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Direction-selective units in goldfish retina and tectum opticum — review and new aspects

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The output units of fish retina, i.e., the retinal ganglion cells (detectors), send highly processed information to the primary visual centers of the brain, settled in the midbrain formation tectum opticum (TO). Axons of different fish motion detectors terminate in different tectal levels. In the superficial layer of TO, axons of direction-selective ganglion cells (DS GCs) are terminated. Single unit responses of the DS GCs were recorded in intact fish from their axon terminals in TO. Goldfish DS GCs projecting to TO were shown to comprise six physiological types according to their selectivity to sign of stimulus contrast (ON and OFF units) and their preferred directions: three directions separated by 120°. These units, characterized by relatively small receptive fields and remarkable spatial resolution should be classified as local motion detectors. In addition to the retinal DS GCs, other kinds of DS units were extracellularly recorded in the superficial and deep sublaminae of tectum. Some features of their responses suggested that they originated from tectal neurons (TNs). Contrary to DS GCs which are characterized by small RFs and use separate ON and OFF channels, DS TNs have extra-large RFs and ON-OFF type responses. DS TNs were shown to select four preferred directions. Three of them are compatible with those already selected on the retinal level. Complementary to them, the fourth DS TN type with rostro-caudal preference (lacking in the retina) has been revealed. Possible functional interrelations between DS GCs and DS TNs are discussed.

Keywords: Goldfish; retina; motion detectors; direction-selective ganglion cells; direction-selective tectal neurons.

1. Motion Detection and Direction Selectivity in the Fish Retina — Early Publications

Information about different properties of visual objects: size, direction of motion, form, color, etc., is processed by different types of specialized retinal ganglion cells (detectors). Some types of the detectors, direction-selective ganglion cells (DS GCs), strongly respond to visual objects moving in a particular (preferred) direction, and their responses are inhibited by stimuli moving in the opposite, or null direction. One of the most extensively studied DS units, are the DS GCs of mammalian retina which project to the midbrain superior colliculus. It was shown that these units respond to

both the leading and the trailing edges of a stimulus moving along the preferred direction through their receptive field (Barlow & Levick, 1965). In other words, these DS GCs are excited by stimuli that are either lighter or darker than the background. Due to this contrast independence, this cell type is referred to as the ON-OFF DS GC (Vaney *et al.*, 2001; Masland, 2004). These GCs that are characterized by relatively small RFs and are tuned to a broad range of stimulus velocities, are considered as fast DS units that function as local motion detectors (Vaney *et al.*, 2001). Fast mammalian DS GCs were shown to group into four physiological subtypes with different preferred directions aligned with the horizontal and vertical ocular axes (Oyster & Barlow, 1967). Direction-selective circuitry of these units, based on asymmetric null side inhibition mediated by the starburst amacrine cells (SACs) has been previously examined in great details in mammals (Lee *et al.*, 2010; Briggmann *et al.*, 2011; Yonehara *et al.*, 2013).

The DS GC system in the fish has been investigated less thoroughly. The first studies of motion detection in the fish retino-tectal system were initiated in our laboratory in the 1960s. Experiments were performed on intact animals (*in vivo* conditions). Different types of retinal movement detectors were revealed in the early studies in the pike (Zenkin & Pigarev, 1969) and six species of marine fish (Maximova *et al.*, 1971). Single unit responses of the motion detectors were recorded extracellularly from their axon terminals in the superficial layers of the midbrain tectum opticum (TO) using low impedance (200–500 KΩ) microelectrodes prepared according to the procedure developed by Gesteland *et al.* (1959). The electrodes were made using micropipettes filled with a Wood's metal and tipped with a platinum cap of 2–10 μm in diameter. These electrophysiological studies of the tectal visual centers revealed four distinct types of retinal projections: axon terminals of four different types of retinal GCs were clustered at different depths of the tectal retino-recipient zone. In the superficial layers, responses of direction-selective units were constantly recorded. Beneath these units, detectors of another type were located which responded to a small contrast spot moving in various directions, i.e., these GCs are not direction selective and resemble "local edge detectors" (LEDs) recorded in the early studies of the frog retino-tectal system (Lettvin *et al.*, 1959). In the even more deep tectal layers, the responses from color-opponent elements were usually detected. And finally, in the deepest layers, the responses of the sustained units were recorded. These cells, referred to as "light-spontaneous" and "dark-spontaneous" units responded by sustained discharges to the diffuse ON and OFF flashes, respectively. No physiological differences in the DS GC circuitry related the ecological or evolutionary differences in the studied fish species were revealed. In the experiments that followed, the responses from axon terminals of another type of retinal movement detectors were recorded underneath the sublaminae of the DS units, approximately in the same zone where the responses of LEDs were previously recorded. These GCs, denoted as orientation selective units (OSUs), of the fish retino-tectal system respond selectively to contrast lines of particular orientation, similar to the cortical "complex" cells of mammals (crucian carp — Maximova & Maximov, 1981;

goldfish — Maximova, 1998). Their responses to moving stimuli were much more prominent than those evoked by stationary lines. OSUs were proved to divide into two subtypes according to their preferred stimulus orientation (approximately horizontal or vertical).

This review will concentrate on the DS GCs that are most extensively studied fish motion detectors. As it was mentioned above, responses of the DS units are constantly recorded in the superficial layers of the TO. It has been considered that these responses come from the axon terminals of retinal GCs projecting to the tectum. Clustering of DS GCs with the caudo-rostral preferred direction was shown for the superficial DS units in the pike (Zenkin & Pigarev, 1969), as well as in the marine fishes investigated in Maximova *et al.* (1971). No clusters of DS GCs with other preferred directions were observed in these studies. DS elements recorded in the superficial tectal sublaminae were characterized by relatively small receptive fields, ranging from 2° to 10°. They were shown to be color blind, i.e., they did not respond to contrast colored spots displayed on a colored background. On the other hand, these units demonstrated remarkable contrast sensitivity that is typical for motion detectors. Finally, it should be noted that these superficial DS responses were not unique in the fish tectum. In the deeper tectal layers, approximately in the sublaminae where the sustained units are located, responses from another type of DS units that are presumably of the TO were recorded. The amplitudes of spikes in the discharges of these units that sometimes exceeded 1mV were much higher than those of the retinal elements (around 300 μV). These putative tectal DS neurons were characterized by the receptive fields of a very large size (of up to 60°) that is not a characteristic for the units of the retinal origin. Similar to the superficial DS units, these DS neurons preferred the caudo-rostral direction of the stimulus' movement (Fig. 1). It should be emphasized that in the studies that followed the differentiation between the retinal and the tectal DS units was elaborated in more detail (see Chapter 5 of the review). DS GCs of the fish retina have also been mentioned in a few papers by other authors. Although all of them noted the dominance of the

Fig. 1. Responses of tectal DS neuron of mullet to stimuli moving in different directions. Stimuli, dark spots moved in caudo-rostral and opposite, rostro-caudal, directions (arrows indicate directions of stimulus movement relative to fish orientation). One can see that movement of spots in caudo-rostral direction always evokes prominent spike discharge of DS neuron, whereas the stimulus motion in the opposite direction does not induce response of the unit.

Source: Data from Maximova *et al.* (1971).

caudo-rostral preference of the direction of movement of the visual stimuli, in their recordings (goldfish — Jacobson & Gaze, 1964; Cronly-Dillon, 1964; Wartzok & Marks, 1973; trout — Liege & Galand, 1971) no clear classification of these cells either by type of response (ON, OFF, or ON-OFF) or by preferred directions was made in these early publications.

2. Classification of Goldfish DS GCs by Preferred Directions and their Selectivity to Sign of Contrast

In order to ensure more precise evaluation of the properties of different types of fish retinal movement detectors, the experimental setup providing on-line data acquisition and processing was developed. This complex setup guided by mutually connected and synchronized computer modules was described in detail elsewhere (Maximov *et al.*, 2005b; Damjanović *et al.*, 2009a; Maximov & Maximov, 2010). Same as before, responses of detector GCs were recorded extracellulary from their axon terminals in the retino-recipient layer of the TO using low-impedance microelectrodes. As from the year 2003, in a series of studies we have systematically investigated the responsive properties of some hundreds of movement detectors in the retina of *Carassius gibelio* (wild form of goldfish) using the newly developed experimental setup (Maximov *et al.*, 2005a, 2005b, 2009, 2013; Damjanović *et al.*, 2009a, 2009b, 2015). Types of different movement detectors were determined on the basis of their polar diagrams (directional tuning curves). Polar response pattern of the unit was measured with contrast edges moving in 12 or more different directions across the RF. Mean number of spikes in the response recorded over three repeated runs in each direction (N) as a function of direction φ was approximated by a second-order harmonic function:

$$N(\varphi) = a_0 + a_1 \cdot \cos(\varphi - \varphi_1) + a_2 \cdot \cos(2 \cdot \varphi - 2 \cdot \varphi_2). \tag{1}$$

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 polar response patterns. Typical examples of polar response patterns measured for different GCs projecting to the fish TO are shown in Fig. 2(a). It is customary to divide visual neurons by their polar response patterns, into nonselective, direction-selective, and orientation-selective (Barlow *et al.*, 1964; Maximova *et al.*, 1971; He *et al.*, 1998). Three types differ from each other by relative contribution of different harmonics [Fig. 2(a)]. The amplitudes of the first and second harmonics reflect the strengths of the directional and orientational components, respectively (He *et al.*, 1998), and so, can be considered as classifying features. As one can see from the distribution shown in Fig. 2(b), according to their polar patterns, GCs projecting to the tectum indeed constitute three clear clusters: (1) those with small relative amplitudes of both first and second harmonics — nonselective units (resemble LEDs of frog); (2) those with pronounced relative amplitude of the first harmonic — direction-selective units; (3) those with pronounced relative amplitude of the second harmonic — orientation-selective units.

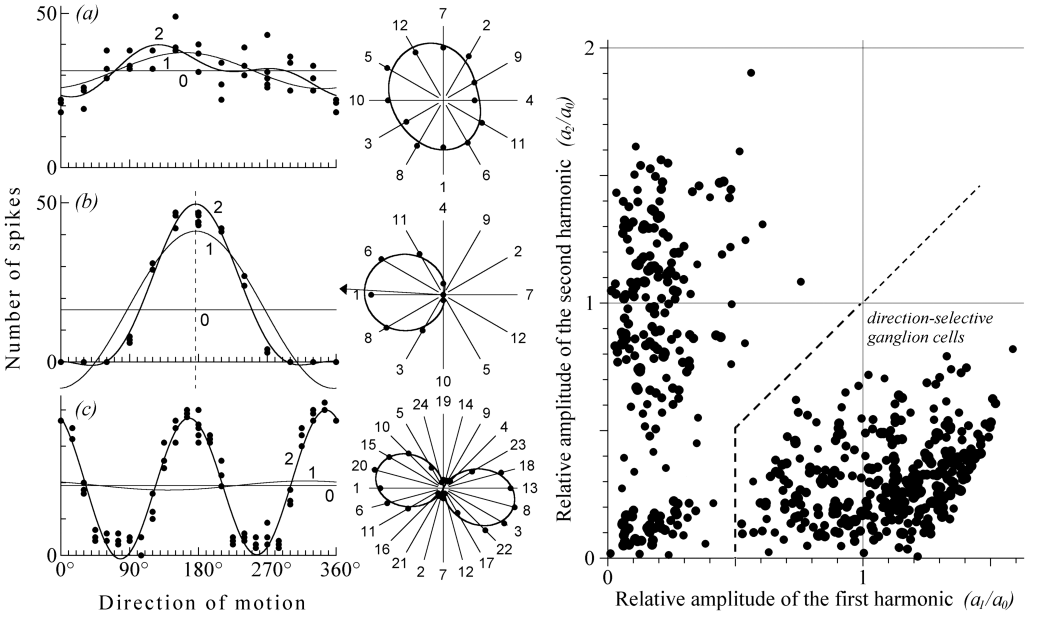
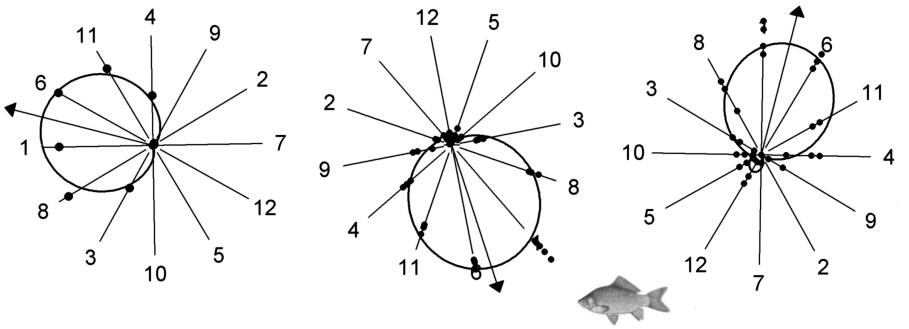


Fig. 2. Examples of three principal types of polar response patterns observed in goldfish retinal motion detectors. (a) Responses of various types of goldfish motion detectors were measured with contrast edges moving in 12 or more different directions across the receptive field. Diagrams were plotted in Cartesian (left) and polar (right) coordinates using the same experimental data. Dots mark number of spikes in the response either separately for each run in each direction (Cartesian plots), or a mean value over repeated runs (polar plots). Solid lines are approximations of experimental data by harmonic functions of zero- (0), first- (1) and second- (2) order (only second-order approximations are shown in the polar plots). Numbers at the ends of radius-vectors in the polar plot indicate a sequence of presentations of different directions. Types of units and stimulation: (a) leading edge detector, responses to movement of black stripes against a white background; (b) DS unit of the ON type selective to caudo-rostral movement (preferred direction is shown by a dashed line in the Cartesian plot and by an arrow in the polar plot), responses to white edges moved in 12 directions against a black background; (c) detector of vertical line (OS unit), responses to white stripes moved in 24 directions against a black background. (b) Scatter diagram of amplitude of the second harmonic vs. amplitude of the first one for 522 polar patterns measured for GCs of various types.

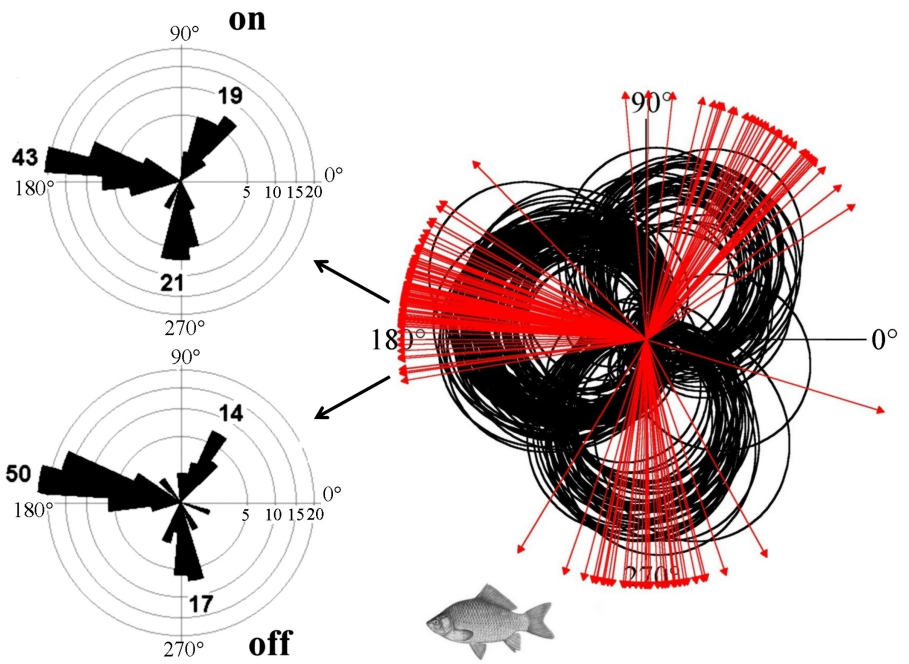
Source: Data from Maximov *et al.* (2005b).

Axon terminals of three types of motion detectors were clustered at different depths of retino-recipient zone in accordance with arrangement suggested in Maximova *et al.* (1971): direction-selective units were recorded superficially, while projections of LEDs and OSUs were located in the underneath sublaminae. According to this classification, DS units fall into the domain, where $a_1 > \frac{1}{2}a_0$ and $a_1 > a_2$ [Fig. 2(b)].

More than 400 of DS GCs in the retina of *C. gibelio* were investigated by means of new setup till the present time (Maximov *et al.*, 2005a, 2005b; Damjanović *et al.*, 2009a). Polar diagrams of different direction-selective units recorded in the goldfish are presented in Fig. 3(a). Preferred directions calculated by the phase of the first harmonic of the Fourier transform are marked by arrows. Besides the clustering of caudo-rostral preferred direction observed in above-mentioned early



(a)



(b)

Fig. 3. (Color online) Preferred directions of goldfish DS GCs. (a) Polar response patterns of three goldfish DS GCs: ON-type DS unit preferring caudo-rostral direction (left), OFF-type unit preferring dorso-ventral direction (middle) and ON-type DS unit preferring ventro-dorsal direction (right). Other conventions are same as in Fig. 2(a). (b) Clustering of polar response patterns calculated for 164 goldfish DS GCs (right panel; preferred directions calculated for directional tuning curves are marked by red arrows). ON- and OFF-type DS GCs were presented in practically equal quantities among tested units (see histograms of preferred directions for both types of DS units presented on the left panel). Orientation of fish relative to directions of stimulus movement is demonstrated.

studies (Zenkin & Pigarev, 1969; Maximova *et al.*, 1971) another two clusters of preferred directions were identified — ventro-dorsal and dorso-ventral. It emerged that fish fast DS GCs differ from analogous units of mammals in some aspects. In contrast to fast mammalian DS GCs comprising four physiological subtypes with different preferred directions aligned with the horizontal and vertical ocular axes

(Oyster & Barlow, 1967), direction-selective units projecting to goldfish tectum appeared to be divided into three distinct groups, characterized by the preferred movement directions, respectively: caudo-rostral, ventro-dorsal, and dorso-ventral, separated by about 120°. Units that responded to the caudo-rostral direction of stimulus movement were the most numerous [Fig. 3(b)]. Unlike mammalian mixed ON-OFF type of the fast DS units, two separate types, pure ON and pure OFF units, were equally encountered in the fish retina. [Fig. 3(b); the data processed in 164 cells]. The results of our recent experiments performed in carp, roach, and barbell fish *Labeobarbus intermedius* indicated that DS GCs of these fishes coincided with retinal DS units of *C. gibelio* (Damjanović *et al.*, 2015). Results confirming our findings have been recently published by Nikolaou *et al.* (2012). Using calcium imaging techniques, visually evoked activity of the retinal GC axons innervating tectum of zebrafish was recorded. Three subtypes of retinal DS units, characterized by preferred directions similar to those described in *C. gibelio* were identified. The proportion between the DS GC subtypes was practically the same as that shown in *C. gibelio* (units with the preference to caudo-rostral direction were the most numerous). The authors did not classify zebrafish retinal DS units according to their selectivity to sign of contrast (ON, OFF, or ON-OFF). However, the results of the study indicate that the system of DS GCs comprising six physiologically distinct subtypes might be universal retinal DS circuitry developed during evolution of the teleost fish species.

Nevertheless, the results of the recent study of Tsvilling *et al.* (2012) revealed specific features of the DS mechanism in archer fish retina. Results of the study proved the full dominance of DS units with caudo-rostral preferred direction. Two other preferred directions of DS units characterized in goldfish and zebrafish (ventro-dorsal and dorso-ventral) were not clustered. Consequently, DS GCs preferring caudo-rostral direction were determined as fundamental DS units playing an important role in predatory behavior of archer fish. The newest study of DS mechanism in archer fish retina (Pinski *et al.*, 2015) revealed further discrepancies with retinal DS system of goldfish. Results of this study contradict the "detector concept" of Lettvin *et al.* (1959). In their fundamental work, Lettvin and colleagues showed that the movement detectors of the frog retina projecting to TO responded distinctly to moving contrasts and gave no response to the diffuse ON/OFF flashes. The same was noted for the movement detectors (most of them — DS units) of the goldfish retina projecting to TO. Goldfish retinal DS units responded distinctly to moving contrast edges, bars, or spots. On the other hand, responses to small stationary flashing spots were usually much weaker than to moving stimuli (Damjanović *et al.*, 2009a). Finally, the goldfish DS units did not respond when their whole receptive field area was transiently lightened (for ON-units) or darkened (for OFF-units) (Maximov *et al.*, 2005b). On the contrary to this, the archer fish DS units investigated in the study of Pinski *et al.* (2015) did respond to diffuse ON/OFF flashes with prominent transient ON- and OFF-peaks. Consequently, the archer fish DS ganglion cells were defined as ON-OFF units. This result differs from the above-mentioned data for the goldfish in

which the DS units were shown to use separate ON- and OFF-channels. All foregoing arguments qualify retinal DS mechanism of archer fish as fundamentally different from the DS mechanism in the goldfish retina. However, it is unlikely that the DS system of the archer fish might be unique among DS systems of other fish species. In our view, it is most likely that the above-mentioned discrepancies in the archer fish and the goldfish DS systems are due to the differences in the methods of acquiring and processing of the data in the studies on these two species. In our studies on the goldfish, we record the responses of the DS GCs from their individual axon terminals located in the TO, from a fish that has been subjected only to minor surgical procedures, and which eyes remain intact during the experiment. On the contrary, in the studies of the DS system in the archer fish, all of the recordings were performed, apparently, from the GC bodies in an isolated retina using a multi-electrode array.

3. Spatial Properties and Contrast Sensitivity of Goldfish DS GCs

Irrespective of the above-mentioned differences between the fish DS GCs projecting to TO and the mammalian fast DS GCs projecting to the superior colliculus, according to numerous physiological characteristics of fish DS GCs resemble the fast mammalian DS units and should be classified as local motion detectors. First of all, DS GCs of *C. gibelio* were shown to be characterized by relatively small responsive receptive field (RRF) areas. In the work of Damjanović *et al.* (2009) RRF sizes of goldfish DS units were evaluated on the basis of four different methods. Figure 4 demonstrates the results obtained when canonical method of the RRF mapping with a contrast flashing spot was used ("random checkerboard"). The spots were flashed on and off sequentially in nodes of square grid in a quasi-random order. Number of spikes evoked by each sequential turning on and off the spot was counted. In Fig. 4(a) are shown results obtained in one OFF DS unit. The ellipse presents an estimate of the unit RRF area, its diameter being evaluated as a geometric mean of its length and width. Histogram of RRF size distribution estimated by this method for 99 DS units is represented in Fig. 4(b). The RRF sizes varied from 1.8° to 7°, with the mean value of $4.3 \pm 1.1°$. In other three methods, moving stimuli (contrast edges or spots) were used to evaluate RRF sizes of more than 200 DS GCs. It should be noted that all applied methods gave consistent estimates of RRF sizes — mean values of RRF diameters for all four procedures ranged between 4° and 4.8°. These angle values corresponded to rounded retinal area with the diameter of approximately 300 μm. ON-OFF DS ganglion cells with RF sizes similar to those described in goldfish DS units were observed in rabbit (Amthor *et al.*, 1984), mouse (Weng *et al.*, 2005; Lee *et al.*, 2010), and rat (Sun *et al.*, 2011).

Second property characterizing goldfish DS GCs as local motion detectors was their extremely high spatial resolution. Spatial resolution of goldfish DS GCs was evaluated in the study of Maximov *et al.* (2013). Spike activity of different movement detectors including DS units was recorded in response to the movement of square-wave gratings of various spatial frequencies into the unit RF and drifting them

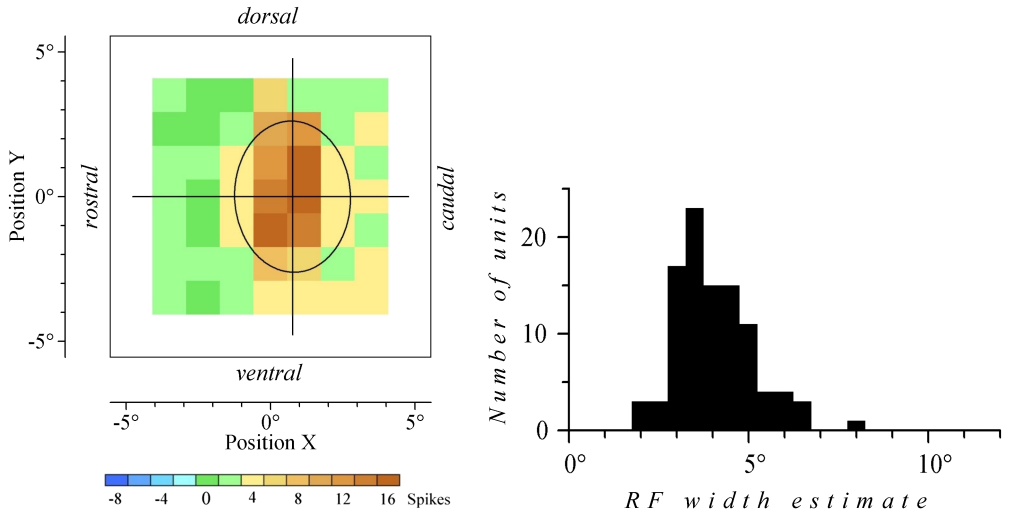


Fig. 4. Canonical method of the receptive field mapping with a flashing spot (random chekerboard). (a) Results obtained in an OFF DS GC of goldfish. Cell responsiveness across the stimulation area, recorded by RF mapping with one flashing black spot against light background. Cell responses over the entire stimulation area, measured by this method, are represented in the form of topographic map [see the scale at the bottom of Fig. 4(a)]. The ellipse presents an estimate of the unit RRF area, its diameter being evaluated as a geometric mean of its length and width. Detailed explanation in the text. (b) Distribution of the RRF sizes evaluated by canonical method for 99 DS GCs of goldfish.

Source: Data from Damjanović *et al.* (2009).

through it at a certain speed in a preferential direction [Fig. 5(a)]. In case of stable recordings, the DS units provided reproducible number of spikes in response to repeated stimulation. The measurement began with the presentation of the moving edge (wide stripe, exceeding unit receptive field in width). Then, a series of gratings of increasing spatial frequency was presented automatically. The finest grating used had a frequency of 1.8 cycles per degree. At the end of the procedure, a measurement for the moving edge was repeated. In order to analyze quantitatively the detection and resolution of gratings, the records of spike responses to drifting grating stimuli were Fourier analyzed to calculate the responses at zero and the first harmonic component of the Fourier decomposition of the response. To do this, in each record the first discharge of response to the movement of the leading edge of the grating was discarded, and for the rest of response the magnitudes of the zero and the first harmonic components were calculated. The dependences of the magnitude of the zero harmonic component (which coincides with the mean spike rates of the response) and the magnitude of the first harmonic component (which coincides with the fundamental response frequency) on the spatial frequency of stimuli presented spatial frequency characteristics of the response. Examples of such characteristics obtained in one OFF DS GC selective to dorso-ventral motion direction and one ON DS GC selective to caudo-rostral movement are shown in Fig. 5(b). The figure also shows the theoretical spatial-frequency characteristics, calculated for linear model of GC RFs.

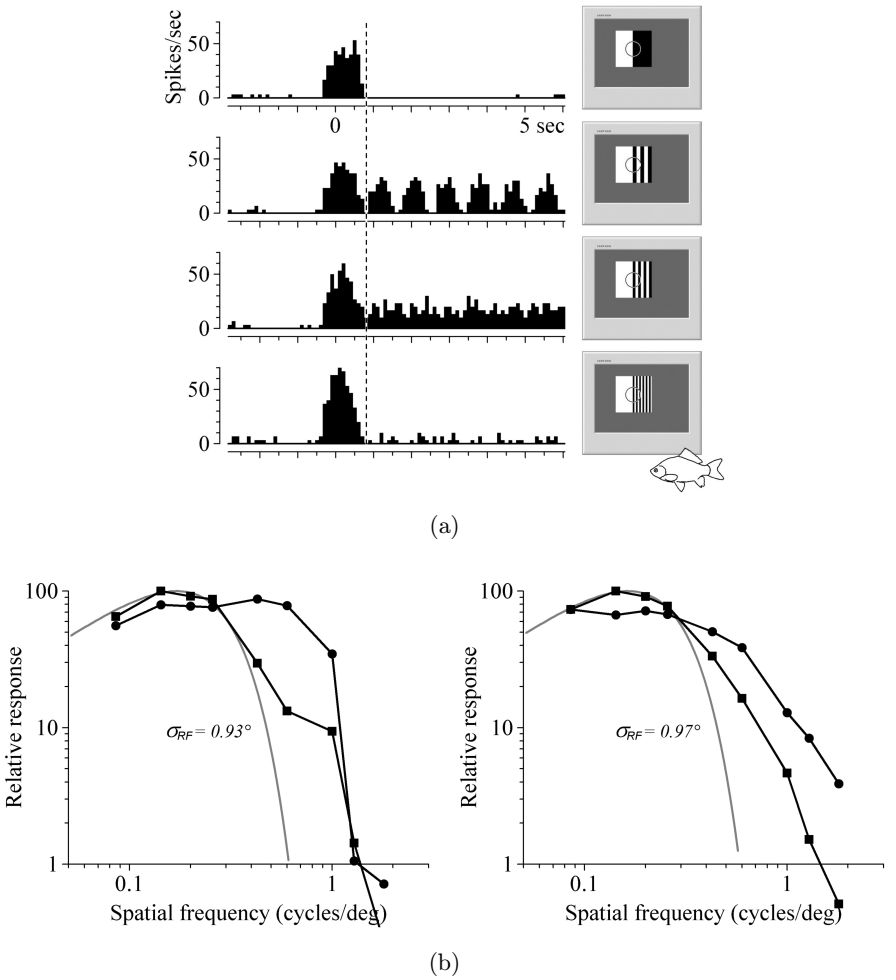


Fig. 5. Spatial properties of goldfish DS GCs. (a) A schematic view of the experimental paradigm. The stimulation began with the presentation of the moving edge i. e. wide stripe, exceeding stimulation area in width (see the stimulus on the top). Subsequently, square-wave gratings of various spatial frequencies moving at a certain speed in a preferential direction (caudo-rostral in the present case) were presented to fish in the square stimulation area. Peristimulus histograms of recorded responses are presented near corresponding stimuli. The first discharge of response to the movement of the leading edge of the grating was discarded, and for the rest of response the magnitudes of the zero- and the first-harmonic components were calculated (beginning moment of data processing is marked by vertical dashed line). Detailed explanation in the text. (b) Dependences of the mean spike rate (the zero harmonic) and of the amplitude of the fundamental frequency (the first harmonic) on the spatial frequency of the gratings for two DS GCs plotted in double logarithmic co-ordinates. Left graph — a unit of the OFF-type selective to dorso-ventral movement stimulated by horizontal black gratings drifting at the speed of 2,75°/s in a downward direction; right graph — a unit of the ON-type selective to caudo-rostral movement stimulated by vertical white gratings drifting at the speed of 2.75°/s in the caudo-rostral direction. Gray smooth curves — theoretical curves of spatial-frequency characteristics for the linear model of RF; rectangles — the first harmonic; circles — the zero harmonic.

Source: Data from Maximov *et al.* (2013).

Linear RFs were approximated from the responses to moving contrast edges (the traces of the first and the last sessions of the experiment). For this purpose, peristimulus histogram of spike discharges evoked by the moving edges was fitted by the Gaussian function with the use of a least-squares minimization algorithm. The best Gaussian fits were considered as optimal approximations of unit RRFs. According to the value of parameter "σ" of the best Gaussian fits [σ_{RF} in Fig. 5(b)] the theoretical curves of spatial-frequency characteristics for the linear model of GC RFs were calculated [see Fig. 5(b)]. One can see that the units demonstrated in Fig. 5 maintained a high level of the mean spike rate close to the maximum at high spatial frequencies, where the responses of the linear model were decreased by more than an order of magnitude [see curves for the zero harmonic components in Fig. 5(b)]. Reproduction of some frequency i.e., resolution acuity (presence of the first harmonic component in the cell response) was always worse than the detection acuity (mean spike rates of responses), what is clearly demonstrated in Fig. 5(b) (compare curves for the first and zero harmonics in both presented units). However, the curves for the first harmonic also fell off much slower at high frequencies than the theoretical curves. In other words, the real cell could reproduce such frequencies that the linear model could not. Accordingly, we can make a conclusion that in present cells visual acuity for detection and resolution of drifting gratings was much higher than the acuity provided by the linear RF of the appropriate size. Such behavior was a characteristic for all the DS GCs investigated. The results of the previous study (Damjanović *et al.*, 2009a) showed that for DS GCs there is a considerable convergence of cones onto GCs (up to several hundreds of cones per GC), which would worsen the resolution. However, as shown in the study Maximov *et al.* (2013) goldfish DS units likewise other movement detectors responded to movement of gratings of the spatial frequencies, to which they should not, if they were linear integrators. Results of the present study were consistent with results of numerous behavioral experiments with the use of optomotor drums which have shown that fish distinguish periodic gratings at all spatial frequencies, which can be resolved by their cone mosaic (Neave, 1984; Schaerer & Neumeyer, 1996; Dobberfuhl *et al.*, 2005; Haug *et al.*, 2010). It was considered as the evidence that the visual system of fish can resolve such gratings. However, in order to follow a moving high-frequency grating in the optomotor drum, the visual system should only be able to detect the grating and determine in which direction it moves. This ability does not require resolving individual stripes of the grating. It is indeed this property that motion detectors investigated in the study Maximov *et al.* (2013) do possess. There are gratings of such a high spatial frequency, that these detectors cannot resolve them, though still can detect. Minimum resolvable angle for the goldfish DS GCs (determined as a period of the first indistinguishable grating) was considerably lower than that determined by sizes of unit RFs, and amounted 42′, being approximately twice as high as the theoretical limit defined by cone density. In other words, acuity of DS GCs themselves is close to the limit determined by the density of cones. The same was shown for another type of goldfish retinal movement detectors, OSUs. The question arises: what mechanism underlies so high spatial

resolving power of fish movement detectors, exceeding the resolution limited by cell RF sizes by an order of magnitude? From the all above-mentioned it is evident that the implicit assumption of fish movement detectors as simple linear integrators is false. RFs of fish GCs seem to be composed of many nonlinear subunits with significantly smaller zones of signal summation (Maximov, 2010). The concept of spatial subunits was first expressed by Hochstein and Shapley (1976) in connection with a widespread nonlinear pathway with high spatial resolution in the Y-type GCs of the cat retina. Since then, it became clear that the nonlinear RF seems to be expressed by most GC types in all mammalian species (Demb *et al.*, 1999; Schwartz *et al.*, 2012).

Besides, the extremely high spatial resolution goldfish DS GCs are characterized by remarkable contrast sensitivity. High contrast sensitivity of DS GCs was demonstrated already in Maximova *et al.* (1971). However, for the systematic, more precise measurements of DS GC contrast sensitivity separate experimental procedure was recently developed. This procedure, designed in a form of program tool, was as follows. Stimuli were wide contrast stripes of different brightness, exceeding in diameter receptive field of the studied DS unit. Stripes of different brightness were moved, three times each, in a preferred direction over the DS GC receptive field illuminated by neutral gray light, and number of spikes evoked by leading and trailing edges of stimuli were counted. On the basis of recorded responses graphs, representing dependence of the mean number of spikes on the brightness of stripes, were constructed (see Fig. 6, representing data for an ON DS unit). On the graphs were separately presented amplitudes of responses evoked by leading ("IN") and

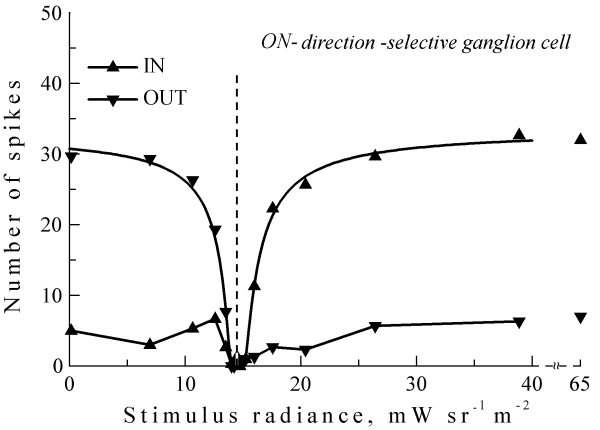


Fig. 6. Contrast sensitivity of goldfish DS GCs. Intensity–response profile showing the responses of one goldfish ON-type DS GC as function of the light intensity, stimulus radiance. The ordinate indicates the number of spikes (mean of three runs) in the cell discharge in response to the movement of achromatic stripes of various intensities over a fixed gray background through the receptive field in a preferential direction. Two branches of the curve correspond to responses to the leading (in) and trailing (out) edges of the stimulus. Presented DS GC was selective to caudo-rostral movement, stimulated by vertical edges moving in the caudo-rostral direction. The background radiance was equal to 14.5 mW sr^{-1} m^{-2} (marked with dashed line), and the speed of the stimuli was 11°/s.

Source: Data from Maximov *et al.* (2005b).

trailing edges ("OUT") of applied stimuli. The data recorded for stripes darker or lighter than the gray background light were separately approximated by the two-parameter hyperboles (steep profiles in Fig. 6). Crossing points of hyperboles with abscissa defined the increment and decrement threshold values. More than 100 DS units were studied and recorded threshold contrasts for all data varied between 1.1% and 6.4%, with the mean value of approximately 3% of background brightness. Such high contrast sensitivities recorded in goldfish DS GCs attest to the fact that fish retinal DS units work practically according to the all-or-nothing principle similar to other movement detectors.

4. Properties of Inhibition Underlying Direction Selectivity in Goldfish Retina

The crucial role of the null-side inhibition in generation of direction selectivity was proved for mammalian fast DS GCs. The asymmetric delayed inhibition from the null side was shown experimentally to be mediated by "starburst" amacrine cells (SACs) (Yoshida *et al.*, 2001; Euler *et al.*, 2002; Lee & Zhou, 2006; Lee *et al.*, 2010). Two possible inhibitory mechanisms mediated by the SACs that are not mutually exclusive could produce the suppression of dendritic spikes in DS GCs. According to the "presynaptic model", presynaptic inhibition of excitatory synaptic inputs from bipolar cells to a local dendritic region of DS GC should suppress spike initiation (Fried *et al.*, 2002, 2005). The second possible inhibitory mechanism underlying direction selectivity is based on post-synaptic processing, i.e., post-synaptic inhibition from SACs within a local dendritic region of DS GC should block spike initiation (Borst, 2001; Taylor *et al.*, 2000). In the recent work of Yonehara *et al.* (2013), concerted activity of bipolar cells, DS GCs, and SACs in the DS circuitry of mouse retina was recorded using calcium imaging techniques. Results of that study confirmed that the first stage of cardinal direction selectivity is localized to dendrites of retinal GCs and so arguments supporting evidence in favor of the postsynaptic model were provided. DS mechanisms of fish retina were investigated more thoroughly only recently in the study Damjanović *et al.* (2015). As shown in Fig. 7 (results recorded in an ON DS GC) units were stimulated by narrow stripes, moving across gray stimulation area in preferred or null directions in the procedure composed of three steps. In the first two steps, single stripe moved in the preferred and null directions, respectively (top and middle panel of Fig. 7). In the final step of the procedure, DS units were stimulated by paired stripes that moved simultaneously in opposing directions, one of them passing stimulation area in the preferred, and the other one in the null direction (bottom panel of Fig. 7). It was shown that the cell response, evoked by the stripe coming from the preferred side of RF was inhibited by the stimulus coming from the opposite direction. Inhibitory effect mediated from the null direction was recorded while stimuli were approaching, and it ceased after stripes crossed each other in the center of the stimulation area. In the majority of units recorded (in total 52 cells were studied), inhibitory effect induced by the null-side

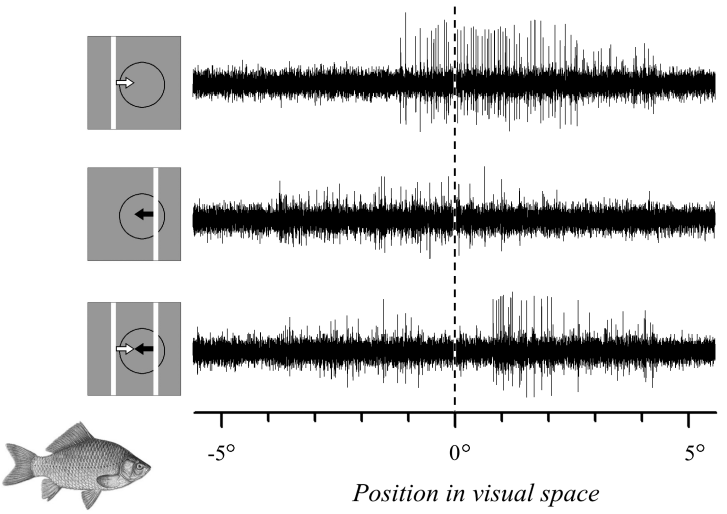


Fig. 7. Stimulation procedure with paired stripes moving in opposing directions. Results obtained in one ON DS GC of goldfish. DS unit was stimulated by white stripes, moving in either preferred or null directions across gray stimulation area, which occupies approximately $11 \times 11^\circ$ of the fish visual field. Stimuli: top panel — single stripe moving in the preferred direction; middle panel — single stripe moving in the null direction; bottom panel — paired stripes moving simultaneously in opposing directions. Opposing stimuli met in the center of the square stimulation area (marked by the vertical dashed line) and subsequently moved away from each other. Stimulation areas are schematically presented by gray square regions. Rounded area in the square represents the unit responsive receptive field. Responses of the unit are shown near corresponding stimuli. Width of stimuli was $30'$; velocity of stimulus movements was 5.5°/s. Orientation of fish relative to presented stimuli is demonstrated. One can see that the cell response, evoked by the stripe coming from the preferred side of RF was inhibited by the stimulus coming from the opposite direction. Detailed explanation in the text.

Source: Data from Damjanović *et al.* (2015).

stimulus was initiated in the RF periphery. As a rule, inhibitory influences sent from the RF periphery were spread across the entire central area of RF. Results of the study indicated that the inhibitory mechanism underlying direction selectivity in goldfish retina does not essentially differ from the analogical mechanism described in mammals. However, applied experimental procedure could not settle a question which of two circuitries underlie null-side inhibitory effects described in fish DS GCs — the one based on the single postsynaptic mechanism (Yonehara *et al.*, 2013) or the second based on coordinated pre- and postsynaptic processing (Euler *et al.*, 2002; Fried *et al.*, 2002, 2005; Poznanski, 2005, 2010).

5. Classification and Spatial Properties of Goldfish Direction-Selective Tectal Neurons

In addition to the retinal DS GCs described above, other types of DS units were recorded in the tectum. Some features of the responses of these latter units suggested that the recordings were made from tectal neurons (TNs). As shown already in the study of Maximova *et al.* (1971), while the responses of the DS GCs are recorded from

their axon terminals in the tectal superficial layers, the responses of the putative tectal DS neurons are usually recorded from their cell bodies in the deep layers of TO. However, in more recent studies (Maximov *et al.*, 2005a, 2005b; Maximova *et al.*, 2012) it was revealed that responses of the TNs with direction-selective properties can be recorded from the tectal superficial layers as well, mainly from the sublaminae located above the zone of DS GC projections. The main differences in the responses of putative tectal and retinal DS units are illustrated in Fig. 8. The OFF-DS unit of presumably retinal origin, the response of which is presented in the figure, preferred the caudo-rostral direction of the moving stimuli. It responded prominently to the leading edge of black broad stripe moving over the neutral gray background within the RF and did not respond to the trailing edge of the stimulus [Fig. 8(a), upper trace]. On the other hand, the putative tectal DS unit, which preferred the dorso-ventral direction, responded to the moving edges of any sign of contrast (ON-OFF type of unit). This unit had a large RF, as can be judged by the duration of the spike train [Fig. 8(a), lower trace]. In general, DS units of tectal origin recorded in a number of our studies (Maximova *et al.*, 1971, 2012; Maximov *et al.*, 2005a, 2005b) were characterized by very large sizes of their RFs. Figure 8(b) shows the differences between the two types of DS units in the form of individual spikes. In extracellular recordings, arriving from retina axonal spikes usually have triphasic waveform with a positive deflection before the main negative wave [Fig. 8(b), upper trace]; whereas the spikes that are recorded in the vicinity of the cell body of the TNs are biphasic and lack such a deflection [Fig. 8(b), lower trace]. In general, in our experiments the

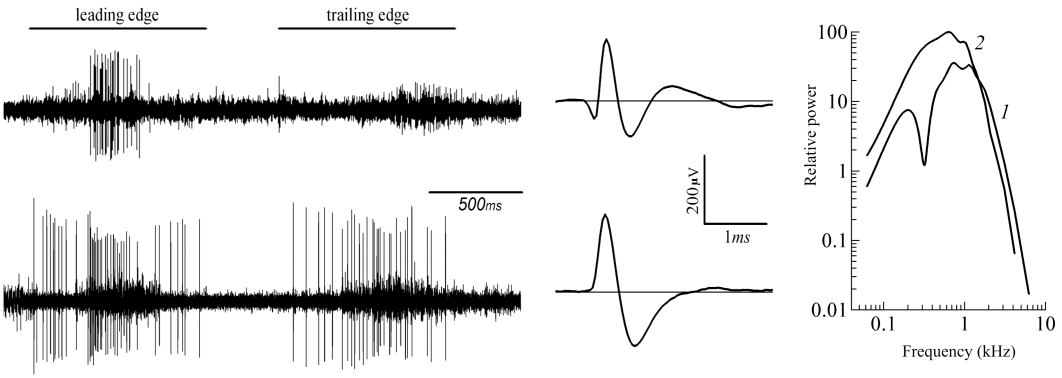


Fig. 8. Responses of two goldfish DS units of different origin. (a) Firing patterns of two DS units in response to movement of leading and trailing edges of the broad stripe ("edge stimulus"). The first unit (upper trace) is a putative retinal OFF-type DS GC stimulated by caudo-rostral movement of a broad black stripe on a neutral gray background with a speed of 11°/s, and the second (lower trace), a tectal DS neuron stimulated by downward movement of a broad white stripe on a black background with the same speed. (b) Averaged spike forms for retinal DS GCs (upper trace $N = 42$), and tectal DS neurons (lower trace $N = 61$) shown in expanded time scale (negativity upward). (c) Power spectra for spikes of DS GC (1) and tectal DS neuron (2).

Source: Data from Maximov *et al.* (2005b) and Maximova *et al.* (2012).

biphasic spikes had a longer duration and, consequently, a low-frequency power spectrum, while arriving triphasic spikes of the retinal GCs were characterized by a high-frequency spectrum [Fig. 8(c)]. As to features of spike trains recorded in the retinal and tectal DS units, the arriving DS GC spikes were as a rule approximately equal in amplitude, whereas the amplitude of the spikes generated in the DS neurons decreased substantially as spike rate increased [Fig. 8(a)].

From all of the above-mentioned one can conclude that contrary to the DS GCs which are characterized by small RFs and use separate ON and OFF channels, DS TNs have extra-large RFs and are characterized by ON-OFF type responses. The latter indicates the convergence of both types (ON and OFF) of DS GCs as excitatory inputs to DS TNs. However, the results of our recent experiments indicated that the fish retino-tectal DS mechanisms need a more accurate explanation.

A thorough classification of the tectal DS neurons according to their preferred directions was implemented only recently. It was shown that in the goldfish, DS neurons of the presumably tectal origin are characterized by four preferable directions, while the retinal DS GCs have only three. Three types of DS TNs that have putative inputs from the corresponding DS GC types prefer practically the same directions as those already selected on the retinal level. Complementary to them, the fourth DS TN type with the rostro-caudal preference (lacking in the retina) has been found. A histogram showing the distribution of preferred directions in 70 recently recorded tectal DS neurons is shown in Fig. 9(b). The interpretation of the retino-tectal DS mechanism is additionally complicated by the fact that the DS TNs form two populations that are settled at different depths of the tectum. As mentioned above, the responses of tectal DS neurons were mainly recorded from the deep tectal layers, and sometimes — from the superficial retino-recipient layers of the tectum. It was shown that three types of DS neurons that preferred the directions compatible to those selected by the retinal DS GCs were presented in both tectal DS populations, while among the superficial DS neurons those with rostro-caudal preferred direction

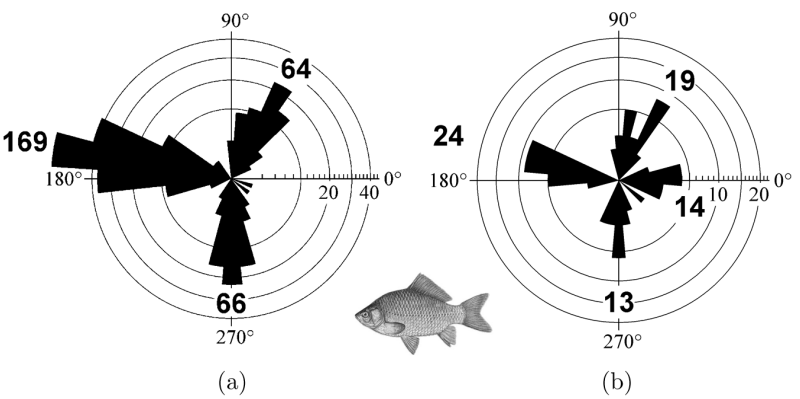


Fig. 9. Histograms of preferred directions for retinal DS GCs and tectal DS neurons represented in polar coordinates. (a) Distribution of preferred directions calculated in 299 DS GCs. (b) Distribution of preferred directions calculated in 70 tectal DS neurons. One can see that the fourth, rostro-caudal preferred direction (lacking in the retina) emerged among tectal DS units. Detailed explanation in the text.

were absent. DS neurons of the tectal origin were identified also in the zebrafish in a number of electrophysiological studies (Grama & Engert, 2012; Gabriel *et al.*, 2012; Kassing *et al.*, 2013). As a rule, cell bodies of the zebrafish DS neurons recorded with the calcium imaging techniques were located in the deep tectal layers (the periventricular zone). The prevalence of neurons with relatively strong input from the caudo-rostral retinal DS GCs was reported in all of the above-mentioned studies. However, recently, in more detailed calcium imaging study Hunter *et al.* (2013) identified two populations of tectal DS units in the zebrafish larvae. The major part of the recorded cells were located in the deep, periventricular zone of TO, while other DS units were identified in the tectal superficial layers located above the zone of DS GC projections. As in the goldfish, zebrafish DS neurons had four preferred directions, three of them compatible with those already selected on the retinal level. Similar to our findings, the authors identified the fourth population of DS tectal cells with the emergent rostro-caudal preference not explicitly present in any of the DS GC inputs. Moreover, the four types of DS neurons were recorded only in the deeper tectal layers as it is the case in the goldfish. In other words, the results of Hunter *et al.* (2013) were consistent with our recent findings, what, taking into account the similar DS circuitries revealed on the retinal level in two fish species (Maximov *et al.*, 2005a, 2005b; Nikolaou *et al.*, 2012), indicates that the retino-tectal DS systems of the goldfish and zebrafish do not essentially differ from each other. Finally, it should be emphasized that our recent data revealed remarkable spatial resolution in the goldfish DS TNs. Spatial resolution of the DS neurons was evaluated by means of the same procedure as in DS GCs. Some of the recorded DS neurons detected all applied drifting gratings, i.e., mean spike rates of their responses practically did not change with the increase in spatial frequencies of the stimuli (Fig. 10).

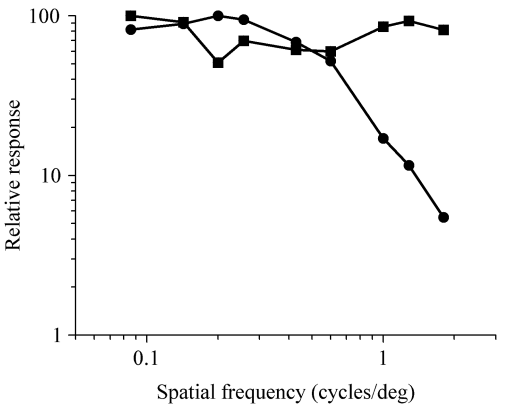


Fig. 10. Spatial properties of tectal DS neurons. Zero harmonic (mean spike rates of responses) recorded at different spatial frequencies of drifting gratings in a tectal DS neuron selective to the ventro-dorsal direction, stimulated by horizontal black gratings, drifting at the speed of 2,75°/s in an upward direction (rectangles) and an ON DS GC selective to the caudo-rostral direction, stimulated by vertical white gratings, drifting at the speed of 2,75°/s in the caudo-rostral direction (circles). One can see that the DS neuron maintained a practically unchanged level of the mean spike rate at high spatial frequencies, where the responses of the DS GC significantly decreased.

6. Summary and New Aspects of Research

Here, we briefly summarize the findings of our research. The properties of goldfish retinal DS GCs projecting to the tectum discussed above, namely, the relatively small RF sizes and high spatial resolution characterize these units as local motion detectors similar to the fast DS GCs of the mammalian retina projecting to the superior colliculus. This assumption can be supported by the fact that the goldfish DS units were shown to respond to a broad range of velocities of moving stimuli (from 2–30°/s) (Maximov *et al.*, 2005b), similarly as shown for fast DS GCs of the mammalian retina (see review of Vaney *et al.*, 2001). Direction selectivity in the fish DS GCs was shown to be produced by the null-side inhibition (Damjanović *et al.*, 2015), and in this respect these units also resemble the fast DS GCs of mammals (Fried *et al.*, 2002, 2005; Poznanski, 2005, 2010).

However, it is important to note that our experiments as well as study of Nikolaou *et al.* (2012) revealed some essential differences between fish and mammalian DS GCs. Both, the goldfish and zebrafish DS GCs are characterized by three preferred directions and use separate ON and OFF channels, while the mammalian retinal DS units are represented by four types of ON-OFF cells with the preferred directions separated by about 90° (Oyster & Barlow, 1967). Nevertheless, the fourth rostro-caudal preferred direction is present in the fish visual system, though not at the level of the retinal DS-cells, but among the DS neurons of the fish tectum. At least three types of the goldfish tectal DS neurons with similar preferred directions to those already existing on the retinal level could be considered as putative targets of the retinal DS GCs. These DS TNs, characterized by remarkable spatial resolution, seem to collect responses from ON- and OFF-DS GCs throughout the large segments of the visual scene. On the other hand, rostro-caudal DS TNs lacking evident excitatory DS inputs could have their direction selectivity generated solely on the tectal level using combined inputs from the ventro-dorsal and dorso-ventral retinal DS units. However, results of our recent studies testify that fish retino-tectal DS system requires more accurate interpretation. Still, it remains unclear how to interpret two populations of DS neurons settled at different depths of the goldfish and zebrafish tectum (goldfish — our newest data; zebrafish — data from Hunter *et al.*, 2013). Apparently, these two DS populations differ in the number of types of DS units characterized by different preferred directions. Both in the goldfish and zebrafish the deeper tectal layers include four types of DS neurons. On the other hand, among the superficial DS neurons, those with the rostro-caudal preferred direction are absent. Differences between two populations of DS TNs indicate that superficial and deep tectal DS units could be related to separate functional tasks. Accordingly, it remains to be clarified, if the DS TNs receive direct inputs from retinal DS GCs, or at least in one population of tectal DS neurons the responses are computed from non-DS retinal inputs using tectal asymmetric inhibition as suggested by Grama & Engert (2012). Working on zebrafish tectum, the authors suggested a model allowing the existence of a special type of tectal interneuron, which, similar to the retinal SACs responds to moving

stimuli in the null-direction and is asymmetrically connected to the DS tectal output neurons. The fact that the circuits underlying direction selectivity in the retina and visual brain areas can fundamentally differ was demonstrated in mammals. In contrast to the retinal DS GCs which receive asymmetric inhibition, directional responses in some cells of the primary visual cortex arise primarily from the facilitation of the excitatory inputs triggered by preferred motion. It was shown that these units gather excitatory inputs from the non-directional neurons in the cortex and/or lateral geniculate nucleus to create directional preferences (De Angelis *et al.*, 1995; Peterson *et al.*, 2004; Elstrott & Feller, 2009).

All of the discussed above indicates that all or some of the fish tectal DS neurons could be functionally independent from the retinal DS units. Functional organization of direction selectivity in the fish tectum will be the main topic in the future studies. For this purpose, interactions in the RF of tectal DS neurons will be investigated by the method already used for the DS GCs, i.e., stimulation with pairs of narrow stripes moving in opposite directions. In order to better understand the organization of the DS TN inputs, another experimental procedure will be additionally applied. In recent studies, it was shown that the goldfish retinal DS units being "color blind" are connected with all three chromatic cone types (Maximov *et al.*, 2014, 2015). All types of DS GCs were confirmed to receive inputs mainly through the long-wave cones with weak negative (opponent) contributions of the middle-wave and short-wave cones. Using a method of selective stimulation of different cone types (see Maximov *et al.*, 2015), we intend to test to what extent are the associations with different chromatic channels in two populations of the DS TNs consistent with the cone inputs of the DS GCs. As a whole, the planned experiments should give us additional information on the mechanisms underlying direction selectivity in the fish retino-tectal system.

Acknowledgments

Research on the physiology of the fish visual system has been carried out in our laboratory for more than 40 years. During this period, the chief of our group Dr. Vadim Maximov was the team leader whose scientific attitudes, as well as meticulous experiment planning and data analysis are behind all the research findings. The main aim of this review was to summarize the main results of the research related to the mechanisms of direction selectivity in the goldfish visual system. The author is grateful to Elena Maximova, Paul Maximov, Anna Kasparson, and Alexey Aliper for many helpful discussions and valuable comments and suggestions on the manuscript. Supported by the Russian Foundation for Basic Research (grant No. 13-04-00371).

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