Electronic version of an article published as
Journal of Integrative Neuroscience, Vol. 14, No. 1 (2015) 31–52

DOI: 10.1142/S0219635215500053

Color properties of the motion detectors projecting to the goldfish tectum: II. Selective stimulation of different chromatic types of cones

Vadim Maximov*, Elena Maximova, Ilija Damjanović,
Alexey Aliper and Paul Maximov

Institute for Information Transmission Problems
Russian Academy of Sciences
Bolshoi Karetny Per., 19, Moscow 127994 GSP-4, Russia
**maximov@iitp.ru*

[Received 19 August 2014; Accepted 6 October 2014; Published 30 December 2014]

Sensitivity to the sign of contrast of direction-selective (DS) and orientation-selective (OS) ganglion cells (GCs) was investigated with selective stimulation of different chromatic types of cones. It was shown that the DS GCs that were classified with the use of achromatic stimuli as belonging to the ON type responded to selective stimulation of the long-wave cones as the ON type also, while the stimulation of middle-wave or short-wave cones elicited the OFF type responses. Character of the responses of DS GCs of the OFF type was exactly the opposite. OS GCs, which responded to achromatic stimuli as the ON–OFF type, responded to selective stimulation of the long-wave cones as the ON–OFF type as well, responded to middle-wave stimulation as the OFF type and to stimulation of short-wave cones it responded mainly as the ON type. At the same time, under color-selective stimulation, both DS and OS GCs retained the directional and orientation selectivity with the same preferred directions. The results obtained are in favor of the idea that the signals from the different chromatic types of cones are combined in the outer synaptic layer of the retina at the inputs of bipolar cells using sign-inverting and/or sign-conserving synapses, while specific spatial properties of motion detectors are formed in the inner synaptic layer.

Keywords: Goldfish; color vision; retina; ganglion cells; tectum opticum; motion detectors; direction selectivity; orientation selectivity.

1. Introduction

Color vision in vertebrates is based on several types of retinal cone photoreceptors which contain photopigments with different spectral sensitivities. Most fishes are predominantly visually orientated. With few exceptions, they have highly developed color vision, which plays an important role in predator avoidance, prey detection and visual orientation. Splendidly colored species extensively utilize their color vision capacities in social behavior and species interactions including territoriality, pair formation, intra- and interspecific communications. Some fish, including young

*Corresponding author.

goldfish, have tetrachromatic vision (Bowmaker *et al.*, 1991), and the fish retina is known to be well-equipped with many neural mechanisms for color processing, starting with several types of chromaticity horizontal cells (Tomita, 1965) and ending with ganglion cells (GCs), the outputs of the retinal neuron network, many of which are color-coded (Daw, 1967). On the basis of experiments on isolated retina it is generally accepted that the majority of goldfish retinal GCs have wavelength-opponent center-surround organization (Wagner *et al.*, 1960; Spekreijse *et al.*, 1972; Bilotta & Abramov, 1989).

It is natural to expect that color-opponent GCs send their signals to those areas of the fish brain which are involved in color processing. The brain of teleosts displays several well-developed visual centers, retinofugal terminals being located in about a dozen distinct brain nuclei (Springer & Gaffney, 1981; Northcutt & Wullimann, 1988; Collin, 1989; Deguchi *et al.*, 2005). Most of them are not yet investigated electrophysiologically, and their color properties are unclear, but some nuclei contain so few neurons that they can hardly be supposed to perform such complex visual functions as color discrimination and color recognition. On the contrary, the tectum opticum (TO) is a prominent target of retinal outputs in teleosts and is considered to be a prime candidate for such functions. Accordingly, views about its leading role in the color processing have been repeatedly expressed (Coughlin & Hawryshyn, 1993, 1994; Gibbs & Northmore, 1998; McDonald & Hawryshyn, 1999; Northmore, 2011). Fortunately, the fish retinotectal system has been intensively studied in single-unit recordings (Jacobson & Gaze, 1964; Zenkin & Pigarev, 1969; Maximova *et al.*, 2012) that enables to consider the color properties of different types of GCs projecting to the TO separately. Axons of different GCs terminate at different depths of the TO to form layers with specific features. Most of these GCs have an intricate structure of their receptive fields (RFs), extracting very subtle features of the retinal image — that is, possess the properties of feature detectors (Zenkin & Pigarev, 1969). In all fish species investigated, the same stratification of responses of GCs can be found: (i) a layer of direction-selective (DS) units of ON and OFF types with three different preferred directions of movement, (ii) a layer of rather heterogeneous units sensitive to moving contrast — detectors of light or dark spots, orientation-selective (OS) units of ON–OFF type with two preferred orientations (detectors of horizontal and vertical lines), etc, (iii) a layer of units responding by sustained discharges in darkness or in light. Yet there were contradictory evidences as to the color properties of these GCs. The first experiments with color stimuli in many fish species have revealed only one rare type of cells with color-opponent concentric RFs among a good dozen of different types of GCs projecting to the tectum (Maximova *et al.*, 1971). At the same time, the best explored motion detectors (DS GCs and OS GCs) were considered color-blind. Only recently it was shown in color matching experiments that being color blind they also possess weak color-opponent properties (Maximov *et al.*, 2014).

Units are usually classified as ON, OFF or ON–OFF by their responses to achromatic stimuli (Hartline, 1938). So in fish, there are two separate sets of DS

GCs: ON units respond to moving of a light edge into the RF and OFF units respond to moving of a dark edge (Maximov *et al.*, 2005a,b). As for OS GCs, both types (detectors of horizontal and vertical lines) respond to moving of light and dark edges into the RF and are therefore classified as ON–OFF units (Maximov *et al.*, 2009). However, for units that receive signals from several chromatic types of cones, classification by means of achromatic stimuli is of little use. Moreover, even stimulation with color stimuli is not always effective, since because of the overlap of the spectral sensitivity curves of cones, each such stimulus inevitably excites all types of cones. In particular, it appears that the motion detectors of the fish retina respond the same way to all colored stimuli presented on a black background — namely, with the same polarity as to the white stimulus (Maximov *et al.*, 2014). In other words, the color opponency discovered in color matching experiments is not detectable under these conditions of stimulation. This is explained by the fact that it is the long-wave cones that make the main contribution to the responses of the motion detectors so that the GC response even to blue stimulus is determined by the work of long-wave cones. Contribution of middle-wave and short-wave cones is negligible. To see their contributions, one needs to try to stimulate separate chromatic types of cones selectively.

2. Materials and Methods

2.1. *Preparation and recordings*

The studies were performed on a wild form of the goldfish, *Carassius gibelio* (Bloch, 1782). In all, 56 fish were used in experiments. All procedures with fish were approved by the local ethical committee of the Institute for Information Transmission Problems. The maintenance of the fish and the surgical and experimental procedures have been described in detail in the previous paper (Maximov *et al.*, 2014). Briefly, in the experiments, an immobilized fish, placed in a transparent Plexiglas tank with its eyes submerged in water, looked at the monitor screen through the transparent tank wall. Single-unit responses of DS and OS retinal units were recorded extracellularly from their axon terminals in retinorecipient layers of a contralateral lobe of the TO.

2.2. *Visual stimulation*

Visual stimuli were presented to the fish on a computer-controlled 17 inch CRT monitor LG Flatron 775FT with a refresh rate of 75 Hz from the distance of about 30 cm. From this distance, the screen occupied $43 \times 32^\circ$ of the fish visual field. To stimulate the DS or OS GCs, color stripes or edges moving or flashing over a color background were presented on the screen within a square area of stimulation with angular dimensions of $11 \times 11^\circ$. The stimulation area was usually placed such that the RF of the recorded unit was located in its center. Color of the rest of the monitor screen outside the stimulation area usually was the same as the background.

2.3. *Color specification*

Previously, it was shown (Maximov *et al.*, 2007) that the red, green and blue guns of the stimulating monitor were independent and any emission spectrum $I(\lambda)$ for monitor values of R, G and$B$, specified in the range from 0 to 255, was well approximated by the formula:

$$I(\lambda) = \left(\frac{R}{255}\right)^{\gamma_R} \cdot r(\lambda) + \left(\frac{G}{255}\right)^{\gamma_G} \cdot g(\lambda) + \left(\frac{B}{255}\right)^{\gamma_B} \cdot b(\lambda) + c(\lambda),$$

where $r(\lambda)$, $g(\lambda)$ and $b(\lambda)$ are the emission spectra of three phosphors of the monitor (Fig. 1(a)) and exponents of powers γ_R, γ_G and γ_B for different guns have different values, a little larger than 2; the light radiation of a dark screen, described by the spectrum c(λ), was about 100 times weaker than maximum radiation emitted by each phosphor.

Besides the RGB color coordinate system, all colors, set on the stimulating monitor, were specified in a physiological color coordinate system of the goldfish — a three-dimensional color space with coordinates L, M and S (corresponding to long-, middle- and short-wavelength sensitive cones, respectively) whose values can be calculated using the following equations:

$$L = \int_0^\infty I(\lambda) \cdot l(\lambda) \cdot d\lambda, \quad M = \int_0^\infty I(\lambda) \cdot m(\lambda) \cdot d\lambda, \quad S = \int_0^\infty I(\lambda) \cdot s(\lambda) \cdot d\lambda,$$

where the cone spectral sensitivity functions $l(\lambda)$, $m(\lambda)$ and $s(\lambda)$ are known (Fig. 1(a)).

2.4. *Selective stimulation of different chromatic types of cones*

One of the key techniques is the selective stimulation of individual color channels. Basically, because of the strong overlap of the cone spectral sensitivity curves, any radiation will excite all three types of cones. In other words, there is no such natural radiation, and especially such a combination of emissions of the monitor phosphors, which would excite only one type of cone and would not excite the other two (Fig. 1(b)). The exception is the long-wavelength cones, which can be selectively stimulated by bright monochromatic (laser) radiation with a wavelength of about 700 nm and above. Fortunately, the motion detectors projecting to the fish tectum do not respond to uniform and constant illuminations, but respond only to changes (temporal or spatial) occurring in their RF. In particular, they respond to moving contrast edges. To stimulate such units, it is possible to choose a pair of colored radiations for the stimulus and for the background, which would differ for only one (any) type of cones, but "from the point of view" of the other two types of cones that pair (the stimulus and the background) would represent a homogeneous unchanging surface.

For such selective stimulation we calculated seven specific monitor colors. One of them, "gray" or "neutral", served as a background on which stimuli were presented

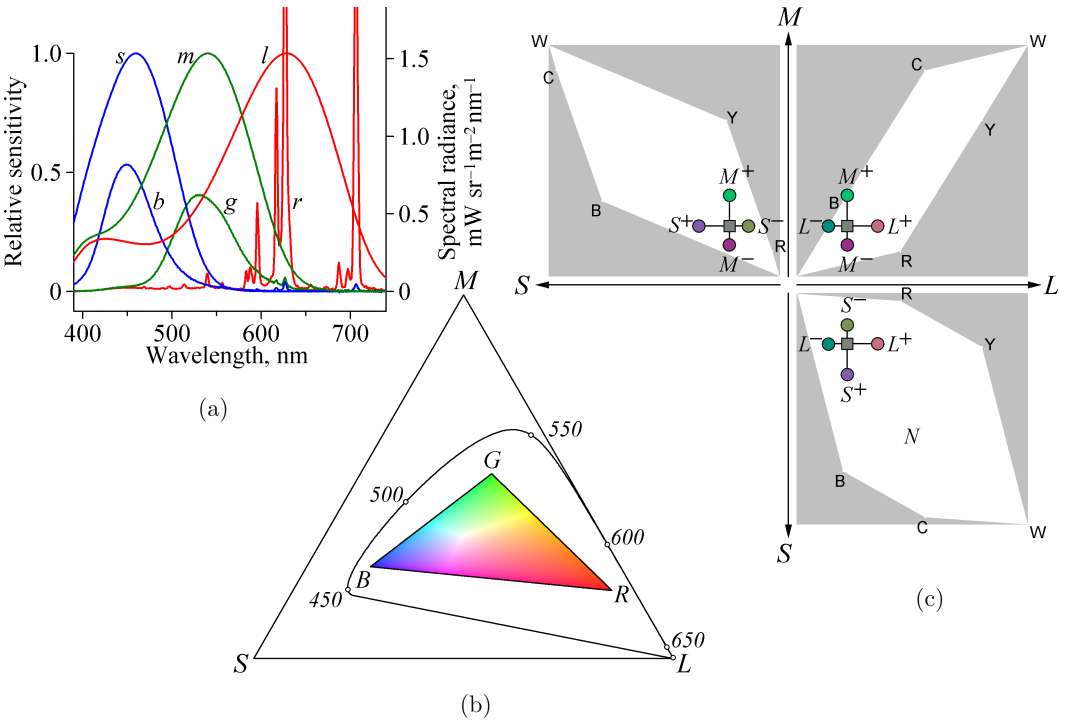

Fig. 1. Monitor color specification. (a) Spectral sensitivities of the *C. gibelio* cones (l, m and s) and emission spectra of three phosphors of the monitor at maximum brightness (r, g and b). Functions of relative spectral sensitivity for three types of goldfish cones with absorption maxima at 622–623, 535 and 454 nm (Maximova *et al.*, 2005) were calculated using a standard template (Govardovskii *et al.*, 2000) for the visual pigment of vitamin A2 and taking into account the spectral transmission of the goldfish ocular media (Douglas, 1989). (b) An equilateral chromaticity diagram of the goldfish. Vertices of the triangle L, M and S correspond to colors of physically impossible radiations that selectively excite separate types of goldfish cones. The smooth curve inside the triangle is the spectral locus, with wavelengths shown in nanometers; it limits the area of physically achievable chromaticities. Multicolor triangle within this area indicates the gamut of the display. (c) Three two-dimensional projections of the three-dimensional physiological color space of the goldfish. The axes in these diagrams are the relative excitations of the short-wavelength (S), middle-wavelength (M) and long-wavelength (L) cones. Light polygons inside the coordinate planes LM, MS and LS are projections of a 3D parallelepiped enclosing the colors achievable on the monitor. Their vertices correspond to the standard RGB colors: R — red, B — blue, Y — yellow, C — cyan, W — white. Colored circles and squares mark positions of "selective colors" of stimuli and background used in the present work. Detailed explanations are in the text.

within the RF. The remaining six colors were used as colors for stimuli. Each of these colors differs from the neutral one for only certain type of cones. Three of these colors (incremental colors) were 1.6 times more intense than the neutral one for a given type of cones, and the intensity of the other three (decremental colors) was 1.6 times lower than the intensity of the neutral color. The incremental colors will be denoted in this paper as $L+$, $M+$ and $S+$, and the decremental ones, as $L-$, $M-$ and $S-$ for the long-wave, middle-wave and short-wave cones, respectively. The neutral color will be denoted as N. The mutual arrangement of these colors in the goldfish color space is shown in Fig. 1(c).

2.5. *Procedures*

When a good DS or OS unit was isolated (as can be judged from the absence of interspike intervals shorter than the period of absolute refractoriness) and an approximate position of its RF was found, the first step was always to measure its directional tuning curve (polar diagram) with contrast edges moving in different directions across the RF. This allowed to confirm the type of the recorded unit and to determine the size and accurate location of its RF. Then the position of the area of stimulation was centered relative to the RF, and the unit was investigated by edges of six selective colors moving over a neutral background or by stripes and spots of the same colors flashing against the background. Actually when stimulating by moving edges, stimuli were wide stripes exceeding the stimulation area in width. Cell responses were recorded during the stimulus movement across the stimulation area. In this case, only one edge always moved in the stimulation area. At first, the leading edge of the stimulus gradually went across the RF of the unit, which initiated the IN-response. After some delay, the trailing edge crossed the RF resulting in a gradual substitution of the stimulus by background, which initiated the OUT-response of the unit.

2.5.1. *Polar diagram measurements*

A typical procedure for the measurement of a polar diagram by moving edges was as follows. The monitor and the stimulation area on its screen were placed in the visual field of the fish in such a way as to cover the estimated RF, and the values of the following stimulation parameters were specified: the speed of movement of the edge, its color, as well as the color of the background and the surrounding outside the stimulation area, the initial direction of movement, the total number of different directions of movement (usually 12 or 24) and the number of repetitive runs in each direction. After that, measurement was performed automatically for different directions in a quasi-random order. At the end of the procedure, a measurement for the first direction was repeated in order to check the unit response level. The mean number of spikes, N, in the response (over several repeated runs in each direction) as a function of direction φ was approximated by a second-order harmonic function:

$$N(\varphi) = a_0 + a_1 \cdot \cos(\varphi - \varphi_1) + a_2 \cdot \cos(2\varphi - 2\varphi_2).$$

The amplitudes of the zero (a_0), first (a_1) and second (a_2) harmonics, and the phases of the first (φ_1) and second (φ_2) harmonics characterize the directional tuning curve.

According to their polar diagrams, GCs are subdivided into nonselective, DS and OS. The three types differ from each other by the relative contribution of different harmonics. The amplitudes of the first and second harmonics reflect the relative strength of the directional and orientational components, respectively, and thus, can be considered as classifying features. DS and OS units that fall into the domains, where $a_1 > 1/2a_0$ and $a_1 > a_2$, or $a_2 > 1/2a_0$ and $a_1 < a_2$, respectively, were the subject of the present study. The preferred directions and preferred orientations of

the DS and OS GCs under study can be determined from the phases of the first and the second harmonics.

2.5.2. *Determination of the RF center*

Position of the RF in the stimulation area was calculated online using the same experimental data, obtained during polar diagram measurements. The RF center was estimated from the sequences of time points of spike appearances in all of the trials for all directions of movement. The idea of an automatic procedure that determined the position of the RF center is as follows. A squared deviation of the time of spike appearance from the time when the stimulus passes through the assumed RF center is calculated for each of the applied directions. The center of the RF was determined as a point in the visual field, where the mean square deviation calculated for all directions was minimal. After the measurement of the polar diagram and determination of the position of the RF, the position of the stimulation area on the monitor screen was centered with respect to the RF, and all subsequent procedures were conducted with the centered RF.

2.5.3. *Measurement of responses to stimuli of selective colors*

Investigations of the unit's responses to stimuli of selective colors were conducted under the general scheme. Values of the parameters of stimulation, which remained unchanged during the whole measurement, were specified in advance. In the case of stimulation with moving edges or stripes, the parameters were the direction of movement (usually coincided with the preferred direction of the unit under investigation), the speed of movement and the number of repetitive runs of each color. Upon stimulation with flashing colored stripes or spots, the size and position of the stripe (spot) in the stimulation area, the magnitude of an idle time interval before applying the stimulus, the duration of stimulation and the number of repetitive runs with each color were specified. The measurement began with the presentation of the $L+$ color. Then, the remaining selective colors were presented sequentially: $M+$, $S+$, $L-$, $M-$ and $S-$. At the end of the procedure, a measurement for the $L+$ color was repeated in order to check the unit response level.

By means of this procedure, when using moving edges as stimuli, 61 DS GCs (40 cells of the ON type and 21 cells of the OFF type) and 30 OS GCs (25 detectors of horizontal line and 5 detectors of vertical line) were investigated. Because as a rule several experiments were made on each cell, a total of 183 such measurements were made on the DS GCs and 97 measurements were made on the OS GCs. In addition, 165 experiments were carried out on 39 OS GCs with flashing colored stripes.

3. Results

3.1. *Absence of color coding in the motion detectors*

Usually, color-coding of some unit implies that there are clear differences between the responses of the unit to stimuli which are the same in all respects, except for their

color. In particular, it is thought that different polarity of cell responses evoked by flashes of different colors given in darkness (color opponency) is a sufficient reason to consider such cells as color-coding.

In this respect, the retinal motion detectors lack color coding. Although the middle-wave and/or short-wave cones do contribute to the spectral sensitivity curve of the detectors with the sign opposite to the contribution of the long-wave cones (Maximov *et al.*, 2014), this contribution is rather small. As a result, responses of the motion detectors to any natural light are determined mainly by the long-wave cones. There is no apparent color-dependent difference in responses, and so, by the form of response it is impossible to understand what color was presented. This is illustrated in Fig. 2, where the examples of responses of DS GCs of ON and OFF types to pure

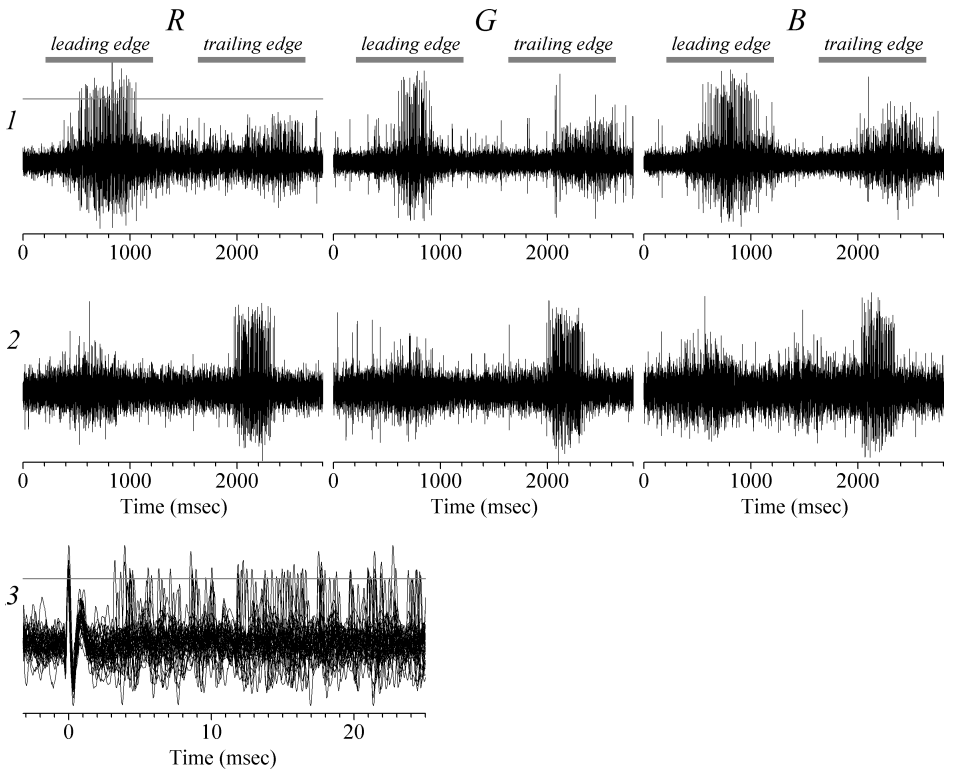

Fig. 2. Spike responses of DS GCs to movement of pure monitor colors (*R*, *G* and *B*) on a black background. Stimuli were moving so that at first their leading edge entered in the RF, and the black background was replaced by edge color; after that their trailing edge moved in the same direction — the edge moved out of the RF and its color was replaced by the black background. Gray bars above the discharges mark time intervals during which the leading or trailing edges were moving within the area of stimulation. (1 — upper panel) A DS GC of the ON-type with caudo-rostral preferential direction. Responses to movement of the vertical edge from tail to head at the speed of 11°/s. A thin horizontal line in 1, *R* indicates a threshold used for amplitude discrimination of spikes in this unit. (2 — middle panel) A DS GC of the OFF-type with ventro–dorsal preferential direction. Responses to movement of the horizontal edge in bottom–up direction at the speed of 11°/s. (3 — bottom panel) Superimposed runs of the same record as in 1, *R*, synchronized by each spike that has passed the threshold of discrimination, shown in the extended sweep.

monitor colors are given. It can be seen that the DS GCs of the ON-type respond to moving of pure blue or green monitor colors into their RFs and are unresponsive to their removal in the same way as they respond to red monitor color (Fig. 2(1)).

Here, it should be noted that this lack of color dependency of the response pattern cannot be attributed to a non-single-unit record. Indeed, apart from the responses of the DS GCs of the ON-type, spikes of smaller magnitude from other cells are also visible in the oscillograms of Fig. 2, particularly those responding to trailing edge of the stimuli. However, if we consider only high spikes, they should be regarded as generated by one and the same cell. If there was a mixture of cells, then, because of uncorrelatedness of their responses in the record, a spike of one cell could follow a spike of another cell with an arbitrarily small time interval. In Fig. 2(3), it can be seen that there were no interspike intervals in the spike train shorter than 3 ms, which evidenced in favor of single-unit recording (and that the refractory period of this DS GCs was about 3 ms).

On the contrary, DS GCs of the OFF-type do not respond to moving of any monitor colors into their RF, but respond by spike trains only to their removal (Fig. 2 (2)). Again, based on these spike trains, it is impossible to understand what color was presented. As for OS GCs, in all experiments, both detectors of horizontal and vertical edges give ON–OFF responses to edges of any monitor color.

3.2. *Color opponencies revealed with color-selective stimulation*

To reveal opponent signals from middle-wave and short-wave cones it is necessary to eliminate strong signals from the long-wave ones — to equalize the background and the edge colors for long-wave ones. Figure 3 illustrates such an experiment, made on the same DS GC of the ON-type, which is shown in Fig. 2(1). In this case, the cell was stimulated with colored edges of incremental colors $L+$, $M+$ and $S+$, moving over the neutral background. It is seen that in the case of selective stimulation of long-wave cones (L) the cell responds only to the edge moving into its RF, similar to non-selective stimulations (Fig. 2(1)). But to selective stimulation of middle-wave (M) and short-wave (S) cones it responds primarily to removal of the edges from the RF.

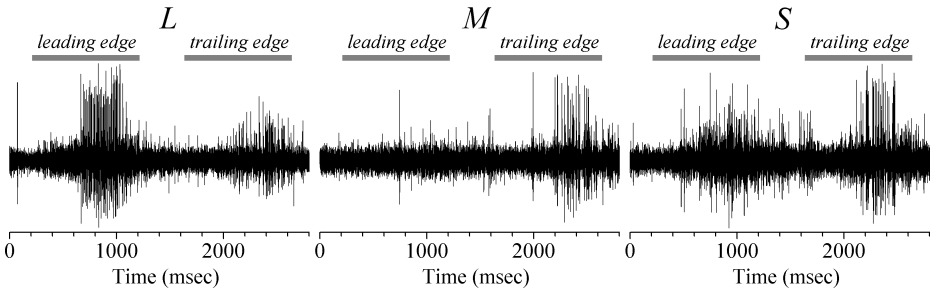

Fig. 3. Spike responses of the same DS GCs of the ON-type as shown in Fig. 2(1) to movement of colored edges, selectively stimulating L, M and S cones of the goldfish. Vertically oriented edges were moved from tail to head on the neutral background at the speed of 11°/s. Other conventions are as in Fig. 2.

Besides having different polarity, these responses are usually much weaker than in the case of selective stimulation of the long-wave cones. Completely symmetric pattern was observed in DS GCs of the OFF-type. Here, cells respond to selective stimulation of middle-wave and short-wave cones mainly to moving of the edge into their RFs. These experiments confirm the conclusion obtained in the previous study that in DS GCs, signals of middle-wave and short-wave cones are opponent to the signals of long-wave ones (Maximov *et al.*, 2014).

Another example of responses of DS GC of the ON-type to the color-selective stimulation by moving edges is shown in Fig. 4(a). Here responses are shown to moving of the color edges into the cell RF. Condensed discharges to stimulation of middle-wave and short-wave cones appear only to the decremental colors $M-$ and $S-$.

The first thing that strikes the eye in experiments with selective stimulation of OS units with moving edges of optimal orientation is that the indifference to the sign of stimulus contrast exists only within the long-wave color channel. Selective stimulation of the middle-wave and short-wave cones evoked more or less pure OFF or ON responses, respectively. Thus, Fig. 4(b) shows that responses of a detector of horizontal line to increment and decrement for long-wave cones ($L+$ and $L-$) contain approximately the same number of spikes, while middle-wave stimulations ($M+$ and $M-$) gave dramatically different numbers. The second thing that strikes the eye when performing experiments with selective stimulation of OS units is that unlike DS GCs their middle-wave and short-wave channels are mutually opponent. This can be

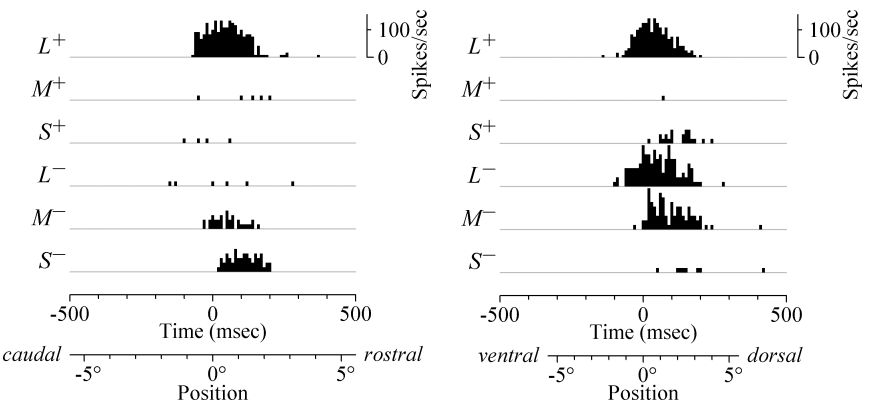

Fig. 4. Responses of the motion detectors to movement of colored edges on the neutral background. Peristimulus histograms of the discharges display the density of evoked spikes along the time or position scales. The time scale: zero point corresponds to the time when the stimulus leading edge passes through the center of stimulation area. The position scale: zero point corresponds to the position of the center of stimulation area. The scale enables to fix the position of stimulus leading edge in the visual space at the moment of spike appearance. Histogram with 10-ms bins was compiled from the responses to 12 presentations for $L+$ stimulus and 6 presentations for the others. (a) Responses of a direction-selective unit of the ON-type with caudo-rostral preferred direction to movement of vertical edges from tail to head at the speed of 11°/s. (b) Responses of a detector of horizontal line to movement of horizontal edges in top-down direction at the speed of 16°/s.

seen in Fig. 4, where the DS GC of the ON-type has noticeable responses to decremental colors $M-$ and $S-$, but its responses to incremental colors $M+$ and $S+$ were practically absent, while in the detector of horizontal line noticeable responses were observed to stimuli of the opposite contrast: $M-$ and $S+$. It should be noted that the presence of some responses both to decremental and incremental colors of the short-wave channel (with those to increments being much larger) seems to reflect an overall pattern of the OS GCs physiology. In the short-wave channel, the small response to decremental color was observed regularly. In middle-wave channel, responses to $M+$ were usually absent. This feature shows the different physiology of middle-wave and short-wave color channels of the OS GCs.

3.3. *Polar diagrams at color-selective stimulation*

The fact that the preference to sign of stimulus contrast can vary when switching from one chromatic type of cones to another, raises the question: what properties of motion detectors at the same time remain unchanged? Does the direction and orientation selectivity remain if polar diagrams are taken with the use of color-selective middle-wave or short-wave stimuli? And if so, whether preferred directions are retained? In favor of the possibility of some surprising changes of preferred direction and preference to sign of contrast in DS GCs, we highlight experiments in which application of picrotoxin unmasked an OFF response in DS GCs of the ON type in the rabbit retina, and this OFF response was direction selective, but its preferred direction was opposite to that of the ON response (Ackert *et al.*, 2009). Further, if the signals in the middle-wave and short-wave channels are so small that they are muted by slightest signals of the long-wave channel, then does this not mean that middle-wave and short-wave signals are generally of little significance for the motion detector and do not participate in the organization of the direction or orientation selectivity?

To explore this question in goldfish, we measured polar diagrams by edges of selective incremental colors for leading and trailing edges for all types of motion detectors. Examples of such diagrams are shown in Fig. 5. It is seen that during transition from stimulation of the long-wave cones to stimulation of the middle-wave and short-wave cones the direction and orientation selectivity, as well as their preferred directions, remained unchanged. At the same time, the sign of the response is reversed in the DS GCs: ON cells gave OFF responses and OFF cells gave ON responses to middle-wave and short-wave stimuli. The OS GCs always responded with an OFF type response to stimulation of middle-wave cones and with the prevalence of an ON response to short-wave cones stimulation.

3.4. *Responses of detectors of oriented lines to flashing stripes of selective colors*

The motion detectors respond not only to moving stripes and edges, but also to flashing spots or stripes within the RF. In DS GCs, the flashes of achromatic spots

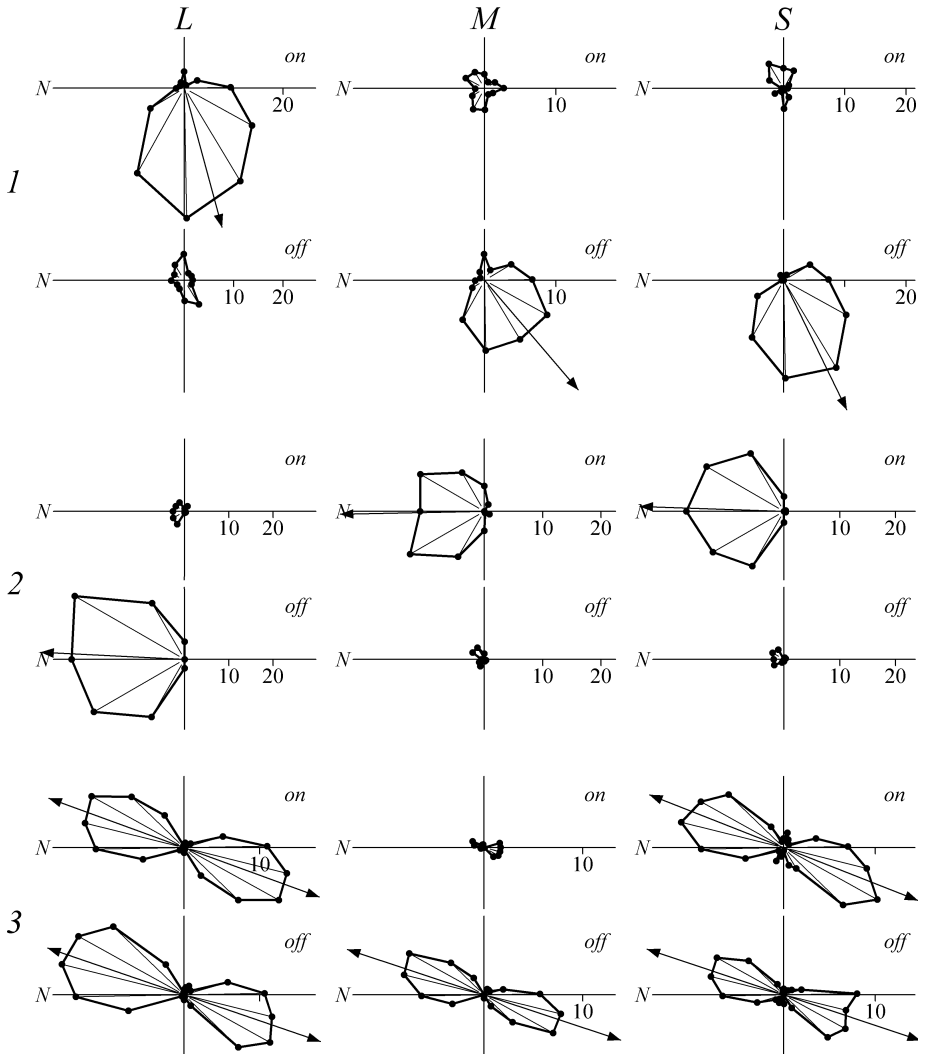

Fig. 5. Polar diagrams measured with selective incremental colors for motion detectors of the fish retina. (1) DS GC of the ON type with dorso–ventral preferential direction. Responses to color edges moving in 12 directions at the speed of 11°/s against a neutral background. (2) DS GC of the OFF type with caudo-rostral preferential direction. Responses to color edges moving in 12 directions at the speed of 11°/s against a neutral background. (3) Detector of vertical line. Responses to color edges moving in 24 directions at a speed of 16°/s against a neutral background. Diagrams marked with label "*on*" were built from the cell responses to the movement of leading edges into the RF, those marked with label "*off*" were built from the responses to the movement of trailing edges. Dots on rays of different direction mark the mean number of spikes evoked in response for each of the tested directions. Preferred directions of the cells are shown by black arrows. The letter "N" indicates nasal direction. Scales represent the average number of spikes in the response of the cell.

cause transient responses where polarity allows to attribute cells to ON or OFF type. However, flashes of spots of different sizes do not represent a specific stimulation for the units selective to direction of movement that can be evidenced by a large variety of responses to such stimuli in different cells, which is not comparable with the clear

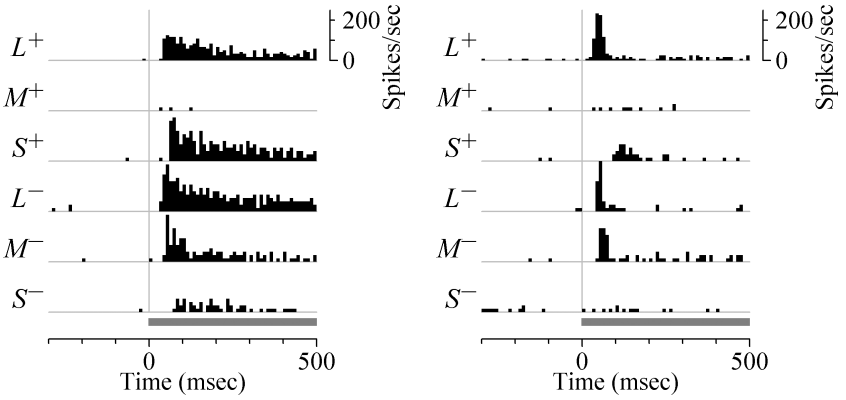

Fig. 6. Responses of detectors of (a) horizontal and (b) vertical lines to flashes of colored stripes of preferred orientation on the neutral background. The stripes width was 1°. Duration of the flashes was 0.5 s (marked by gray horizontal bars). Peristimulus histograms of the discharges display the density of evoked spikes along the time scale. Other conventions are as in Fig. 4.

pattern observed when stimulated by moving stimuli. In OS GCs, the flashes of achromatic stripes (both light and dark) of preferred orientation usually cause sustained responses with more or less prominent transients. Sometimes, the sustained response may be absent, but sometimes the cell can respond within hours to a thin pencil line drawn in its RF.

Examples of responses of the OS GCs to color-selective stimulation with stripes of preferred orientation are shown in Fig. 6. Diagram (a) shows an example of response with the most pronounced sustained component while diagram (b) shows an example of response with the most pronounced transient component. These differences in the form of responses are not associated with the type of detectors of oriented lines. Responses of both types were equally frequent among detectors of horizontal and vertical lines. As in the case of moving stimuli, the OS GCs always responded to increments and decrements of stimulation of the long-wave cones, but responded only to decremental stimulation of middle-wave cones and responded with the prevalence of response to increments of short-wave cone stimulation.

3.5. *Latencies of detectors of oriented lines to flashing stripes of selective colors*

The noteworthy points in the Fig. 6 are that the latent periods of responses are large and the differences of these latent periods for different colors are significant. When examining by achromatic stimuli, the latent periods of responses were found to be not dependent on contrast (at least for incremental or decremental contrasts exceeding 10%) and hardly dependent on the width of presented stripes (except for very narrow stripes with width less than 15 angular minutes).

In order to estimate values of the latent periods for different selective colors, 78 experiments of the type as shown in Fig. 6 were carried out on 12 OS cells (with 3 to

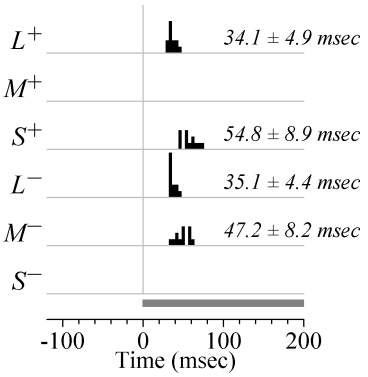

Fig. 7. Distributions of response latencies of 12 detectors of oriented lines to flashes of colored stripes of preferred orientation presented on the neutral background. Designations for stripe colors are given on the left. Histogram bars indicate the number of cells in which the average position of the first spike in the discharges falls at a given time. Bin size, 4 ms. Numbers to the right are the mean latency ± s.d. for all cells investigated.

10 measurements on each cell). In each experiment, the value of the latent period was determined by the time when the first spike in the spike discharge appeared in response to flash of stripes of all selective colors (except for the colors $M+$ and $S-$). The procedure for finding the first spike in the discharge is described in the Appendix. Then, for each cell the value of average latency was determined by averaging over all the experiments on this cell. Histograms of latencies (the amount of cells falling within the given time interval) for each color are shown in Fig. 7. Finally, these numbers were averaged for all 12 cells and dispersions of these figures were calculated. The resulting figures are shown in the same Fig. 7. Although the absolute values of the latent periods vary markedly from one experiment to another and from one cell to another (and at that the dispersion of values for stimuli $M-$ and $S+$ was always significantly higher than for stimuli $L+$ and $L-$), within each experiment, the values of latent periods for stimuli $M-$ and $S+$ were always greater than for the stimuli $L+$ and $L-$. Statistically significant differences in latency were also observed between the responses to stimuli $M-$ and $S+$.

4. Discussion

The experiments of this work with selective stimulation of different cone types have provided the first electrophysiological evidence that movement detectors projecting to the fish tectum possess color-opponent properties. Although color-opponent neurons usually are associated with color vision, in the case of the motion detectors this opponency is hardly used directly for color coding. In low-saturated natural environment (outside of the experimental setup with saturated monitor colors) all motion detectors of the goldfish will behave as color-blind. Functions of the DS and OS GCs are apparently quite different and are not related to color vision. Nevertheless, the color features of the responses of these cells carry information about the

details of wiring of the retinal circuitry. Therefore, based on our experimental data we will attempt to gain an idea about the possible mechanisms of synaptic organization of the color opponency used in DS and OS GCs.

There are three ways to get color-opponent signals in the retina. The first way uses negative feedback from horizontal cells, where the second-order neuron is synaptically connected with one chromatic type of cones, while the signal from the another cone type comes through interneurons — horizontal cells (Stell & Lightfoot, 1975; Stell *et al.*, 1975; Maximov & Byzov, 1996; Kamermans & Spekreijse, 1999; Li *et al.*, 2009). The second way is that signals from ON and OFF channels originating from different chromatic types of cones are collected only at the level of the inner plexiform layer (IPL) by bistratified GCs ramifying in the ON and OFF sublaminae of the IPL as it was discussed in connection with the blue pathway in primate retina (Dacey & Lee, 1994). The third way is to collect signals from different chromatic types of cones in one bipolar cell at the very input, in the outer plexiform layer (OPL), using different types of synapses (sign-conserving and sign-inverting) with cones (Wong & Dowling, 2005). Spatial properties of the RF of GCs (which, in particular, are responsible for the differences between the various types of DS and OS GCs) are organized in the IPL by using several types of amacrine cells. Thus, in mammalian retina, each of the DS neurons is served by two independent networks of starburst amacrines, ramifying in the ON and OFF sublaminae of the IPL and, nevertheless, forming the directional selectivities with identical preferred directions (Demb, 2007). There are evidences that fish use similar mechanisms of the organization of the directional selectivity (Damjanović *et al.*, 2015). The orientational selectivity of GCs apparently is also formed in the IPL both in rabbit (Levick, 1967; Bloomfield, 1994; Venkataramani & Taylor, 2010) and in goldfish (Maximov, 2010).

The easiest way would be to assume that ON and OFF responses to different colors, say, in DS GCs of the ON type of the fish retina are organized the same way as ON and OFF responses in bistratified DS GCs of the ON–OFF type of the mammalian retina (Vaney *et al.*, 2001). Here, the path of ON bipolar cells is used for the organization of an ON response. These cells terminate in the ON sublamina of the IPL on starburst cells and on dendrites of GCs, interaction between which provides the directional selectivity. Correspondingly, the path of OFF bipolar cells is used to create an OFF response. These cells terminate in the OFF sublamina of the IPL on the other branch of dendrites of GCs and starburst cells of another type. Schematically, this model is shown on the left drawing of Fig. 8(a). Corresponding model for the DS GCs of the OFF type is shown on the central drawing of Fig. 8(a). To avoid cluttering the pictures, starburst amacrines, whose dendrites costratify with the axons of DS GCs, are not drawn. For all their ideological simplicity, these models have a number of disadvantages that make them improbable. The main disadvantage is that besides the individual types of bipolar cells per each color channel (which are inevitable in this scheme), the scheme requires also separate chromatic types of the starburst cells in each sublaminae to create directional selectivity for each of the selective colors. This is not only too cumbersome, but corresponding architecture

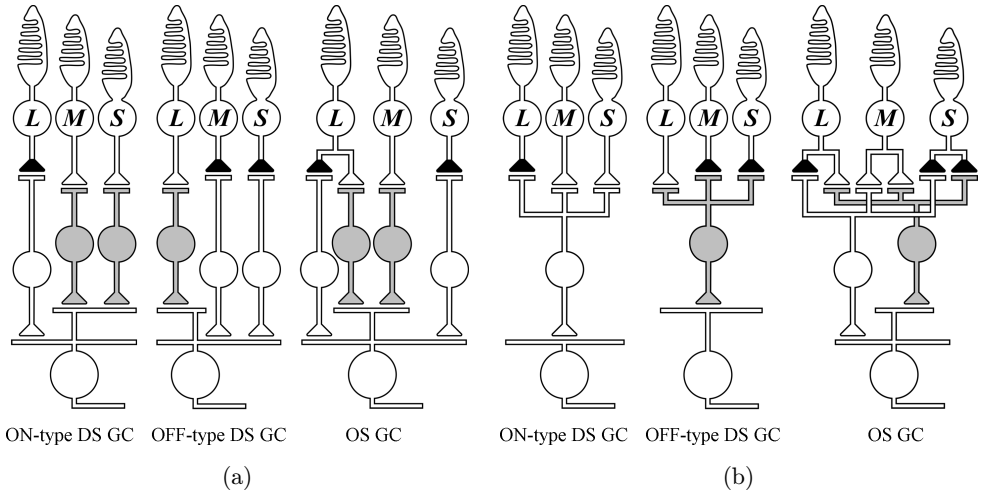

Fig. 8. Wiring diagrams showing possible innervation of different motion detectors with three different chromatic types of cones (L, M and S) through the bipolar cells. (a) Signals originating from different chromatic types of cones are collected by bistratified ganglion cells from the ON and OFF bipolar cells in the IPL. (b) Signals of different chromatic types of cones are collected by each bipolar cell already in the OPL. Three layers of neurons (from top to bottom): cones, bipolar cells and ganglion cells are separated by two synaptic layers: the outer plexiform layer (OPL) and the inner plexiform layer (IPL), where these neurons transmit signals to each other. Sign-inverting synapses in the OPL are shown by black triangles. Accordingly, in (a), ON bipolar cells (which receive signals from cones through sign-inverting synapses) are painted white and OFF bipolar cells (which receive signals from cones through the sign-conserving synapses) are painted gray. In (b), color-opponent bipolar cells are subdivided into ON (white) and OFF (gray) types according to how they are connected with long-wavelength cones. Two levels of branching of ganglion cells dendrites correspond to ON (lower level) and OFF (upper level) sublaminae of the IPL.

seems to be hardly feasible at all, since each of these chromatic types of starburst amacrines should cofasciculate in a certain way with the same dendrites of DS GCs.

Furthermore, there is a certain discrepancy between the schemes shown in Fig. 8(a) and the real morphology. The supposed DS GCs must have a bistratified morphology, to collect signals from both the ON and OFF bipolar cells. In the paper by Maximova *et al.* (2006) it was shown that this is likely not the case: in the goldfish retina there are two separate morphological types of DS GCs whose dendrites ramify in either ON, or OFF sublaminae of the IPL, but not in both.

As for the OS GCs, similar straightforward scheme of organization of different selectivity to the sign of stimulus contrast in different color channels in these cells is shown on the right drawing of Fig. 8(a). Nothing is known about the types of amacrine cells and how the orientation selectivity in the IPL is organized. However, in this case it is obvious that for different selectivities to the sign of contrast in different color channels, this scheme will also require duplication of these amacrine cells, which also makes the scheme rather cumbersome.

An alternative to these cumbersome schemes can be to collect signals with opposite signs from different color channels as early as in the OPL. As already

mentioned, the change of sign can be done either by using different kinds of synapses of bipolar cells with different types of cones, or with the help of interneurons. The schemes that use different types of sign-conserving and sign-inverting synapses with cones are shown in Fig. 8(b). They do not require specific types of bipolar cells for each color channel. In the case of DS GCs these schemes can be made with just one type of bipolar cells for each type of GCs (ON or OFF types). And what is more important here, these schemes do not require special types of chromatic amacrine cells in the IPL. In this case, the coincidence of preferred directions or orientations in different color channels is provided automatically since specific spatial properties of the GCs are built in the IPL, where color signals are already combined. The structure of the OS GCs should be somewhat more complicated because of the ON–OFF nature of their responses to the long-wave selective colors. It looks like it will require separate types of ON and OFF bipolar cells. Yet, we still have little data to imagine exactly how these cells are connected with different types of cones. One possible scheme is shown on the right drawing of Fig. 8(b). Thus, the union of the color channels with opposite signs already at the input of the bipolar cells gives us a paradigm within which one can build wiring diagrams for the DS and OS GCs that are not too complicated.

The presence of color-opponent bipolar cells in the fish retina was shown by Kaneko (1973) and Kaneko & Tachibana (1981). The question of whether the existence of two synapses with different selectivity to the sign of contrast at the same bipolar cell is possible has a long history. Now it is known that the sign-inverting and sign-conserving synapses differ in their presynaptic morphology, the postsynaptic receptor biochemistry (ionotropic and metabotropic glutamate receptors) and their functions, generating depolarizing or hyperpolarizing signals in response to stimulation of cones (Stell & Lightfoot, 1975; Stell *et al.*, 1975; Saito *et al.*, 1985; Hidaka *et al.*, 1986; Shimbo *et al.*, 2000). Finally, the evidence that both sign-inverting and sign-conserving glutamate receptors can co-localize to the same bipolar cell and that both can mediate light responses was obtained by Wong & Dowling (2005). All of this taken together makes the circuits shown in Fig. 8(b) very plausible.

Distinct differences in the magnitude of the latent periods of the responses to flashing stimuli of different colors imply another scheme for organizing color opponency in the OPL. This should refer only to the scheme of OS GCs, since flashing spots and stripes were not adequate stimuli for DS GCs and did not give consistent results. The shortest latencies in the OS GCs occurred when stimulated by flashes that affect the long-wave cones. One can assume that this time is spent on the passage of the visual signal in the direct path from cones to GCs. Latencies were measured from the moment of sending a control signal to stimulating monitor until the appearance of the first spike in response. The shortest latency was approximately 35 ms, of which an average of about 7 ms constituted hardware delays, and the remainder goes to the signal transduction in the cones and two synaptic delays in OPL and IPL. At the same time, responses to flashes of stripes, which differ in color from the background for the middle-wave cones (decremental color $M-$) appeared an

average of more than 10 ms later. It is natural to assume that this delay is due to some interneuron transmitting the signal from the middle-wave cones in this direct pathway. Short-wave signal undergoes additional delay, which suggests an additional intermediate cascade from the short-wavelength cones to middle-wave cones (with a sign inversion).

Similar relations of the values of the latent periods of the responses to different colors were described for color-opponent bipolar cells in the carp (Shimbo *et al.*, 2000). All this is very similar to the cascade model of organization of color-opponent horizontal cells, proposed by Stell *et al.* (1975). Here, horizontal cells themselves served as interneurons. Unfortunately, this scheme, as it is, cannot serve for an explanation of the color opponency in bipolar cells and motion detectors, because ratios of the latencies here are straight reverse to that of horizontal cells: in the opponent bipolar cells or in the OS GCs the responses to long-wave stimuli have a latency shorter than the responses to middle- or short-wave ones, whereas the latency of the red component in the RG-type horizontal cells is longer than that of the green component. In order to explain the selectivity to the sign of contrast and delays observed in the detectors of oriented lines one would have to find some other cells serving as interneurons rather than horizontal cells of different types operating in a cascade circuit (Stell *et al.*, 1975).

Appendix A. Automatic Estimation of Response Latencies from Sample Responses to Flashes of Lines

The latent period of the response was defined as the time interval between the onset of the stimulus and the first spike in the discharge. This is not difficult in the absence of incidental spikes before the discharge. Unfortunately, sparse incidental spikes superimposed on the response can complicate an automatic procedure for finding the first spike of the discharge. In order to segregate the evoked spikes from incidental ones, generated before the evoked train, a special procedure based on the maximum likelihood method was designed.

Statistical model. Let the sequence of spikes in the record be a result of two random processes described by a step function of time: (i) the process with low probability of spike generation before the train and (ii) the process with high probability of spike generation during the train, evoked by stimulus. Time is assumed to be discrete. Let the low and the high probabilities of spike generation at the time points be p_1 and p_2, and the time of the starting point of the discharge be t. Then for the given statistical model, a likelihood function can be defined as the product of probabilities that neuron fire or not fire at any time point:

$$L(p_1, p_2, t) = p_1^{m_1}(1-p_1)^{t-1-m_1} p_2^{m_2}(1-p_2)^{T-t+1-m_2},$$

where T is the duration of recording in ms, m_1 and m_2 depend on the sample data and are equal to the numbers of spikes recorded before and during the discharge, respectively.

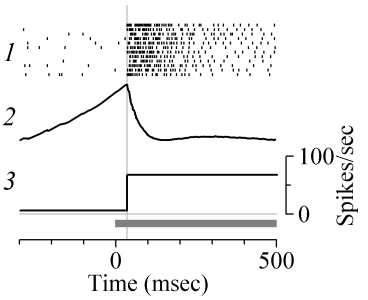

Fig. 9. Example of determining of the starting point of the discharge in response of a detector of horizontal line to flashes of horizontal stripes. (1) Raster plots of 12 trials of responses of the detector to flashes of incremental color $L+$ on a neutral background with duration of 500 ms. The stripe width was 1°. (2) The log-likelihood function computed by these data. (3) The restored step function of random processes describing the statistical model.

To find the most likely position of the start of the discharge t, it is necessary to maximize the likelihood function. Values of the probabilities p_1 and p_2, for which the function reaches its maximum value, are easy to find: they are $p_1 = \frac{m_1}{t-1}$ and $p_2 = \frac{m_2}{T-t+1}$. After substituting these values, the expression for the likelihood function depends only on one variable t. To find the maximum of this function it is convenient to use the log-likelihood function, that has the form:

$$\begin{aligned}\ln L = {} & m_1 \ln m_1 - (t-1)\ln(t-1) + (t-1-m_1)\ln(t-1-m_1) \\ & + m_2 \ln m_2 - (T-t+1)\ln(T-t+1) \\ & + (T-t+1-m_2)\ln(T-t+1-m_2).\end{aligned}$$

This log-likelihood function was numerically computed by the sample data set. The maximum value of the function was found by a brute force search of all 800 time points.

An example of application of the procedure of search of the starting point of the discharge in response of the detector of horizontal lines to flashing stripes is shown in Fig. 9.

It should be noted that despite the rather crude statistical model (in particular, a smooth decrease in the spike frequency during the discharge does not meet the assumption about the constancy of the spike generation probability), in all cases examined, the position of the first spike found by the procedure corresponded to the beginning of the spike discharge from a human point of view.

Acknowledgments

The study was supported by the Russian Foundation for Basic Research (Grant No. 13-04-00371).

REFERENCES

Ackert, J.M., Farajian, R., Völgyi, B. & Bloomfield, S.A. (2009) GABA blockade unmasks an OFF response in ON direction selective ganglion cells in the mammalian retina. *J. Physiol.*, **587**, 4481–4495.

Bilotta, J. & Abramov, I. (1989) Spatio-spectral properties of goldfish retinal ganglion cells. *J. Neurophysiol.*, **62**, 1140–1148.

Bloomfield, S.A. (1994) Orientation-sensitive amacrine and ganglion cells in the rabbit retina. *J. Neurophysiol.*, **71**, 1672–1691.

Bowmaker, J.K., Thorpe, A. & Douglas, R.H. (1991) Ultraviolet-sensitive cones in the goldfish. *Vis. Res.*, **31**, 349–352.

Collin, S.P. (1989) Anterograde labelling from the optic nerve reveals multiple central targets in the teleost. *Letbrinus cbrysostomus* (Perciformes). *Cell Tissue Res.*, **256**, 327–335.

Coughlin, D.J. & Hawryshyn, C.W. (1993) Ultraviolet sensitivity in the Torus semicircularis of juvenile rainbow trout (*Oncorhynchus mykiss*). *Vis. Res.*, **34**, 1407–1413.

Coughlin, D.J. & Hawryshyn, C.W. (1994) The contribution of ultraviolet and short-wavelength sensitive cone mechanisms to color vision in rainbow trout. *Brain Behav Evol.*, **43**, 219–232.

Dacey, D.M. & Lee, B.B. (1994) The 'blue-on' opponent pathway in primate retina originates from a distinct bistratified ganglion cell type. *Nature*, **367**, 731–735.

Damjanović, I., Maximova, E., Aliper, A., Maximov, P. & Maximov, V. (2015) Opposing motion inhibits responses of direction-selective ganglion cells in the fish retina. *J. Integr. Neurosci.*, **14** (in press).

Daw, N.W. (1967) Goldfish retina: Organization for simultaneous color contrast. *Science*, **158**, 942–944.

Deguchi, T., Suwa, H., Yoshimoto, M., Kondoh, H. & Yamamoto, N. (2005) Central connection of the optic, oculomotor, trochlear and abducens nerves in medaka, *Oryzias latipes. Zoolog. Sci.*, **22**, 321–332.

Demb, J.B. (2007) Cellular mechanisms for direction selectivity in the retina. *Neuron*, **55**, 179–186.

Douglas, R.H. (1989) The transmission of the lens and cornea of the brown trout (*Salmo trutta*) and goldfish (*Carassius auratus*) — effect of age and implications for ultraviolet vision. *Vis. Res.*, **29**, 861–869.

Gibbs, M.A. & Northmore, D.P. (1998) Spectral sensitivity of the goldfish Torus longitudinalis. *Vis. Neurosci.*, **15**, 859–865.

Govardovskii, V.I., Fyhrquist, N., Reuter, T., Kuzmin, D.G. & Donner, K. (2000) In search of the visual pigment template. *Vis. Neurosci.*, **17**, 509–528.

Hartline, H.K. (1938) The response of single optic nerve fibers of the vertebrate eye to illumination of the retina. *Am. J. Physiol.*, **121**, 400–415.

Hidaka, S., Christensen, B.N. & Naka, K. (1986) The synaptic ultrastructure in the outer plexiform layer of the catfish retina: A three-dimensional study with HVEM and conventional EM of Golgi-impregnated bipolar and horizontal cells. *J. Comp. Neurol.*, **247**, 181–199.

Jacobson, M. & Gaze, R.M. (1964) Types of visual response from single units in the optic tectum and optic nerve of the goldfish. *Quart. J. Exp. Physiol.*, **49**, 199–209.

Kamermans, M. & Spekreijse, H. (1999) The feedback pathway from horizontal cells to cones: A mini review with a look ahead. *Vis. Res.*, **39**, 2449–2468.

Kaneko, A. (1973) Receptive field organization of bipolar and amacrine cells in the goldfish retina. *J. Physiol.*, **235**, 133–153.

Kaneko, A. & Tachibana, M. (1981) Retinal bipolar cells with double colour-opponent receptive fields. *Nature*, **293**, 220–222.

Levick, W.R. (1967) Receptive fields and trigger feature of ganglion cells in the visual streak of the rabbit's retina. *J. Physiol.*, **188**, 285–307.

Li, Y.N., Matsui, J.I. & Dowling, J.E. (2009) Specificity of the horizontal cell-photoreceptor connections in the zebrafish (*Danio rerio*) retina. *J. Comp. Neurol.*, **516**, 442–453.

Maximov, V.V. (2010) A model of receptive field of orientation-selective ganglion cells of the fish retina. *Sens. Syst.*, **24**, 110–124 (in Russian).

Maximov, V.V. & Byzov, A.L. (1996) Horizontal cell dynamics: What are the main factors? *Vis. Res.*, **36**, 4077–4087.

Maximov, V.V., Maximova, E.M., Damjanović, I. & Maximov, P.V. (2014) Color properties of the motion detectors projecting to the goldfish tectum: I. A color matching study. *J. Integr. Neurosci.*, **13**, 465–484.

Maximov, V.V., Maximova, E.M. & Maximov, P.V. (2005a) Direction selectivity in the goldfish tectum revisited. *Ann. NY Acad. Sci.*, **1048**, 198–205.

Maximov, V.V., Maximova, E.M. & Maximov, P.V. (2005b) Classification of direction-selective units recorded in the goldfish tectum. *Sens. Syst.*, **19**, 322–335 (in Russian).

Maximov, V.V., Maximova, E.M. & Maximov, P.V. (2007) Colour properties of the direction-selective motion detectors projecting to the goldfish tectum. *Sens. Syst.*, **21**, 19–28 (in Russian).

Maximov, V.V., Maximova, E.M. & Maximov, P.V. (2009) Classification of orientation-selective units recorded in the goldfish tectum. *Sens. Syst.*, **23**, 13–23 (in Russian).

Maximova, E.M., Govardovskii, V.I., Maximov, P.V. & Maximov, V.V. (2005) Spectral sensitivity of direction-selective ganglion cells in the fish retina. *Ann. NY Acad. Sci.*, **1048**, 433–434.

Maximova, E.M., Levichkina, E.V. & Utina, I.A. (2006) Morphology of putative direction-selective ganglion cells traced with DiI in the fish retina. *Sens. Syst.*, **20**, 279–287 (in Russian).

Maximova, E.M., Orlov, O.Yu. & Dimentnman, A.M. (1971) Investigation of visual system of some marine fishes. *Voprocy Ichtiologii*, **11**, 893–899 (in Russian).

Maximova, E.M., Pushchin, I.I., Maximov, P.V. & Maximov, V.V. (2012) Presynaptic and postsynaptic single-unit responses in the goldfish tectum as revealed by a reversible synaptic transmission blocker. *J. Integr. Neurosci.*, **11**, 183–191.

McDonald, C.G. & Hawryshyn, C.W. (1999) Latencies and discharge patterns of color-opponent neurons in the rainbow trout optic tectum. *Vis. Res.*, **39**, 2795–2799.

Northcutt, R.G. & Wullimann, M.F. (1988) The visual system in teleost fishes. Morphological patterns and trends. In: Atema, J., Fay, R.R., Popper, A.N. & Tavolga W.N., eds. *Sensory Biology of Aquatic Animals.* NY: Springer, pp. 515–552.

Northmore, D. (2011) Optic tectum. In: Farrell, A., ed. *Encyclopedia of Fish Physiology: From Genome to Environment.* Elsevier, pp. 131–142.

Saito, T., Kujiraoka, T., Yonaha, T. & Chino, Y. (1985) Reexamination of photoreceptor-bipolar connectivity patterns in carp retina: HRP-EM and Golgi-EM studies. *J. Comp. Neurol.*, **236**, 141–160.

Shimbo, K., Toyoda, J.I., Kondo, H. & Kujiraoka, T. (2000) Color-opponent responses of small and giant bipolar cells in the carp retina. *Vis. Neurosci.*, **17**, 609–621.

Spekreijse, H., Wagner, H.G. & Wolbarsht, M.L. (1972) Spectral and spatial coding of ganglion cells in goldfish retina. *J. Neurophysiol.*, **35**, 73–86.

Springer, A.D. & Gaffney, J.S. (1981) Retinal projections in the goldfish: A study using cobaltous-lysine. *J. Comp. Neurol.*, **203**, 401–424.

Stell, W.K. & Lightfoot, D.O. (1975) Color-specific interconnections of cones and horizontal cells in the retina of the goldfish. *J. Comp. Neurol.*, **159**, 473–502.

Stell, W.K., Lightfoot, D.O., Wheeler, T.G. & Leeper, H.F. (1975) Goldfish retina: Functional polarization of cone horizontal cell dendrites and synapses. *Science*, **190**, 989–990.

Tomita, T. (1965) Electrophysiological study of the mechanisms subserving color coding in the fish retina. *Cold Spring Harbor Symp. Quant. Biol.*, **30**, 559–566.

Vaney, D.I., He, S., Taylor, W.R. & Levick, W.R. (2001) Direction-selective ganglion cells in the retina. In: Zanker, J.M. & Zeil, J. eds. *Motion Vision: Computational, Neural, and Ecological Contstraints.* Berlin: Springer, pp. 13–56.

Venkataramani, S. & Taylor, W.R. (2010) Orientation selectivity in rabbit retinal ganglion cells mediated by presynaptic inhibition. *J. Neurosci.*, **30**, 15664–15676.

Wagner, H.G., MacNichol, E.F. & Wolbarsht, M.L. (1960) The response properties of single ganglion cells in the goldfish retina. *J. Gener. Physiol.*, **43**, 45–62.

Wong, K.Y. & Dowling, J.E. (2005) Retinal bipolar cell input mechanisms in giant danio. III. ON–OFF bipolar cells and their color-opponent mechanisms. *J. Neurophysiol.*, **94**, 265–272.

Zenkin, G.M. & Pigarev, I.N. (1969) Detector properties of the ganglion cells of the pike retina. *Biophysics*, **14**, 763–772.