Spectral Sensitivity of Direction-Selective Ganglion Cells in the Fish Retina

ELENA MAXIMOVA,[a] VICTOR GOVARDOVSKI,[b] PAUL MAXIMOV,[a] AND VADIM MAXIMOV[a]

[a]*Institute for Information Transmission Problems, Russian Academy of Sciences, 127994 Moscow, Russia*

[b]*Institute for Evolutionary Physiology and Biochemistry, Russian Academy of Sciences, 194223 St. Petersburg, Russia*

ABSTRACT: In color-matching experiments with extracellular recordings from axon terminals of ganglion cells in the tectum opticum of immobilized goldfish, direction-selective ganglion cells were shown to be color-blind. Their spectral sensitivity is determined by a high positive input from the long-wavelength sensitive cones and weak opponent input from other cone types.

KEYWORDS: color vision; color opponency; direction-selective neurons; ganglion cells; goldfish; tectum opticum

Tectum opticum (TO) of the midbrain is the main primary visual center in lower vertebrates that mediates various visually driven behaviors. Therefore it is surprising that TO proved to be color-blind in amphibia, though frogs and toads are known to possess necessary mechanisms for color processing in the retina and demonstrate true color discrimination in behavior. Color vision in fish is even more highly developed. Some fish, including young goldfish, have tetrachromatic vision, and fish retina possesses many neural mechanisms for color processing. Nevertheless, little or no color information arrives at the TO of goldfish, as was shown in color-matching experiments that used colored papers of known reflectances moved over colored background. Only one type of about a dozen of ganglion cells (GCs) projecting into fish TO proved to be color-coding. The others, so-called detectors of moving spots and oriented lines, direction-selective (DS) units, and so on, were demonstrated to be color-blind and sensitive to far red light. Therefore it was hypothesized that long-wavelength sensitive cones drive them. Unfortunately, using the method of "paper colorimetry" with a limited set of specially painted surfaces it was not possible to obtain reliable spectral sensitivity functions. Thus the aim of the current study was to further investigate color properties of DS GCs with the wide range gamut of colors accessible on the CRT monitor.

Address for correspondence: Dr. Elena M. Maximova, Institute for Information Transmission Problems, Russian Academy of Science, 127994 Moscow GSP-4, Russia. Voice: 7-095-952-3303; fax: 7-095-209-0579.
maximova@iitp.ru

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Experiments were carried out on adult goldfishes, subspecies *Carassius auratus gibelio Bloch,* of 10–15 cm length. Microspectrophotometric examination of the retinas revealed short-wavelength sensitive (S), middle-wavelength sensitive (M), and long-wavelength sensitive (L) cones containing three A2-based visual pigments absorbing maximally at 454 nm ($N = 12$), 535 nm ($N = 20$), and 622–623 nm ($N = 38$), respectively. No UV-sensitive cones were encountered in the retina of fishes of this age. In electrophysiological experiments, fish was immobilized by tubocurarin and placed in a Plexiglas tank with aerated water flow through its gills, its eyes underwater. Electrical responses of GCs projecting to the TO were recorded from their axon terminals. Stimuli, color edges moving in the preferred direction on color backgrounds, were presented at the computer-controlled color monitor. Known emission spectra of the CRT phosphors (R, G, and B) and known spectral sensitivities of cone mechanisms permitted specifying any monitor's RGB values in terms of goldfish color fundamentals and representing colors of the stimuli and backgrounds as vectors in the 3-dimensional color space.

DS GCs projecting to the goldfish TO respond to the movement of either a light edge on a dark background (ON-subtype DS GCs) or a dark edge on a light background (OFF-subtype DS GCs). Responses of any DS GC of a given subtype allow the ordering of color stimuli as darker or lighter compared with the color background and easily, in a few steps, find the color that matches the background. In the experiments, a set of colors that matches any background was shown to be a plane in the color space. A relative contribution of different cone types to the spectral sensitivity of DS GCs was estimated from the orientation of the plane in the goldfish color space. The spectral sensitivity of DS GCs appeared to be determined not solely by L cones but also by M and S cones that participate as weakly opponent to L cones. As a result, the sensitivity was reduced in the blue-green end of the spectrum, its maximum being shifted further to the red end, beyond 623 nm. This shift of spectral sensitivity may be considered as an adaptation to the aquatic environment where acute vision is only possible in long wavelengths, due to substantial light scattering in the blue-green region.

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