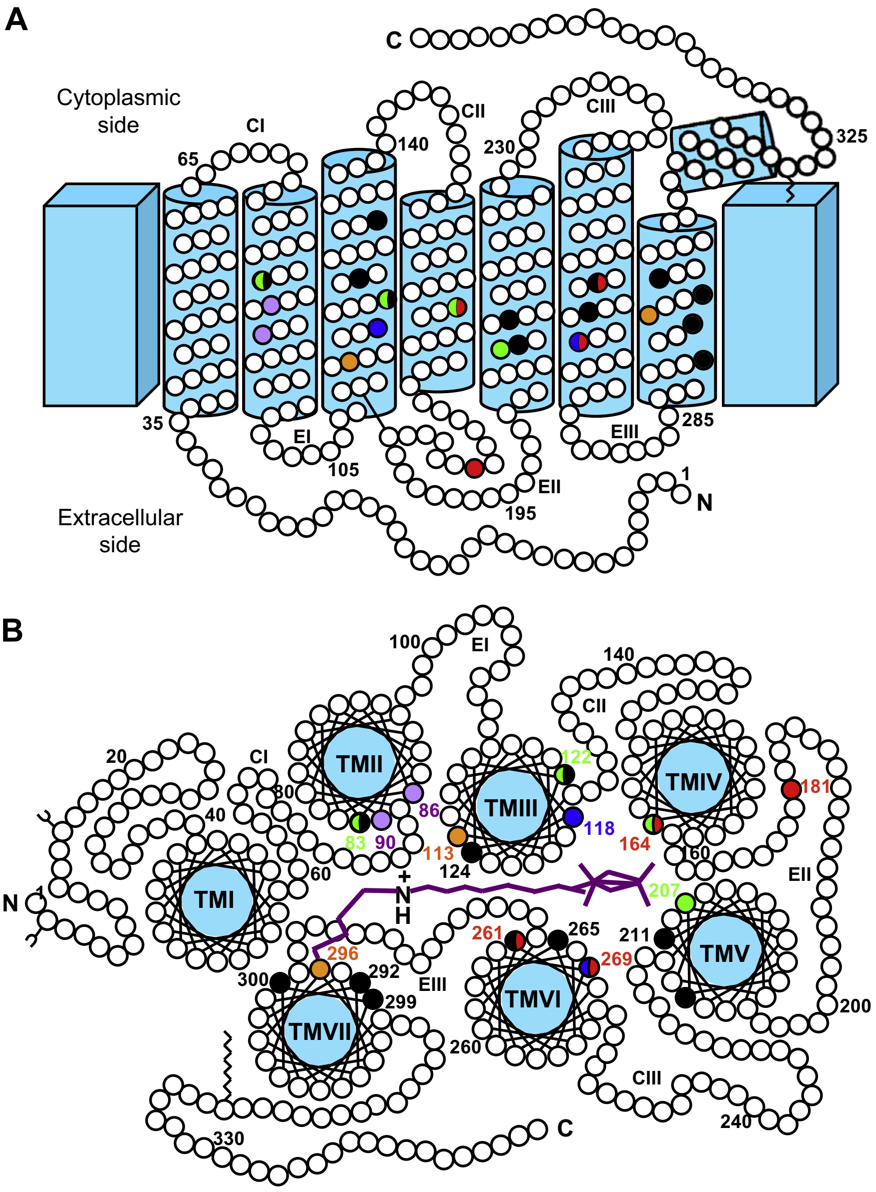

Fig. 1. Schematic diagrams of a visual pigment molecule. (A) Two-dimensional diagram illustrating the seven transmembrane α-helices. (B) View showing the arrangement of the helices around the chromophore, retinal, shown in purple (basic design kindly supplied by W.L. Davies). Although the helices are of different lengths, for simplicity, each helix is shown with only the central 18 amino acids. The numbering is based on mammalian rod opsin. Lysine 296 (orange) is the binding site of retinal and glutamate 113 (orange) provides the Schiff base counter ion. Major sites involved in spectral tuning are colour coded with opsin class: LWS red, RH2 green, SWS2 blue, SWS1 violet and RH1 black. Split colours indicate sites involved in tuning in more than one opsin class. Note how sites tend to cluster around either the Schiff base linkage or the ionone ring of retinal. Figure from Bowmaker and Hunt (2006).