

UDC 612.843.3  
BIBLID 0021-3225 (1998) 34 p. 343-349  
*Conference paper*

## COLOUR VISION IN EARLY VERTEBRATES

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Maximov V. Vadim (1998): *Colour vision in early vertebrates* . - Jugoslav. Physiol. Pharmacol. Acta, Vol. 34, 343-349.

According to the molecular clock, colour vision in vertebrates appeared 500 million years ago. It was only then that the gene of the short-wave visual pigment diverged from the long-wave one, providing vertebrates with a dichromatic color vision.

Soft bodies of the first fishlike vertebrates leave very sparse fossil records. The reconstruction, however, of their morphology can be established from widespread remains of their heavily armoured direct descendants (with bony head shields): heterostracans and osteostracans. At that time the vertebrates already possessed well developed image-forming eyes, rotating in the orbits by means of six extrinsic eye muscles, like in modern vertebrates. The natural moulds disclose also preserved traces of cranial nerves and a brain with well identifiable main parts. Early jawless vertebrates were marine, but lived near the shore, in shallow sandy lagoons or deltas. They probably fed by sucking food from the mud or scraping the bottom. Their vision hardly

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played an essential role in this behavior. Therefore, it is natural to assume that highly developed eyes and brain were necessary to maintain such forms of behaviour as the avoidance of enemies or mating, requiring some means of detection and recognition of predators (or sexual partners) at a distance.

Lighting conditions in shallow water set serious constraints to visual processing. The fact is that surface waves and ripples form complex lenses, focusing solar rays and creating continuously changing contrast patterns at objects under water. In each point, intensity varies with the frequency ranging from fractions of Hz to few dozen Hz near the surface. The frequency range usually decreases with depth. An obvious way to overcome this flicker consists in low-frequency filtering, which smooths out the fluctuations of illumination. Unfortunately, such filtering will inevitably reduce the rate of responses of an organism to external visual stimuli, this reduction being detrimental to the capacity of avoiding enemies and mating. Therefore, selective pressure should lead to alternative ways of visual information processing. One property of the wave-produced changes in underwater illumination can be exploited. It is the fact that the fluctuations are colourless, *i.e.* the light intensity changes synchronously in different parts of the spectrum. Therefore, in spite of the strong fluctuations of light all over the spectrum, the ratio of the light intensities in two different parts of the spectrum remains constant. It depends only on the properties of the illuminated surface (its colour).

Thus, we can guess that two types of receptors, with different spectral sensitivities, appeared about 500 million years ago in the retina of fishlike vertebrates. Signals from these receptors were subtracted from each other (on a logarithmic scale) producing a non-flickering output signal. Such a structure of vision provided certain advantages concerning reaction time, and favoured survival.

*Key words:* colour vision, evolution, photoreceptors, visual pigments

According to the molecular clock, colour vision in vertebrates appeared 500 million years ago (Nathans *et al.*, 1986). At that time, the gene for the short-wave visual pigment diverged from the genes for long-wave pigments, providing vertebrates with dichromatic colour vision. In extant animals the principal functions of colour vision are the detection of objects against their background and the recognition of objects by their colour. Colours in each point of the retinal image are substantial components in the subsequent visual processing. In addition, two spectral classes of photoreceptors occur in the pineal organs, known to control circadian rhythms of various biological functions in some of the lower vertebrates. The advantage of colour perception in this non-image-forming pineal eye is not clear.

A major question regarding extinct vertebrates concerns the original function for colour vision, *i.e.* why did colour vision evolve? To answer this, it is necessary to clarify (i) what type of eyes (image-forming or non-image-forming) were present in ancestral vertebrates, (ii) what functions of visually guided behaviour were required, and (iii) what conditions of light and colour were present in the environment.

Palaeontology provides some information on the morphology of lateral eyes in ancestral vertebrates. Soft body parts of the first fishlike vertebrates are very rare in

fossil records. The reconstruction, however, of the morphology of these animals can be established from the widespread remains of their heavily armoured direct descendants with bony head shields: the heterostracans and the osteostracans from the Silurian and the Devonian (Novitskaya, 1983). At that time the vertebrates already possessed well developed image-forming eyes, that rotated in the orbits by means of 6 extrinsic eye muscles, like in modern vertebrates. Preserved traces of cranial nerves and of the brain, with its main parts clearly defined, can also be seen. By that time vertebrates had also evolved well developed organs for other senses: a lateral line system, two vertical semicircular canals, a pineal organ and a remarkable paired olfactory apparatus that provided the main source of information about the environment (Novitskaya, 1992).

Early jawless vertebrates were marine, but lived very near the shore, in shallow sandy lagoons or deltas. They probably fed by sucking food from the mud or scraping the bottom (Denison, 1956), their vision hardly playing an important role in this behaviour. We can assume, therefore, that the highly developed eyes and the brain were necessary to such a form of behaviour as the avoidance of predators, including some means of their detection and recognition at a distance.

Lighting conditions in shallow water set serious constraints to visual processing. Surface waves and ripples form complex lenses that focus solar rays, creating continuously changing contrast patterns on substrate and under-water objects (McFarland and Loew, 1983). At a fixed point, intensity varies with frequencies ranging from fractions of Hz to a few dozen Hz near the surface. The frequency range

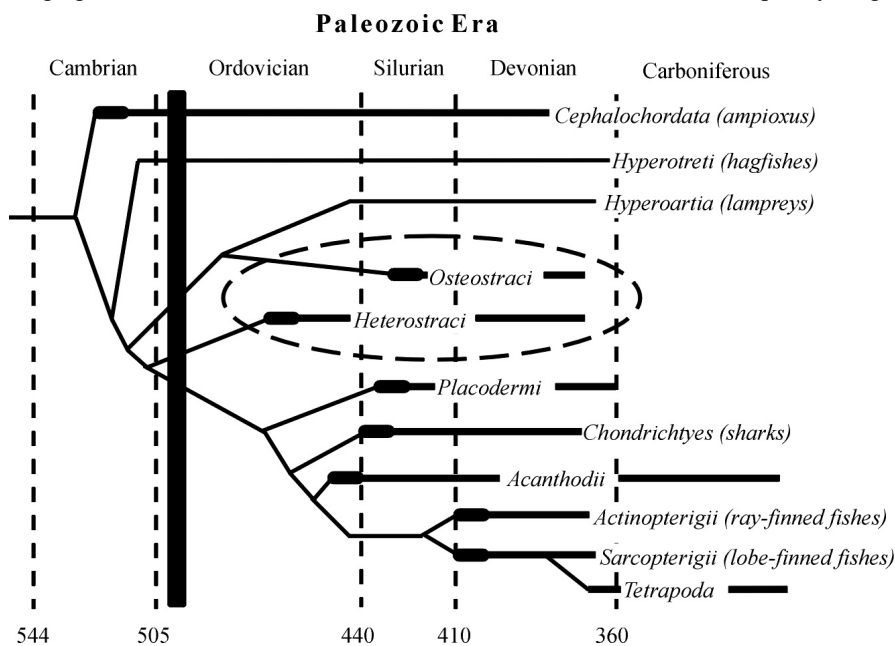


Fig.1. Approximate phylogenetic tree of some early vertebrates. The reinforced lines indicate palaeontological findings - after Novitskaya and Karatajute-Talimaa (1989). The paraphyletic Palaeozoic group of "ostracoderms" is encircled with a dashed line. Figures at the base of the diagram indicate the limits of geological periods in MYA (million years ago). The vertical dashed bar at approximately 500 MYA indicate the point when colour vision in vertebrates probably evolved.

usually decreases with depth. It is evident that the detection of an approaching predator under such lighting conditions is very difficult. Ordinary "enemy detectors" (e.g. so called off-units or "dimming detectors" known in the frog) will give a false alarm in such a situation, responding to each darkening within their receptive field.

There are, however, three ways to avoid predation under such circumstances. The first is to lead an inactive mode of life under conditions of clear weather and direct sunlight, when everything under water is illuminated with flickering light. This type of behaviour is characteristic of the closest living relatives of early vertebrates, the lampreys. Secondly, it is possible to acquire a heavy shield, such as the one in the heterostracans and the osteostracans. Their armour evolved further in the course of the subsequent competitive co-evolution with predators, until it became of no use against the large jawed vertebrate predators that appeared in the late Devonian. The third way to avoid predation is to develop neural mechanisms for image processing capable of eliminating or filtering out the flicker.

An obvious way to overcome the flicker is low-frequency filtering, which will smooth out the fluctuations in illumination. Unfortunately, such filtering will inevitably reduce the rate of responses to external visual stimuli, undesirable when avoiding enemies. Selective pressures would, therefore, lead to alternative ways of visual information processing. One property of the wave-induced changes of underwater illumination could have been of particular importance: the fluctuations are colourless, *i.e.* the intensity of the light changes synchronously in different parts of the spectrum. Therefore, despite the strong fluctuations of light over the entire spectrum, the ratio of light intensities in two different parts of a spectrum remains constant. This ratio is dependent only on the spectral properties of the illuminated surface (its colour).

Thus, we can suppose that two types of photoreceptors, with different spectral sensitivities, appeared in the retina of fishlike vertebrates some 500 million years ago. Signals from these receptors were subtracted from each other, on a logarithmic scale, producing a nonflickering output signal (Fig.2). Such an antagonistic interaction of colour signals is well known in visual systems and is called "colour opponency". An opponency circuit shown in Fig.2 is necessary at the very beginning of the visual signal processing, where it plays the role of a peculiar filter, eliminating the fluctuations in brightness of the visual signal. At the same time, such a filter does not prevent the detection of movements of viewed objects and of other fast changes in the environment itself. Such vision provided certain advantages, concerning particularly the reaction time in detecting predators, and favoured survival.

In extant vertebrates, colour opponency has been detected in the outer retina. However, the circuitry differs slightly from the one shown in Fig.2. The opponency interaction in the retina is carried out with the help of interneurons, the horizontal cells. They obtain signals from cones and return them to cones *via* a feedback mechanism. Horizontal cells must have existed already in the retinas of early vertebrates, since they are present in the retina of lampreys (Walls, 1942) which diverged from other vertebrates 550 million years ago (Forey and Janvier, 1994). Therefore, by the time when the two types of cones appeared in evolution, the retina already possessed the necessary basis to form an opponency interaction of colour signals.

The opponent scheme with interneurons, as a mechanism for overcoming the fluctuations of brightness at early stages of visual processing, has one disadvantage in comparison with the symmetric opponent scheme shown in Fig.2. The interneurons introduce some synaptic delays. As a result, the "red" signal may come with considerable phase shift at high frequencies in comparison with the "blue" signal.

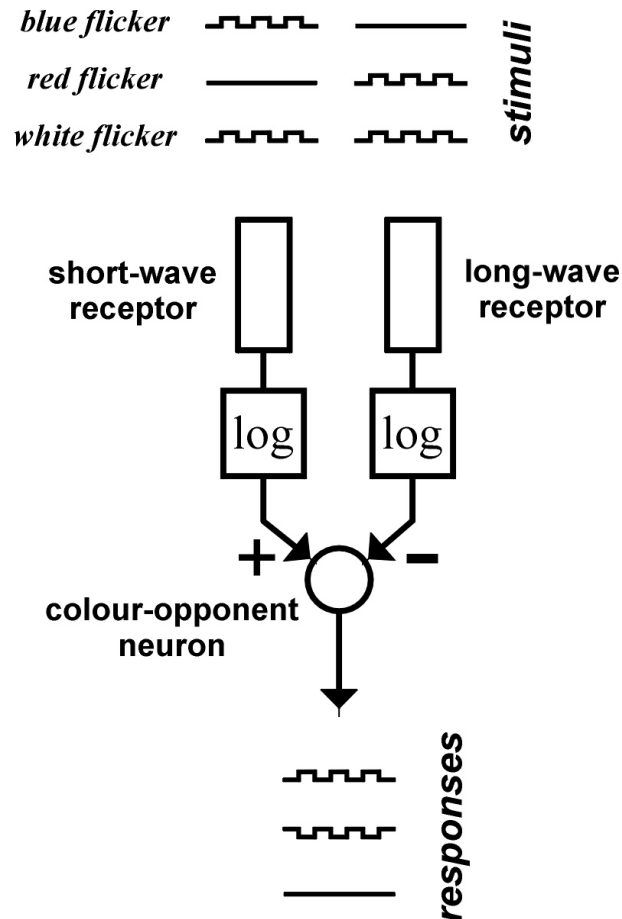


Fig.2. Scheme of colour opponency. The light signals of different colour (time course of the signals are represented above) arrive at photoreceptors of two types (long-wave and short-wave). After converting to their logarithms, the signals are summed with opposite polarities. The resulting output signals are shown at the base of the diagram.

Therefore, it is possible that subsequent evolution of signal processing in the retina followed the path of decreasing these synaptic delays. One possible solution lies in the use of electrical signal transmission instead of chemical transmission. The feedback in a triad synapse between receptor, bipolar and horizontal cell is known to be transmitted by the electrical (ephaptic) way that eliminates delays (Byzov *et al.*, 1977). This adjustment appeared to evolve only to decrease the phase shift. A computer simulation with the use of a model of such a triad synapse (Maximov and Byzov, 1996) has shown that colour opponency involving a horizontal cell as an interneuron provides a fairly good filter for brightness flicker, up to frequencies of several Hz.

*Acknowledgments.* - I would like to thank Drs. L.Novitskaya, R.Andjus, V.Govardovski and A.Parker for valuable discussions and help in English and Serbian.

The work was supported by Russian Foundation for Basic Research (grant 98-04-49298).

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Received December 19, 1998

Accepted January 25, 1999