COLOR PROPERTIES OF MOVEMENT DETECTORS IN THE *CARASSIUS GIBELIO* (BLOCH, 1782) TECTUM OPTICUM STUDIED BY SELECTIVE STIMULATION OF DIFFERENT CONE TYPES. Z. Gačić[1], Elena Maximova[2], I. Damjanović[2], P. Maximov[2], Anna Kasparson[2], and V. Maximov[2]. *[1]Institute for Multidisciplinary Research,* 11000 Belgrade, Serbia*; [2]Institute of Information Transmission Problems, Russian Academy of Sciences,* 101 Moscow, Russia

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The optic tectum or superior colliculus processes image motion and takes part in orienting responses revealed in rapid eye, head, and/or body movemements. This function can proceed without taking into account information about color, and the superior colliculus in mammals is color-blind (Michael, 1973). In the frog, the system carrying chromatic information also originates as a channel separate from the tectal pathway, providing the main information needed for the frog's reactions to moving objects (Maximov et al., 1985). Color blindness of movement detectors projecting to the fish tectum was proved in color-matching experiments for both orientation-selective (Maximova, 1999) and direction-selective (Maximova et al., 2005) units. Recent experiments using selective stimulation of different cone types revealed new features of these projections.

The color vision of Prussian carp (*Carassius gibelio* Bloch, 1782) adults is determined by three types of cones: long-wavelength (L), middle-wavelength (M), and short-wavelength (S), containing three A2-based visual pigments that absorb maximally at about 622, 545, and 434 nm, respectively (Maximova et al., 2005). Color opponent cells were presented at different levels of the fish visual system, and single-unit extracellular recordings from the *C. gibelio* tectum opticum were made in order to examine the possible role of action potential timing in coding chromatic stimuli.

The Prussian carp (10-15 cm standard body length) were immobilized and tubocurarine chloride (0.3 mg/100g) was injected intramuscularly, adjusting the dosage so as to induce respiratory arrest. For electrophysiological recordings, immo-
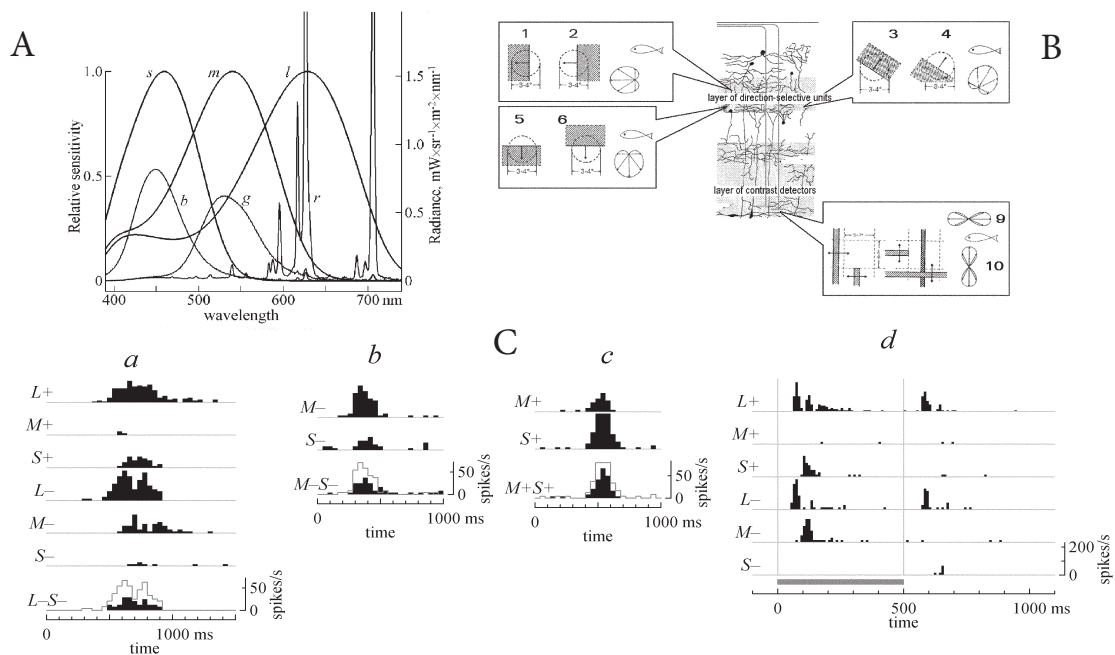

Fig. 1. Emission spectra of CRT monitors, stratification of tectal activity, and transmission of the color signals in the networks of movement detectors in the fish retina. A: Emission spectra of CRT phosphors (r - red, g - green, and b - blue) and spectral sensitivity of C. gibelio cones (l - long, m - middle, and s - short sensitivity wavelength). B: six types of direction-selective (DS) GCs (1-6), selective to the direction of movement and to the sign of contrast (ON and OFF units) and two types of orientation-selective (OS) GCs (7, 8), preferring horizontal or vertical orientations, but nonselective to the sign of contrast (ON-OFF units). Ca: detector of vertical line, stimulation with moving edges, velocity=11 degrees per s (the grey polygonal line repeats the poststimulus histogram for L - for comparison). Cb: detector of horizontal line, stimulation with moving edges, velocity=17 degrees per s. Cc: detector of horizontal line, stimulation with moving edges, velocity=17 degrees per s. Cd: detector of horizontal line, stimulation with horizontal flickering stripes (duration=500 ms).

bilized fish were placed in natural position in a transparent Plexiglas tank inside a Faradey cage, where artificial respiration was provided continuously by forcing aerated water through the gills. In order to reveal the optic tectum contralateral to the stimulated eye, an opening was made with surgical instruments in the skull over the contralateral midbrain. During the surgery, the preparation site on the head was anesthetized by ice. The water level in the experimental aquarium was regulated so as to keep the eyes permanently under the water, but without allowing it to overflow the brain. Action potentials evoked by the stimulus light (edges, bars, and spots of different brightness moving with different speed in different directions presented at a computer-controled CRT monitor applied to the right eye in single units in the left optic tectum) were recorded with a micropipette filled with an alloy of Wood`s metal and tipped with a platinum ball 2-10 μm in diameter (low impendance of 200-500 kΩ). The electrode was lowered slowly into the tectum until a single unit was encountered which responded to a stimulus in the visual field. The emission spectra of three phosphors in standard cathode ray tube (CRT) monitors are largely in accord with the **spectral sensitivities of** *C. gibelio* cones (Fig. 1a), which makes monitors a convenient tool for selective stimulation **of** any types of cones. Seven specific monitor colors were calculated, considering both the emission spectra of the phosphors and the spectral sensitivities of the cones, one of which (gray or neutral) served as a background color, while the remaining six were used as the stimuli colors, each differing from the background only in a certain type of cones. Some of the colors (the increment ones) – designated as L+, M+, and S+ were 1.6 times more intense than the background in their effective brightness for a corresponding cone type. The others (the decrement ones) – designated as L-, M-, and S- were 1.6 times less intense than the background. In the experiments, the stimuli were represented by edges of one of the six colors moving over a neutral background or by bars and spots of the same colors flickering against the background.

Single-unit responses, ascribed to axon terminals of GCs, were recorded from two superficial retinorecipient layers of the tectum opticum of immobilized fish. A variety of units have been functionally identified in the tectum opticum (Cronly-Dillon, 1964; Jacobson, 1964; O'Benar, 1976; Mora-Ferrer et al., 2005). Eight physiological types of movement detectors were investigated: six types of direction-selective (DS) GCs (Maximov et al., 2005), selective to the direction of movement and to the sign of contrast (ON and OFF units); and two types of orientation-selective (OS) GCs (Fig. 1b), preferring horizontal or vertical orientations, but nonselective to the sign of contrast (ON-OFF units). It was found that L cones give the main contribution to responses of all these units. Thus, ON units responded to L+ stimuli (both moving edges and flickering spots in the receptive field, RF), OFF units responded to L- stimuli of the same configurations, whereas ON-OFF units responded to moving edges and flickering bars of preferred orientation regardless of whether the stimulus color was the increment (L+) or decrement (L-) one. At the same time, the latter units appeared to be definitely

selective to the sign of stimulation of M and S cones (Fig. 1C*a*). According to our findings, OS GCs always responded to M- and S+ stimuli (Fig. 1c, lower right), but there was no response to M+ and S- stimuli (or it was significantly weaker). We note that in rainbow trout, according to McDonald and Hawryshyn (1999), color-opponent units exhibited a more or less similar reaction (even though they did not classify the recorded units). Moreover, apart from not evoking response, M+ and S- stimulation produced an inhibitory effect (Fig. 1C*a*, last line; and Figs. 1C*b* and 1C*c*), revealed with additional colors that stimulated two cone types. Finally, DS GCs usually responded to the stimulation of M and S cones also, but their selectivity to the signs of contrast was less unambiguous.

Stimulation by flickering stripes and spots made it possible to measure response latencies in the color channels connected with different cone types. Regardless of the fact that the latencies depended considerably on the parameters of stimulation (on stimulus intensity and especially on stimulus size), the obtained mean values reflected a general rule. The responses of the red channels were the fastest, the OFF channel somewhat outpacing the ON one: mean latency to the onset of L+ was 40 ± 7 (s.d.) ms, while mean latency to the onset of L- was 38 ± 8 ms. The latencies in M and S channels were considerably longer: mean latency to the onset of M- was 53 ± 14 ms, while mean latency to the onset of S+ was 68 ± 16 ms. About 20 ms is spent on transduction in cones, the remainder being attributable to synaptic delays in the neural network of signal processing in the retina (Fig. 1C*f*). To be specific, the signal of the blue channel enters the green channel with the inverse sign and a synaptic delay. After that, the combined signal enters a red channel of some kind (ON or OFF) with an additional synaptic delay. Unfortunately, the ways and details of this processing in the retina are unknown. Experiments with selective stimulation of different cone types showed that movement detectors projecting to the fish tectum possessed color-opponent properties, which distinguishes them from the analogous projections in other vertebrates. In particular, opponent interaction was revealed between the signals of S and M cones.

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