**THE ROYAL
SOCIETY**

Environmental factors which may have led to the appearance of colour vision

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It is hypothesized that colour vision and opponent processing of colour signals in the visual system evolved as a means of overcoming the extremely unfavourable lighting conditions in the natural environment of early vertebrates. The significant flicker of illumination inherent in the shallow-water environment complicated the visual process in the achromatic case, in particular preventing early detection of enemies. The presence of two spectral classes of photoreceptors and opponent interaction of their signals at a subsequent retinal level allowed elimination of the flicker from the retinal image. This new visual function provided certain advantages concerning reaction times and favoured survival. This assumption explains why the building blocks for colour vision arose so early, i.e. just after the active predatory lifestyle was mastered. The principal functions of colour vision inherent in extant animals required a more complex neural machinery for colour processing and evolved later as the result of a change in visual function favouring colour vision.

Keywords: colour vision; colour opponency; light environment; flicker; early vertebrates; evolution

1. INTRODUCTION

According to the molecular clock, colour vision in vertebrates appeared 500 million years (Myr) ago (Nathans *et al.* 1986). At that point the gene for short-wave visual pigment diverged from the common ancestor for long-wave pigments, providing vertebrates with dichromatic colour discrimination. In extant animals with image-forming eyes the principal functions of colour vision are the detection of objects against their background and recognition of objects by their colour. In order to realize these functions the animals have complex neural mechanisms of colour processing in the visual system besides the ability of colour discrimination itself. Even the detection of a coloured object on a coloured background is not such a simple task as one may think (Mollon 1989). Without these pre-existing mechanisms of colour processing the appearance of more than one spectral class of receptor is useless. Therefore, one might assume that colour discrimination originally arose for quite another function and it was only in the course of subsequent evolution that an extension and change of the functions of colour vision took place and the necessary neural machineries evolved.

Before answering the question 'What was the original function of colour vision?', 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 of the animals, and (iii) what conditions of light and colour were present in the environment at that time.

2. THE VISUAL ECOLOGY OF EARLY VERTEBRATES

The colour environment in these early times, albeit lacking in flowers, fruits and butterflies, was apparently no less varied than now. Motley rocks and different algae existed 500 Myr ago in the same way as now and were coloured regardless of the eyes which examined them. In addition, colour vision in invertebrates seems to have arisen even earlier than in vertebrates and, judging from their remains, some extinct marine invertebrates already possessed bright colours which may have been of use for intra- and interspecific communications (Parker 1998).

Some information on the morphology of the lateral eyes in ancestral vertebrates can be obtained from palaeontology. Soft body parts of the first fish-like vertebrates are rare in the fossil record, but reconstruction of the morphology of these animals can be established from the widespread remains of their heavily armoured (bony head shields) direct descendants, e.g. heterostracans and osteostracans which were known in the Silurian and Devonian periods (Novitskaya 1993). At that time the vertebrates clearly possessed well-developed image-forming eyes which were rotated in their orbits by six extrinsic eye muscles as in modern vertebrates. One may also see preserved traces of cranial nerves in fossils and a brain with its main parts, including the optic lobes, clearly defined. By that time vertebrates had also evolved well-developed organs for other senses, e.g. a lateral-line system, two vertical semicircular canals, a pineal organ and a particularly remarkable paired olfactory apparatus which may have provided the main source of information about the environment (Novitskaya 1993).

The early jawless vertebrates were marine, but lived very near to 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 played an essential role in this. Therefore, we can assume that their highly developed eyes and brain were necessary for maintaining forms of behaviour such as the avoidance
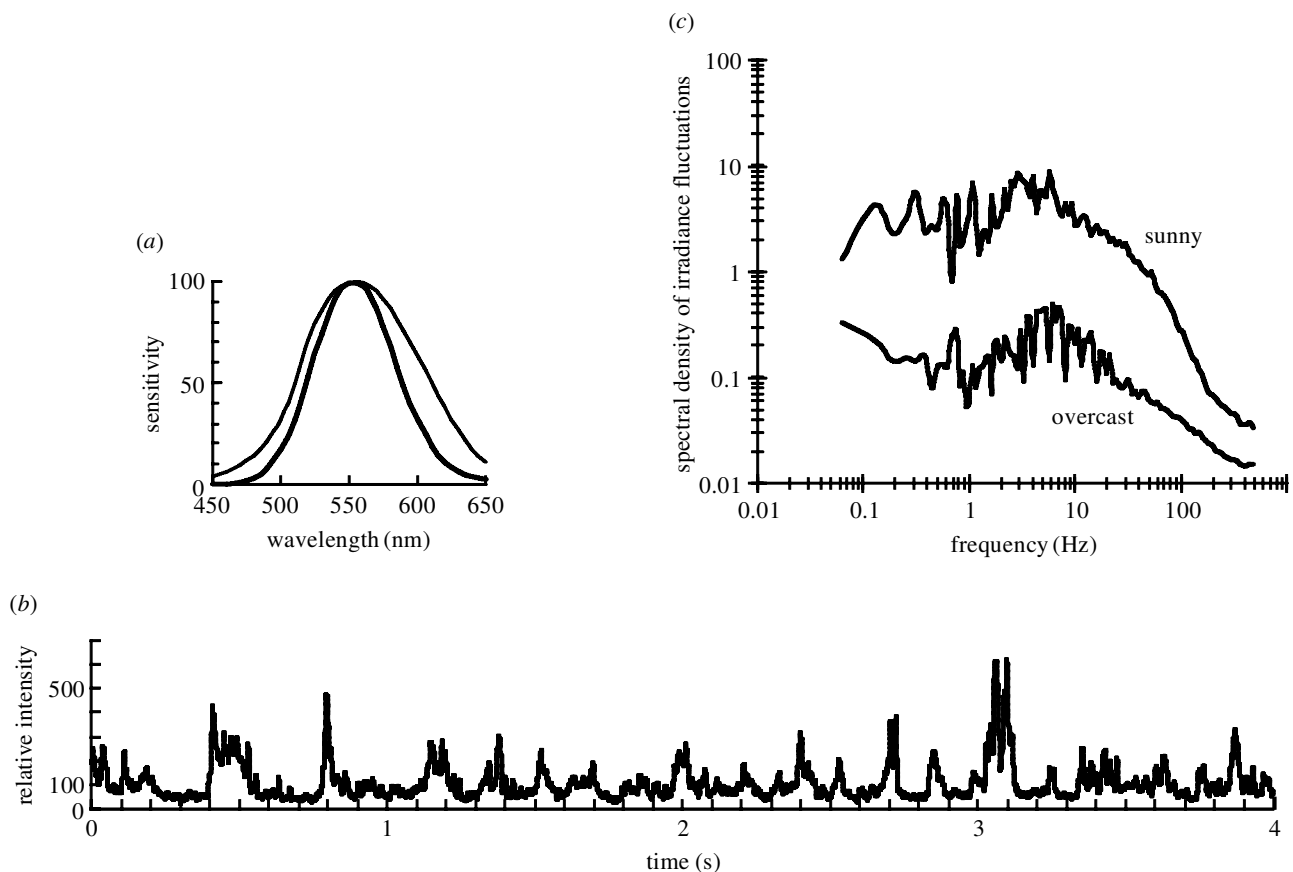
Figure 1. Underwater illumination fluctuations in shallow water measured with an irradiance meter with a cosine collector of 3 mm diameter at 20 cm depth in Moscow ponds under different weather conditions. (*a*) Spectral sensitivities of the photo cell (thick line) and the human photometric standard observer (thin line). (*b*) Irradiance fluctuations during a 4 s period in clear sunny weather normalized to the mean value taken for 100. (*c*) Relative energy spectra of irradiance fluctuations calculated from recordings of 16 s.

of enemies, including some means of detection and recognition of predators at a distance. In extant terrestrial lower vertebrates the detection of enemies is operated by special 'enemy detectors' in the visual system, e.g. the so-called class 3 and class 4 units which are known for the frog midbrain projections. These units are driven exclusively by long wave-sensitive receptors and, thus, are 'colour-blind' (Maximov *et al.* 1985). They only respond to abrupt changes in the illumination of their receptive field. Similar, rather simply arranged detectors can also be expected in the visual system of early vertebrates, thereby implementing their avoidance behaviour.

Unfortunately, the lighting conditions in shallow water set serious constraints on such visual processing. Surface waves and ripples form complex lenses which focus solar rays, creating continuously changing contrast patterns on the substrates and objects under water. At a fixed point, the intensity of the underwater illumination varies by several orders of magnitude with the frequencies falling well into the range of those perceived by animals (figure 1). The fluctuations of the illumination are significantly asymmetrical. The amplitude of the fluctuations is maximal at a depth of *ca.* 1 m (Snyder & Dera 1970). Their frequency ranges from fractions of hertz to a few dozen hertz near the water surface. The frequency range usually decreases with depth (Snyder & Dera 1970).

McFarland & Loew (1983) considered the biological importance of this flicker and found some correlation between its rate and the frequency responses of animals with image-forming eyes. However, little attention was paid to the fact that such lighting conditions badly complicate the extraction of information from an image in a shallow aquatic environment. It is evident that the detection of an approaching potential predator in such lighting conditions is very difficult. Ordinary 'enemy detectors' seem to be completely useless in a shallow-water environment since they will produce false alarms by responding to each instant darkening and lightening of illumination in their receptive field.

In this situation there are three ways of potentially avoiding predation. The first is to lead an inactive mode of life in clear weather conditions under direct sunlight when everything under water is illuminated with flickering light. This mode of life is seen in the closest living relatives of the early vertebrates such as lampreys. Second, it is possible to acquire a heavy defensive shield such as heterostracans and osteostracans evolved. In the course of subsequent competitive coevolution with predators, ostracoderms evolved their armour further until it became no defence against the large-jawed vertebrates which appeared in the Late Devonian age. The third way of avoiding predation is by developing neural mechanisms for image processing which eliminate or filter out the flicker and allow the identification of predators in time for escape.
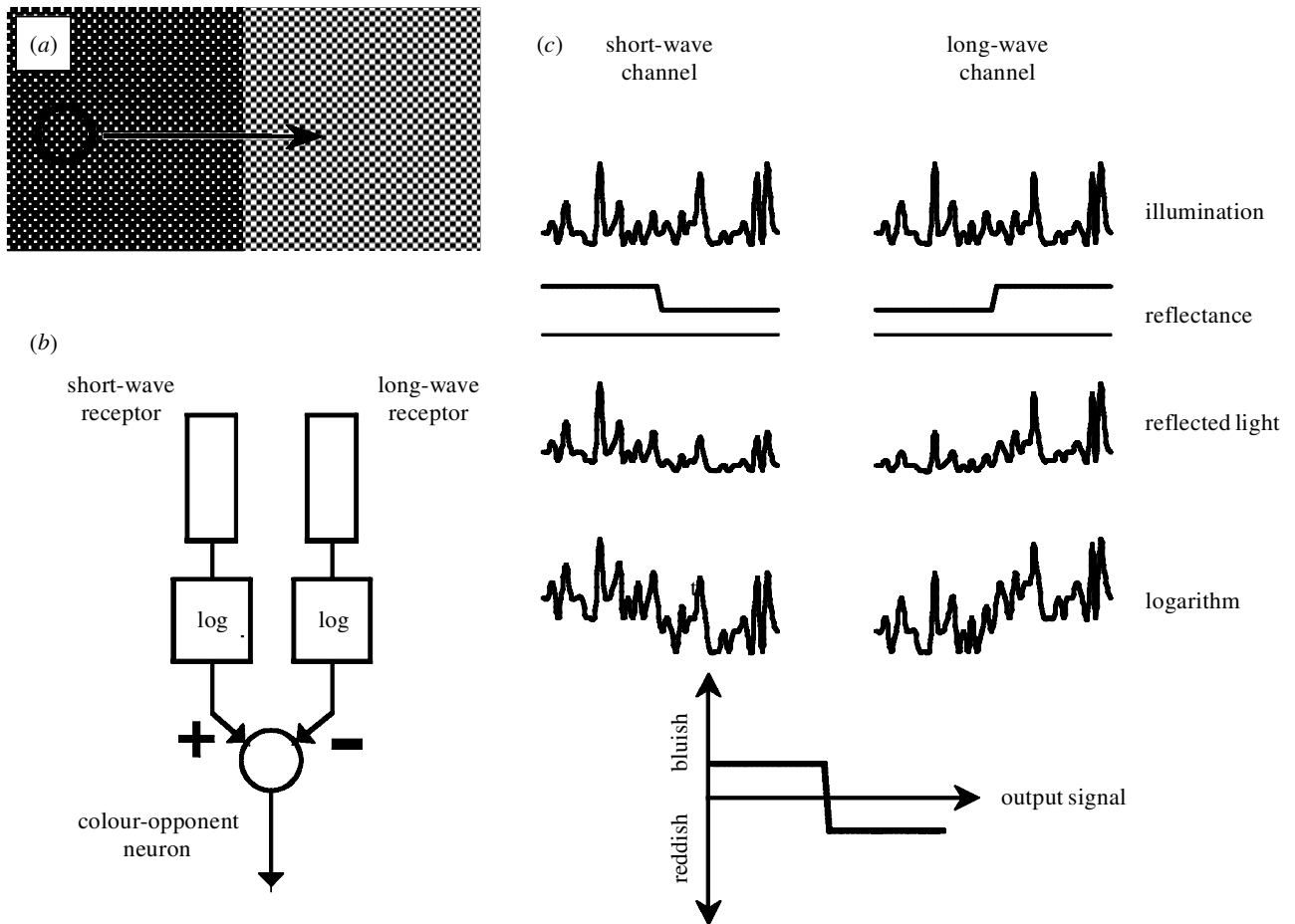
Figure 2. Scheme of colour opponency. (*a*) A bipartite surface painted in different colours; the direction of gaze (marked with a circle) moves from the left half to the right half as indicated by the arrow. (*b*) A colour opponent circuit. (*c*) Time-courses of the signals passing through the channels of the opponent circuit.

3. COLOUR OPPONENCY AS A MEANS OF ELIMINATING FLICKER

An obvious way of overcoming this flicker is low-frequency filtering which will smooth out the fluctuations in the illumination. Unfortunately, such filtering will also inevitably reduce the rate of the responses of an organism to external visual stimuli, which is not so useful when avoiding enemies. Therefore, selective pressures would have led to alternative ways of processing the visual information. One property of the wave-induced changes in underwater illumination would have been important. The fluctuations are colourless, i.e. the intensity of the light changes synchronously in different parts of the spectrum. Hence, despite the strong fluctuations in light over the entire spectrum, the ratio of the light intensities in two different parts of a spectrum remains constant. This ratio is dependent only on the spectral properties of an illuminated surface (its coloration). Thus, the alternative way of eliminating flicker based on this property is possible in the presence of two spectral classes of photoreceptors and consists of calculation of the ratio of their output signals (or the difference of the signals represented on a logarithmic scale).

Thus, we can suppose that, *ca*. 500 Myr ago, two types of photoreceptors appeared in the retinas of fish-like vertebrates with different spectral sensitivities. The

signals from these receptors were subtracted from each other on a logarithmic scale, thus producing a non-flickering output signal. Such an antagonistic interaction of colour signals is well known in present day visual systems and is called 'colour opponency'. In the retinas of early vertebrates an opponent circuit set at the very beginning of visual signal processing may have served to filter out rapid fluctuations in the intensity of the input signal. At the same time, this colour opponent filter would not have prevented the detection of movements of objects and other fast changes in the environment and provided advantages in the reaction time for detecting predators, thus favouring survival of the host.

Figure 2 illustrates the operation of such an opponent scheme in eliminating flicker and allowing the detection of a new object in the visual field. The object is represented by a bipartite surface, the halves of which are homogeneously painted in different colours (figure 2*a*). An opponent device (figure 2*b*) scans the scene from left to right. The 'oscillograms' in the right part of the figure explain what happens at different levels of the visual signal processing. A flickering illumination is achromatic, therefore the upper curves displaying the time-courses of this flicker for both the short- and long-wave channels are identical. Assume that, from the point of view of the short-wave receptor, the left half of the surface reflects twice as much light as the right one and, from the point

of view of the long-wave receptor, it reflects twice as little as the right one. The aim of the visual system is to locate this change of reflectance as the scene is scanned. The light reflected from the surface (i.e. the light captured by the receptors) is a product of the illumination and surface reflectance. At the corresponding curves for the reflected light one can see some decrease in the signal value for the short-wave channel while moving from the left half of the surface to the right half and a corresponding increase for the long-wave channel. However, the heavy fluctuations obscure the moment when sight moves from one half of the target to the other. After converting the output of the photoreceptors to their logarithms, the short- and long-wave signals are summed with opposite polarities. A resulting output signal is shown at the base of the diagram. Positive values of the output signal reflect the prevalence of a short-wave reflectance of the observed surface. As is visible from this curve the very moment of the transition of sight from one-half of the surface to the other is marked by a sharp jump in the signal. Thus, the opponent scheme in figure 2*b* allows instantaneous detection of a change in the reflective properties of surfaces in the visual field under flickering illumination while not having to recourse to low-frequency filtering.

4. COLOUR OPPONENCY VIA HORIZONTAL CELLS

Colour opponency is indeed detected in the outer retina in extant vertebrates. However, the circuitry differs slightly from that shown in figure 2*b* because the opponent interaction in the retina is carried out with the help of interneurons—these are horizontal cells which obtain signals from the cones and return signals back to the cones by the use of a feedback mechanism. Horizontal cells probably already existed in the retinas of early vertebrates, since they also exist in the retinas of lampreys (Walls 1942) which separated from other vertebrates 550 Myr ago. The feedback from the horizontal cells to the receptors is a universal tool for primary visual processing. In the case of achromatic vision, the horizontal cells mediate an antagonistic interaction between neighbouring photoreceptors, thus performing the essential function of improving the contrast discrimination and edge enhancement of an image. An appropriate connectivity which effects an opponent interaction of signals from adjacent cones could have evolved before the cones were divided into two spectral classes. Therefore, by the time two types of cones appeared in evolution, the retina already possessed the necessary basis for forming an opponent interaction of colour signals.

The opponent scheme with interneurons as a mechanism for overcoming the fluctuations of brightness in the early stages of visual processing has one dis-

advantage in comparison with the symmetrical opponent scheme shown in figure 2. The interneurons introduce some synaptic delays. As a result, the long-wave signal may come with a considerable phase shift at high frequencies in comparison to the short-wave signal. Therefore, it is possible that subsequent evolution of the signal processing in the retina followed the path of decreasing these synaptic delays. One solution lies in the use of an electrical signal transmission instead of a chemical one. The feedback in a triad synapse between receptor, bipolar and horizontal cells is indeed supposed to be transmitted by the electrical (ephaptic) way which eliminates delays. A computer simulation with the use of Maximov & Byzov's (1996) model of such a triad synapse 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 hertz.

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