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Ganglion Cells with Sustained Activity in the Fish Retina and Their Possible Function in Evaluation of Visual Scenes

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Background extracellular spike activity of single ganglion cells was recorded from axon terminals in the optic tectum of living immobilized fish. The sizes of the receptive fields of ON and OFF units with sustained responses (USR) amounted to 4–5° and were comparable with those of feature detectors. Generation of spike discharges by USR required contrast between the center and periphery of the receptive field. When there was no contrast, no spike activity appeared. The magnitude of the reaction was monotonically dependent on the level of this contrast. USR of both the ON and OFF types were connected with three types of cone (L, M, S). Both the center and periphery of the receptive field displayed color opponency, the center and periphery of the receptive field being opponent in terms of this characteristic. In other words, USR were double opponent and may thus take part in color discrimination. The simultaneous operation of feature detectors and ganglion cells with baseline activity separated into ON and OFF channels is represented retinotopically and may provide tectum opticum neurons with the visual scene information required for their function of controlling external attention.

Keywords: vision, *Carassius gibelio*, ganglion cells, extracellular reactions, receptive field, contrast sensitivity, tectum opticum, color vision.

Behavior in fish is largely determined by vision [1]. Innate visually controlled forms of behavior include phototaxis, optomotor reactions, prey-catching, and the defensive reflex (avoidance), and are seen in four-day-old young and persist into the adult state [2, 3]. The organization of all these diverse forms of behavior involves the tectum opticum (TO), which is the main primary visual center in fish [4]. Extirpation of the TO or defined TO neurons leads to loss or impairment of these behavioral reactions [5, 6]. TO neurons work with the results of primary processing of images of the surrounding world formed by the optics of the eye on the photoreceptor matrix. This processing is run in parallel by ensembles of bipolar, horizontal, and amacrine cells and is delivered via ganglion cell (GC) dendrites, GC being the output cells of the retina. The fish retina contains about 20 morphofunctional types of GC, each of which forms specific connections between its dendrites and input neurons [7, 8]. The dendritic mosaic of GC of each type completely covers the whole of the retinal surface at the stratification level of the inner synaptic layer (ISL) of the retina, with virtually no overlap (tiling) [9–12]. Thus, this number of morphofunctional types of GC forms, correspondingly, about 20 different "descriptions" of the scene of the surrounding world. These "descriptions" in the form of GC spike reactions are delivered via the optic fibers to the 10 primary visual centers [13, 14]. In fish, 98% of GC axons run to the TO. Axons enter the rostral part of the contralateral TO and are distributed retinotopically, terminating at different levels of the retinorecipient layer (stratum fibrosum et griseum superficiale, SFGS), where they contact dendrites of intrinsic TO neurons [4, 8, 15–18].

Extracellular microelectrode recording from GC axon terminals in the TO of living fish demonstrated reactions

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from 13 different types of feature detector. These were the responses of six types of directionally selective GC, or movement direction detectors, along with two types of line orientation detectors (horizontal and vertical margins), detectors for small white and black spots, color-opponent GC (one of many types described in the retina), and ON- and OFF-type GC with labile background activity [19–22].

The terminals of GC detecting different image features form retinotopic maps of the feature concerned, each type at its own level. The mutual dispositions of individual sources of these retinal reactions relative to each other and intrinsic TO neurons have been evaluated [21]. The set of several maps of features (such as contrast between stimulus and background, its size, direction of movement, and orientation) stacked one on another constitute the retinotectal map of salient features (the saliency map). The TO is believed to use the map of salient features to select the main object visible in the field of vision (the pop-out stimulus) and switch attention to it [6, 23–28].

Observations of freely swimming (and partially immobilized) *Danio* fry (aged 4–12 days after fertilization) led to the concept that the reactions of all specialized GC feature detectors described above are utilized in behavior. In prey-catching behavior, these are small spot detectors and directionally selective GC. Objects smaller than 5° are interpreted as food and induce prey-catching behavior; objects larger than 10° induce avoidance reactions [2, 29]. The reactions of line orientation detectors (vertical and horizontal margins) are probably used in optomotor reactions (fish behavior in an optomotor drum – an experimental version of shoal behavior) [30–33].

For integral perception of a visual scene the animal needs more information than that on potential predators and food objects, which is supplied by feature detectors. Contextual illumination, the uniformity or nonuniformity of this illumination, its intensity, and its color are important environmental factors. This information cannot be represented by directionally sensitive GC, or line orientation detectors, as they operate essentially on the "all or nothing" principle over a wide range of illumination levels independently of the level of illumination, responding only to "their own" stimuli [22, 34–36]. Furthermore, feature detectors generally do not respond to overall changes in illumination.

Information on illumination can arrive in the TO from GC with some labile level of background activity. In some, activity increases gradually to increases in light and is inhibited on darkening, while other cells, conversely, show increases in the dark and are inhibited by light [21, 37].

The present study addresses the properties of OFF and ON units with sustained responses (USR) – receptive field (RF) structure, contrast sensitivity, and connections with different cone types – to answer the question of the presumptive functions of these GC.

Methods. The main study object was the Prussian carp (*Carassius gibelio*). Experiments were also carried out using common carp (*Cyprinus carpio*), common roach (*Rutilus rutilus*), and European perch (*Perca fluviatilis*). Experiments on eight common carp, 29 Prussian carp, four common roach, and two European perch are reported. Experiments were run in computerized apparatus of original design, allowing presentation of different visual stimuli and recording of spike reactions in different formats. Standard experimental procedures used for stimulation (measurement of RPP, contrast sensitivity, etc.) were formulated as program routines. The apparatus consisted of an AC amplifier (bandpass 0.1–3.5 kHz), an analog-to-digital converter (sampling frequency 25 kHz), and a system of three interconnected and synchronized computer modules. It has been described in detail in our previous reports [38–40]. Experimental results were recorded and processed offline using a database. During the experiment, spike patterns were displayed on an oscilloscope screen (C1-73) and played through a loudspeaker.

A fish immobilized with tubocurarine (0.3 mg/100 g body weight) was placed in a natural position in a Plexiglas aquarium and looked with its right eye through the transparent wall at the monitor screen (LG Flatron 775 FT) of the stimulating computer. The distance of the fish to the screen was about 30 cm. The fish was perfused with aerated water via the gills. The water level in the aquarium was kept constant at a level such that the eye was beneath the water, but the water did not enter the brain. A total of about 10 liters of water circulated in the experiment. Studies mostly addressed the lateral visual fields.

Access to the visual lobes of the tectum of the fish was from the left side of the skull, contralateral to the working eye; the parietal-occipital bone was removed and the fatty subcutaneous tissue was extracted and the meninges were dissected. Fish were handled in compliance with the Directive of the European Communities Council of November 24, 1986. The experimental procedures were approved by the Ethics Committee of the Institute of Information Transmission Problems, Russian Academy of Sciences (Protocol No. 1, of April 24, 2018).

Ganglion cell responses were recorded from their axon terminals in the retinorecipient layer – the stratum fibrosum et griseum superficiale (SFGS) of the TO with glass-insulated platinized microelectrodes made in the laboratory, with a platinum cap of diameter 3–5 μm, and impedance of 200–500 kΩ at a frequency of 1 kHz [41]. A micromanipulator (MP-225, Sutter Instrument) was used under a binocular microscope (Olympus SZ51) to bring the microelectrode to the region of interest on the tectal surface in accordance with the retinotopic projection [15]. The microelectrode was cautiously inserted until a unique stable stream was obtained, as assessed from uniform spike size significantly exceeding the noise level sounding on the loudspeaker. The depth of the reactions recorded was assessed relative to the surface of the TO in terms of the indications on the micromanipulator screen.

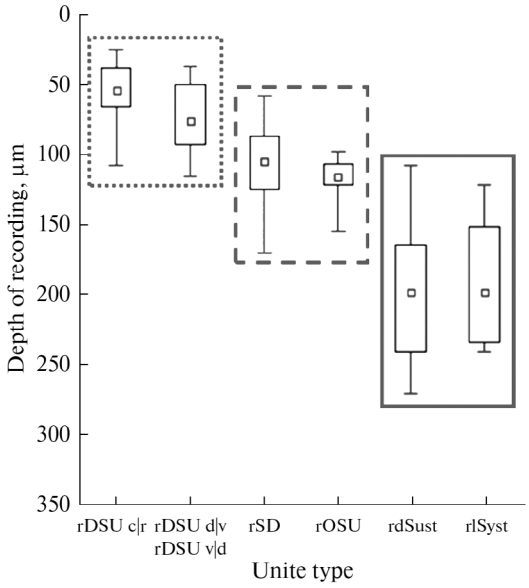

Fig. 1. Three clusters in the retinoreceptive layer of the TO, which were sites of extracellular recording of GC, i.e., detectors of various features, from their axon terminals. Kruskal–Wallis test, $p < 0.05$. Data are presented as median ± interquartile range. The rectangles outline three clusters resolved by statistically significant differences. Left – directionally selective GC; center – line orientation detectors and small spot detectors; right – GC with sustained responses (USR) of the ON and OFF types. Abbreviations: rDSU c|r, rDSU d|v, rDSU v|d – retinal directionally selective units of caudorostral (41 units), dorsoventral, and ventrodorsal preferred directions, respectively (total 25 units); rSD – retinal small spot detectors (29 units); rOSU – retinal orientationally selective units (15 units); rdSust and rlSust – OFF and on-type USR, respectively (45 and 13 units, respectively).

The typical sizes of retinal unit RF were generally less than 10°, so stimuli had to be moved across the whole screen surface (size 45° × 35°) during the experiments. The stimulation area was generally a square with sides of about 11°. Brightness in the remaining part of the screen was held constant. The experiments described in the present article used both achromatic and colored stimuli (this will be discussed in more detail below).

Measurement of receptive fields. The position and size of the RF (or, more precisely, the excitatory zone – the reactive receptive field) was assessed by the random checkerboard method. Small (1.5°) flashing spots (squares) were presented sequentially in pseudorandom order within the square stimulation area of 11° × 11° on the screen, and response magnitudes were recorded (as the number of spikes per unit time). As a rule, 7 × 7 = 49 stimulus positions were tested. In processing the data, the relationship between response magnitude and stimulus position in the stimulation zone was presented as two-dimensional Gaussians. Parameters were determined from the experimental data by computing the moments of distribution – mathematical expectation, dispersion, and covariance. The resulting mathematical expectations characterize the positions of the center of the found RF of the cell in the stimulation zone, while the dispersion and covariance characterized the size and shape of the excitatory region of the RF. The boundary of the excitatory zone of the RF was taken as an ellipse defined by the intersection of the calculated two-dimensional Gaussians with the plane $f = f_{max}/e$, where f_{max} is the maximum of the gaussian function, $e \approx 2.72$, i.e., the base of natural logarithms. The lengths of the major and minor axes of the ellipse are given by $2\sqrt{2}$ of the maximum and minimum mean square deviations computed for the Gaussian. The size of the excitatory zone of the RF was taken as the geometrical mean of the lengths of the axes of the ellipse. The processing results were presented as color maps.

Contrast sensitivity. A special programming tool was used for systematic measurement of contrast sensitivity. On the background of a brightness level specified by the experimenter, stimuli (moving boundaries or flashing spots) of different brightnesses were presented alternately in the center of the RF and plots of the relationship between the mean number of spikes in the GC volley and stimulus brightnesses were constructed [38]. For measurement of contrast sensitivity at the periphery of the RF, brightness was changed through the whole periphery (keeping the brightness at the center of the RF constant).

Results. *General properties*. The responses of units with sustained responses (USR) were recorded at depths of 190–200 μm from the surface, deeper than the six types of directionally sensitive GC, two types of orientationally selective units and the two types of spot detector (Fig. 1).

One of these was activated in the dark and was inhibited by light (OFF type), while others, conversely, were activated in the light and inhibited in the dark (ON type). As a rule, the overall activity of these and others was recorded simultaneously. By sound, i.e., pitch, the spikes of units with dark activity were clearly differentiated by being lower than the sound of units with light activity. Subjective assessment by hearing produced no doubts that background activity increasing on illumination was recorded deeper than dark activity, i.e., that the generator of this activity consisted of GC axon terminals, which are located slightly deeper than the generators of dark sustained responses. However, the results of measurements of the recording depth of ON- and OFF-type USR were in a single cluster (Fig. 1). Extraction of single (unitary) USR responses from the overall chorus of sustained activity requires some skill and our group is the first to achieve this. Indicators of the uniqueness of the stream (apart from assessment by hearing and consistency of spike amplitudes in the discharge) were the absence of spikes during refractory periods on recording of responses during the next sweep (Fig. 2).

Receptive fields of OFF- and ON-type units with sustained responses. USR react not only to changes in general illumination, but also to movement of the boundary or spot within the field of vision. They also respond to small flashing spots, of size about 1.5°. This allows their receptive fields or, more precisely, their central excitatory zones (reactive receptive fields) to be mapped using the standard checkerboard method (see Methods section) (Fig. 3).

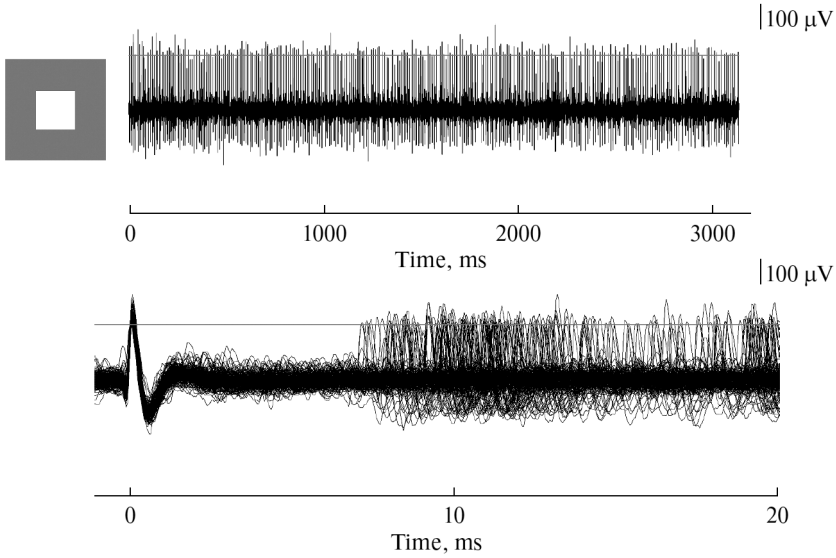

Fig. 2. Criteria for uniqueness of extracellular streams. Above – sustained spike activity in an ON-type USR showing the threshold (250 μV) for amplitude discrimination; below – recording of next-sweep activity (showing the absence of spikes during the refractory period). Left – stimulus configuration (the size of the white spot was 11°).

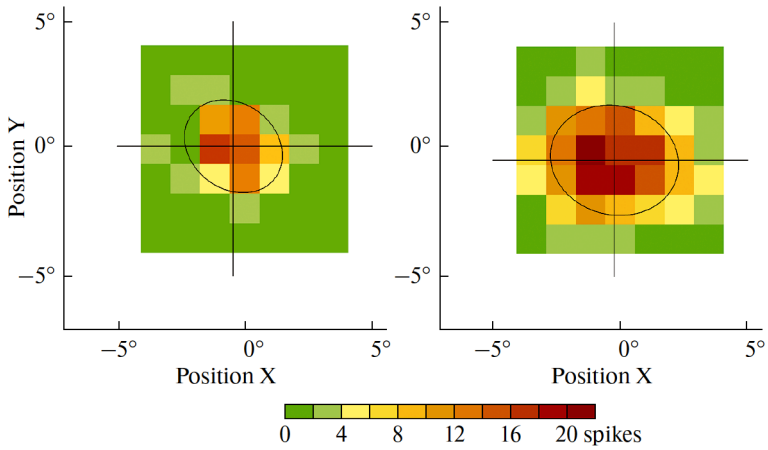

Fig. 3. Receptive fields of OFF- (left) and ON-type (right) USR mapped by the checkerboard method. Ellipses show the boundaries evaluated for the excitatory zones of receptive fields.

The RF of 112 OFF units were mapped with black spots on a white background, along with the RF of 77 ON units with white spots on a black background. The distribution of RF sizes is shown in Fig. 4.

Relationship between USR responses and the nature of illumination. The RF of most GC had central-peripheral opponent organization. Darkening or illumination of the periphery was generally linked with the magnitude of the central response of the GC, though in and of itself it did not elicit a cell response. A distinguishing feature of USR was that stimulation only of the periphery of the field (with the center unaltered) induced a clear reaction. Thus, ON-type USR reacted to illumination of the center of the RF and darkening of the periphery. OFF-type USR responded to darkening of the center of the RF and illumination of the periphery. An indispensable condition for excitation of the USR was the presence of contrast between the center and periphery of the RF (Fig. 5, *A*; Fig. 6, *A*). The most powerful sustained reactions of these and other cells (ON and OFF USR) arose when contrast between the center and periphery of their RF was greatest. This spike activity terminated (or declined dramatically) if the periphery of the RF became indistinguishable, in terms of contrast, from the center (Fig. 5, *B*; Fig. 6, *B*). Unexpected was the first observation that darkening of the whole of the visual field (monitor screen 45° × 35°) did not produce (or terminated) the OFF-type USR reaction. ON-type USR also produced no response to uniform illumination of the screen. This indicates that excitation processes at the center of the RF and inhibition from the periphery are so balanced that simulta-

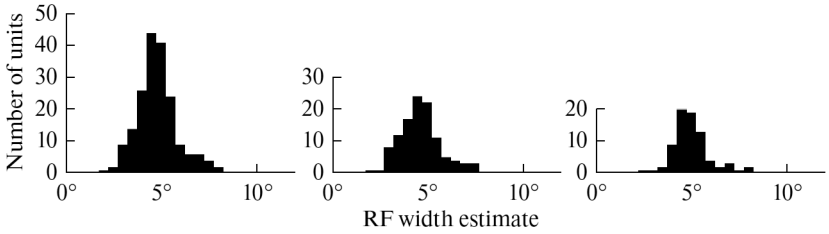

Fig. 4. Receptive field size distribution histograms for 189 USR. Sizes are shown as mean ± mean square deviation. Left: total set of 189 USR of both types (5.0 ± 1.13°); center – set of 112 dark USR (OFF-type) (4.8 ± 1.19°); right – set of 77 light (ON-type) USR (5.2 ± 0.99°).

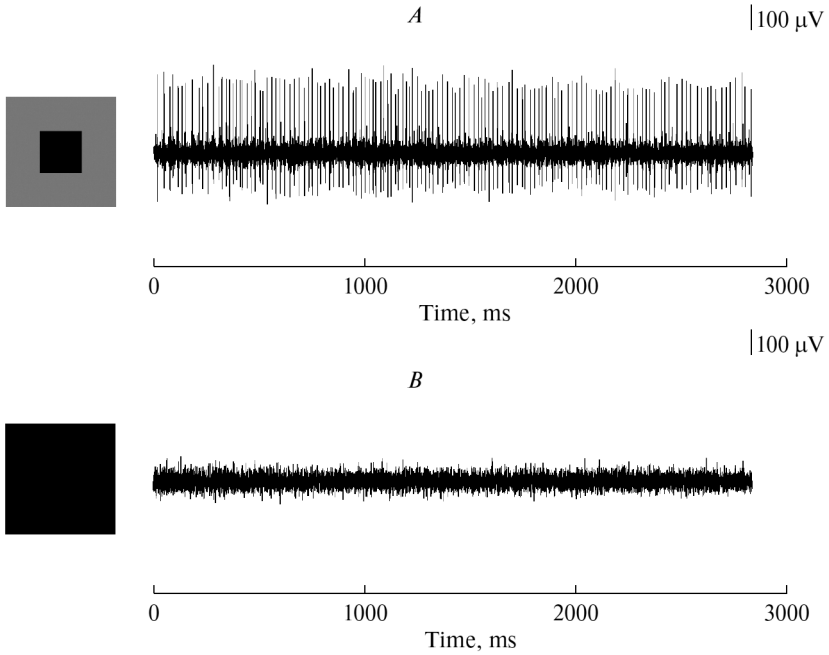

Fig. 5. Conditions for generation of OFF-type USR responses. *A*) Established spike reactions of OFF-type USR with the center of the RF dark and a lighter far periphery; *B*) complete inhibition of the response of this unit on darkening of the far periphery (absence of contrast between center and periphery). Left – stimulus configuration.

neous uniform stimulation of both parts of the RF does not lead to generation of a spike discharge (Fig. 5, *B*; Fig. 6, *B*).

Imposition of minimal contrast between the center of the RF and the periphery immediately elicited USR responses. The contrast sensitivity and dependence of the response on the levels of stimulus:background contrast at the center of the RF were measured in two ways: using a moving contrast boundary with the background unaltered or with a spot flashing at the center of the field, spot size being close to the size of the center of the RF.

The relationship between the magnitude of the response (number of spikes) and the brightness of the center and periphery of the RF was studied. Studies of 114 OFF-type USR and 60 ON-type USR were run to measure contrast sensitivity with changing brightness at the center of the RF and unaltered brightness at the periphery. Studies of 35 OFF-type USR and 23 ON-type USR were carried out using measurements in conditions of changes in the brightness of the periphery and unaltered brightness at the center of the RF. Figure 7 illustrates the results of one of these experiments using an OFF-type USR.

Sometimes, unique ON- and OFF-type USR reactions could be recorded with the electrode in a single position [21]. The positions of the RF in these units were essentially coincident. This may suggest that such a pair of GC converges on a single tectal neuron, which uses the ratio of the spike activity power levels of these units to create its own representation of the illumination in the corresponding area of space.

Four species of fish showed consistent cell characteristics, including RF size, the relationship between reaction power and stimulus intensity at the center of the RF, and the relationship between the response and the contrast between the periphery and center of the RF.

Color properties of ON- and OFF-type USR. Fish display good color vision in their behavior [42]. The retinas of

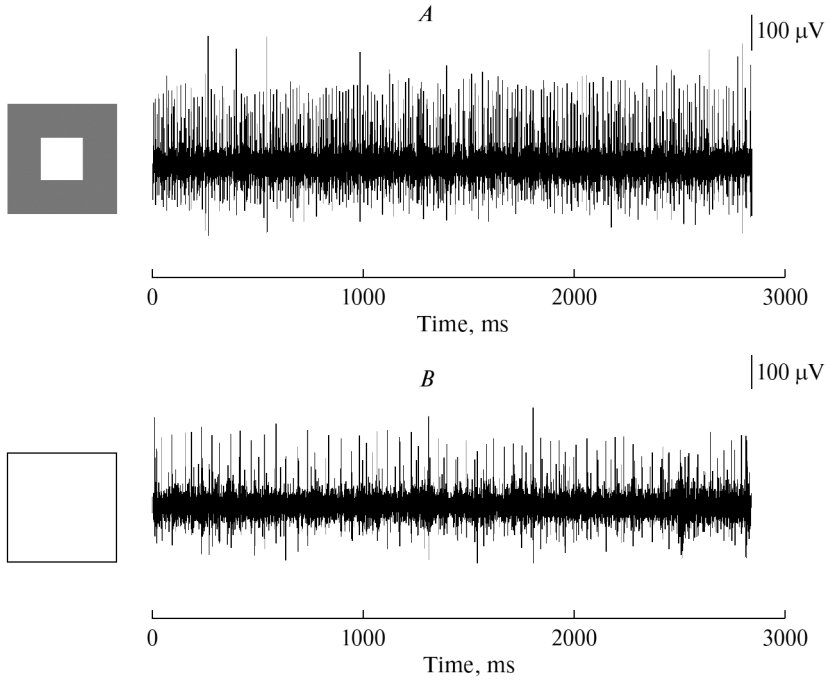

Fig. 6. Conditions for generation of ON-type effects responses. *A*) Established spike reactions of ON-type USR with the center of the RF light and a darker far periphery; *B*) significantly decreased spike activity on illumination of the far periphery of the RF (absence of contrast be center and periphery). Left – stimulus configuration.

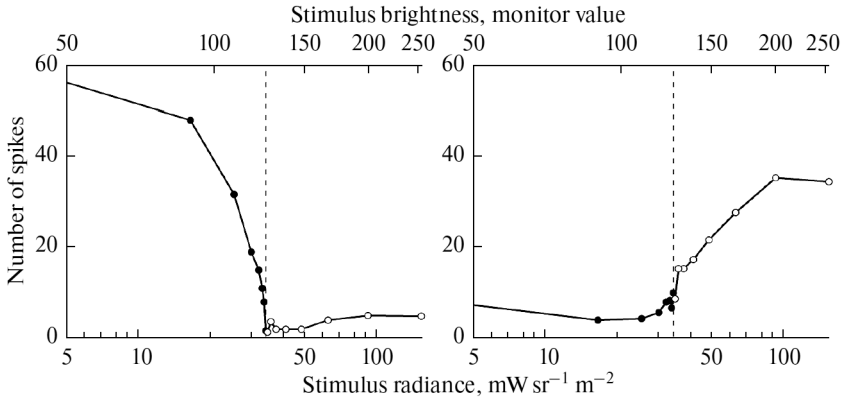

Fig. 7. Dependence of OFF-type USR responses on the contrast of the stimulus and background at the center of the RF and the contrast between the center and the surround. Left – response to flashing spot of size 11° at the center of the RF. The abscissa shows stimulus brightness (in monitor and energy units) and the ordinate shows the number of spikes in the cell response during flashes (700 msec). The vertical dotted line shows background brightness. Right – response to change in the brightness of the far surround (60° × 40°) in the absence of any change in the central area (gray spot of size 11°). The abscissa shows the brightness of the far surround (in monitor and energy units) and the ordinate shows the number of spikes in cell responses during flashes in the far surround (700 msec). The vertical dotted line shows the brightness of the central spot.

adult Prussian carp and common carp contain three types of cone, with peak sensitivities at 623, 535, and 454 nm [43–45]. The rich set of color-opponent cells in the retina (bipolar, horizontal, and ganglion cells) is evidence for the corresponding processing of signals from different types of cone cells [46–53]. At the same time, many types of ganglion cell projecting to the TO, which is connected with all three types of cone, have been shown not to have color-discriminating ability and to demonstrate the principle of univariance [54–56]. We sought to determine the color properties of USR. In the light of the hypothesis that they form information on the illumination of the environment, color discrimination would be very useful.

The spectral sensitivity curves of cones (L, M, and S – long-, medium-, and short-wavelength, respectively) overlap. As a result, excitation of specific types of cones

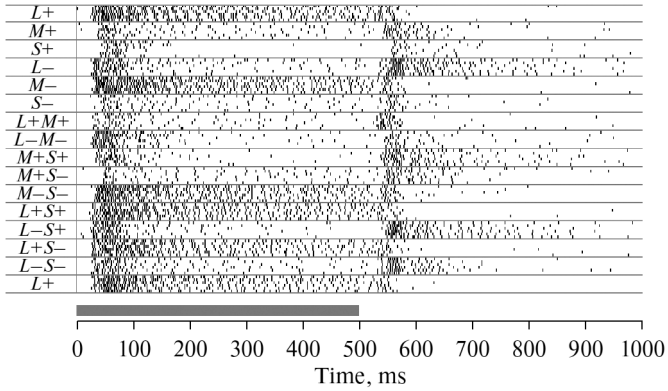

Fig. 8. Raster plots of the responses of OFF-type USR to selective color stimuli presented at the center of the RF with an unchanged gray periphery. The gray bar shows the duration of exposure to the stimulus. Each stimulus was presented six times. The colors of selective incremental (+) and decremental (–) stimuli are shown as letters corresponding to the types of cone excited by them. Attention is drawn to the paradoxical response to presentation of the L+ stimulus.

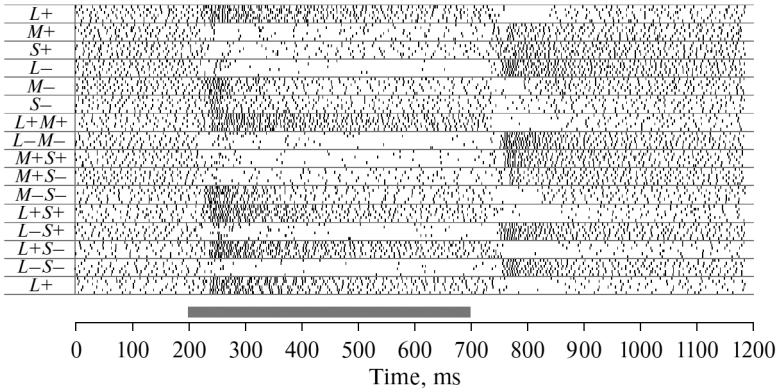

Fig. 9. Raster plots of the responses of ON-type USR to selective color stimuli presented at the center of the RF. Minor background activity is seen before stimulus presentation. For further details see caption to Fig. 8.

with saturated narrowband spectral stimuli from the dark is impossible. It is, however, possible to add or subtract one selected type of cone (or two types) to or from some overall level of excitation. Such incremental (+) and decremental (–) stimuli were determined for L, M, and S cones in the Prussian carp using the capabilities of the monitor (LG Flatron 775FT) [55, 56]. Studies of the color properties of USR using selective stimulation of each of the three types (L, M, and S) of cone were run on 176 OFF-type and 59 ON-type USR. (We studied the color properties of USR in only two species, Prussian carp and common carp, as the spectral sensitivity curves of cones in the common roach and European perch are not accurately known.)

Studies using these stimuli showed that both dark and light USR are connected with all three types of cone, though not identically. Three main types of connection were identified for dark USR: 1) sustained responses were evoked by (L+–, M–, S+) stimuli; 2) others responded to (L–, M+–, S+) stimuli; 3) a further group responded to (L+–, M+–, S+–) stimuli.

The fact that a decrease in the excitation of any type of cone (decremental stimuli) induced responses from OFF-type USR was expected and normal. However, the presence of an ON reaction to an increase in excitation in any of the channels (L, M, and S) in an OFF-type USR was paradoxical (Fig. 8).

Pairwise use of stimuli presented at the center of the RF and exciting different types of cone produced inhibitory and (in rare cases) augmentatory interactions between the signals from different types of cone. Responses to simultaneous excitation with the (L+M+) stimulus were always smaller than responses to each of the stimuli (L+ and M+) used separately. Even when there was no response to the M+ stimulus and the L+ stimulus produced a large response, the reaction to the (L+M+) stimulus was smaller than the reaction to L+ and could even disappear completely (Fig. 8). Taking account of these opponent interactions between inputs, it becomes possible to explain the fact that on achromatic stimulation, simultaneous increases in excitation of all three inputs (L+M+S+) do not induce responses from dark USR. Complex interactions between color channels (particularly opponent interactions between the L and M channels on incremental stimulation of these channels and

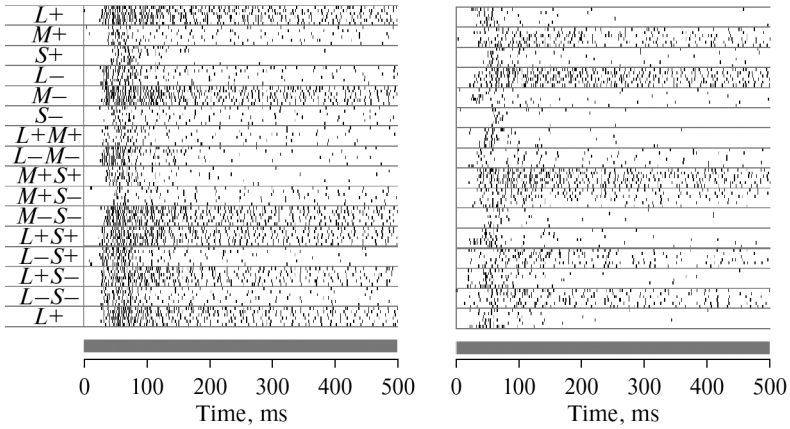

Fig. 10. Color opponency in the center and periphery of the RF of an OFF-type USR. Left – raster plots of the responses of a unit to selective color stimuli presented at the center of an unaltered periphery. Right – raster plots of responses of the unit to selective changes in color of the whole of the periphery with an unaltered center. For details see caption to Fig. 8.

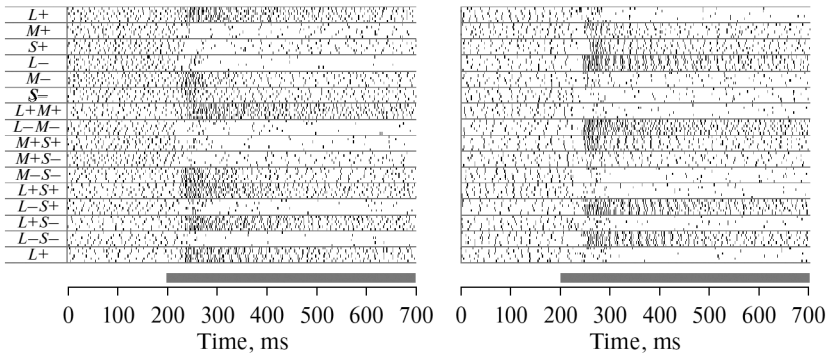

Fig. 11. Color opponency at the center and periphery of the RF of an ON-type USR. Left – raster plots of the responses of the unit to selective color stimuli activated at the center of the RF with an unaltered periphery. Right – raster plots of the responses of the unit to selective changes in the color of the whole periphery with an unaltered center. For further details see caption to Fig. 8.

augmentation with decremental stimulation) are impossible in unistratified OFF GC.

Light USR are also diverse in terms of the relationship between the magnitude of the reaction and selective excitation of L, M, and S cones. This is usually a response to the incremental stimulus for L and the decrement stimuli for M and S cones (L+, M–, S–) (Fig. 9). A response by L cones to the decremental stimulus was also sometimes noted. The occurrence of a quite marked response from ON-type USR to a decrease in excitation in each of the three cone types (L, M, S) remained paradoxical (Fig. 9).

Taking account of these opponent interactions between inputs helps explain the fact that simultaneous increases in excitation of all three types (L+, M+, S+) occurring with achromatic stimuli do not induce any response from dark USR, while decreases in excitation in all three cone types (L, M, S) did not induce any reaction from ON-type USR (some ON-type USR showed decreases in sustained responses in the absence of contrast between the center and periphery of the RF). On achromatic stimulation, dark and light USR operate as OFF and ON units (respectively) and have been presented in our earlier work as ganglion cells unistratified in the inner synaptic layer (ISL) of the retina and receiving input signals – dark from the OFF type and light from the ON type of bipolar cells in the corresponding layers of the ISL. The complex interactions between color channels in reactive USR seen in the present study complicates this interpretation [57].

The existence of color opponency and interactions between light channels found in reactions in the center of the RF of ON and OFF USR suggests that these GCmay have a role in color discrimination.

Opponency of the center and periphery. As already noted, homogeneous illumination (or darkness) of a large part of the screen inhibits spontaneous spike activity in both dark and light USR. Activation of the same color stimuli used for studies of the central part of the RF led to recovery of sustained activity in the whole of the periphery of the RF. This response, induced by stimulation of the periphery of the RF, is opponent in relation to that induced by these stimuli in the center. This is clearly apparent in Fig. 10.

The column at left shows raster traces of a dark USR (the same as that in Fig. 8), while the column at right shows the reactions of the same unit to excitation of the periphery

of its RF using the same stimuli. We see an analogous picture in Fig. 11, which shows the response of a light USR to excitation of the center and periphery of its RF. In this light USR (the same one as in Fig. 9), homogenous illumination did not completely inhibit sustained activity. Presentation of stimulus (L+) at the center of the RF induced an increase in the level of this activity, while at the periphery of the RF it produced significant inhibition. These contradictory (opponent) effects were seen for all stimuli, without exception. Thus, ON- and OFF-type USR were double opponent color cells.

Our data indicate that the opponent influence of the distant surround on USR responses is mediated with involvement of horizontal cells. The fish retina includes three types of cone horizontal cells. Horizontal cells of each type are largely connected with one cone type. These horizontal cells, connected into independent electrical syncytia by gap junctions, transmit the cone excitation signal over large distances. Feedback from horizontal cells to cones mediates the opponency of the center and periphery of the RF of GC [58–60].

Discussion. We have regularly recorded four types of USR of the ON and OFF types deep in the retinorecipient layer of the TO in fish. The characteristics of these cells, such as RF size, the relationship between response power and stimulus intensity at the center of the RF, and the relationship between the reaction and contrast between the periphery and center of the R_f, were completely coincident. In many ways, these units were apparent as positive and negative.

USR have been noted previously in the TO in other fish species [19, 20]. Sustained activity in the deep layers of the TO increasing on darkening has also been described in the frog *Rana pipiens* [61]. GC of two types with sustained responses (maintained activity) with analogous properties have been described in the mouse retina. These are alpha-OFF and alpha-ON GC. It is not known where these GC project or to which primary visual cells, as studies were run on isolated retinas [62, 63].

Dark and light USR in fish on achromatic stimulation are apparent as OFF and ON units (respectively) and we have also presented them (as in mice) as GC unistratified in the OFF and ON subplates of the ISL of the retina, which receives input signals, dark from OFF-type bipolar cells and light from ON-type bipolar cells, in the corresponding strata of the ISL. However, the paradoxical properties affecting the nature of these connections of GC with different cone types seen in the present studies contradict this view. An empirical model of the organization of the connectomes of USR has been proposed [57]. These are bistratified GC, excitation of which is transmitted from ON- and OFF-type bipolar cells, each of which has connections with all three cone types via different types of synapses (ionotropic and metabotropic). The question of the morphological substrate of USR of both types cannot be solved experimentally using our method and requires further study.

It is interesting to note that color-coding ON units in frogs projecting to the nucleus of Bellonci have also been found to show a paradoxical reaction to a decrease in light on insertion of a blue filter in the stimulating beam of white light [64]. This is reminiscent of the response of Prussian carp ON-type USR to the decremental stimulus (M–), which decreases the excitation of mid-wavelength-sensitive cones.

One certain point is that dark and light USR are double opponent GC in relation to color. The existence of neurons of this type in any part of the visual system is a sign of the existence of color vision in animals [65].

The USR studied here differed from the color-opponent units of the R/G type projecting to the TO in fish which we have described previously [66]. These latter are encountered extremely rarely at the same level of the SFGS as spot detectors and line orientation detectors and have no sustained responses. USR form a clearly sounding powerful signal in the depth of the SFGS and are subdivided into ON and OFF types. We have previously suggested that the major color information from the retina in fish arrives not in the TO but in some (unknown to us) specialized nucleus – an analog of the nucleus of Bellonci in frogs [64]. We now see that the TO in fish receives color information from three types of double opponent GC projecting to different sublayers of the SFGS.

In one microelectrode track inserted normal to the TO surface, the RF of sequentially recorded units of different types completely or partially overlapped and were within an area of (5°), i.e., they transmit signals from virtually the same photoreceptor area [21].

The principles of intraretinal image processing are universal and are largely similar in different animals both evolutionarily (fish, amphibia, reptiles, birds, mammals) and ecologically (carnivores and herbivores, aquatic and terrestrial). GC detecting features of visible objects such as size, orientation, movement direction and speed, approach, recession, color, and contrast with background have been described in the retinas of various fish species, turtles, mice, and rabbits [12, 15, 19, 34, 67–74]. It is logical to conclude that detection of these image features provides the grounds for the recognition of visible objects. USR send information relating to uneven illumination and changes in its intensity and color, while feature detectors send information on size, shape, and direction and speed of movement on this background.

The TO is the main primary visual center in fish and has complete information on the surrounding visible environment. This is where the map of salient features is generated and related to the body map. The main object of attention in the field of vision is extracted by neurons in the TO and premotor nuclei and the type of behavioral response is selected.

Conclusions

1. The properties of light and dark units with sustained responses (USR) projecting to the TO in fish were studied. High contrast sensitivity was found, along with a monotonic (within certain limits) dependence of spike activity on the intensity of illumination at the center of the field when contrasting with the periphery.

2. The size of the RF of USR averaged 5°, which is comparable with that of feature detectors.

3. Both ON- and OFF-type USR are connected with the three types of cone.

4. The RF of USR have double opponency in terms of color structure.

5. The existence of a layer of the projections of double color-opponent GC in the TO is evidence for the existence of color discrimination at the level of the TO.

6. The retinotopically represented simultaneous operation of feature detectors and USR with these properties may provide TO neurons with the rich information required on the visual field.

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