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Cardinal difference between the orientation-selective retinal ganglion cells projecting to the fish tectum and the orientation-selective complex cells of the mammalian striate cortex

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

Institute for Information Transmission Problems Russian Academy of Sciences Bolshoi Karetny 19, 127994 Moscow, Russia
**damjanov@iitp.ru*

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Responses from two types of orientation-selective units of retinal origin were recorded extracellularly from their axon terminals in the medial sublaminae of tectal retinorecipient layer of immobilized cyprinid fish *Carassius gibelio*. Excitatory and inhibitory interactions in the receptive field were analyzed with two narrow stripes of optimal orientation flashing synchronously, one in the center and the other in different parts of the periphery. The general pattern of results was that the influence of the remote peripheral stripe was inhibitory, irrespective of the polarity of each stripe (light or dark). In this regard, the orientation-selective ganglion cells of the fish retina differ from the classical orientation-selective complex cells of the mammalian cortex, where the remote paired stripes of the opposite polarity (one light and one dark) interact in a facilitatory fashion. The consequence of these differences may be a weaker lateral inhibition in the latter case in response to stimulation by periodic gratings, which may contribute to a better spatial frequency tuning in the visual cortex.

Keywords: Carassius gibelio; tectum opticum; orientation selectivity; receptive field; inhibitory surround.

1. Introduction

Strong orientation selectivity first emerges in the retina, where two distinct types of orientation-selective ganglion cells (OS GCs) selective to vertical and horizontal edges were described (Levick, 1967). However, physiological properties of these cells have been studied far too insufficiently, with their mechanisms just starting to be attended to (Venkataramani & Taylor, 2010), and the destination of these units in the retina still remaining unknown. Besides this, orientation selectivity is known as one of the key attributes of visual processing performed by the mammalian primary visual cortex (Hubel & Wiesel, 1962), where corresponding cells are selective for all possible orientations and thus, seem to be organized independent of the retinal OS GCs. Comprehensive studies of physiological properties of the orientation-selective cortical cells have greatly contributed to the current understanding of their place in

the functional architecture of the visual cortex and their role in visual perception (Ng *et al.*, 2007). Comparison of the stimulus response properties of orientation-selective cells in the retina and in the visual cortex could make important contributions to a detailed understanding of their mechanisms and their functional roles.

Properties of the OS GCs in the fish retina have been studied in more detail than in mammals. Although responses of the OS GCs sensitive to moving or stationary edges and lines of certain orientation can be investigated when recording from the isolated fish retina (Macy, 1981; Bilotta & Abramov, 1989), it is methodically easier to record responses of the OS GCs extracellularly from their axon terminals in the medial sublamina of tectal retinorecipient layer of immobilized fish. With this method, OS GCs were investigated in pike and goldfish (Zenkin & Pigarev, 1969, 1970), in some marine fish (Maximova *et al.*, 1971), in trout (Galand & Liège, 1975), in crucian carp and common carp (Maximova & Maximov, 1981; Maximova, 1999) and in Japanese dace (Kawasaki & Aoki, 1983). A detailed classification of the OS GCs and investigation of the interaction of signals within their receptive field (RF) in the Carassius gibelio were made in recent studies (Maximov *et al.*, 2009; Damjanović *et al.*, 2009b). It was shown that OS GCs comprised two physiological types that differ in preferred orientations close to vertical and horizontal. These types of OS GCs are known as detectors of vertical and horizontal edges, respectively. In other properties, the two types of the OS GCs did not differ from each other. Both types of the OS GCs were not selective to the sign of stimulus contrast, i.e., have ON-OFF nature, equally well responding to light stripes on a dark background and dark stripes on a light background. In this respect, OS GCs in the fish retina differ from those in the rabbit, where a preponderance of the OFF-type OS-GCs was observed (Levick, 1967; Caldwell *et al.*, 1978; Venkataramani & Taylor, 2010). By this feature, they are more like classical complex cells of the mammalian primary visual cortex (Hubel, 1988).

The responsive receptive field (RRF) of the OS GCs, i.e., central responsive area of the receptive field (RF), mapped by means of contrast edges moving across the RF or stationary stripes flashing in different parts of the RF, had a width between 3 and 6 angular degrees. Stimulation outside the RRF, causing no response in itself, nevertheless affects the behavior of the cells. In particular, an investigation using pairs of stationary stripes of optimal orientation that flashed synchronously at different distances from each other revealed mutual inhibition (Damjanović *et al.*, 2009b). In the experiments, the stripes were of the same sign of contrast relative to the background (both of them light or both dark). At that, the zone of inhibition, on the one hand, extended far beyond the RRF. So that the remote stripe outside the RRF had an inhibitory effect on the stripe presented within the RRF. On the other hand, mutual inhibition was also apparent within the RRF, when a response to two stripes, both lying in the RRF area, may be less than responses to stimulation by any of them alone. This result could be explained by assuming that the RF of the OS GC in fish was functionally divided into subunits sensitive to the appropriately oriented stimuli, that these subunits were subject to the inhibitory influence of neighboring subunits,

and that their output signals were subsequently summed nonlinearly. This scheme was implemented as a one-dimensional computer model (Maximov, 2010). One implication of the model was that the stripes of opposite sign of contrast (not used in the physiological experiment) also interacted in an inhibitory fashion.

The same experimental procedure with paired stripes was initially applied to complex cells in the cat's striate cortex (Movshon *et al.*, 1978). If both stripes were of the same polarity (both light or dark), the complex cells were shown to respond to the paired stimuli less well as compared to either of the stripes, unless the stripes are closely spaced (separated by less than about one quarter of the width of the RF). If the stripes are of the opposite polarity (one light and one dark), the opposite situation occurs: closely spaced stripes cancelled each other, while paired stimuli of larger separation were much more effective. In other words, remote paired stripes of the opposite polarity interacted always in a facilitatory fashion. Striate complex cells with properties similar to that described by Movshon *et al.* were also recorded in a more recent study (Finn & Ferster, 2007). The question arises: what would be the response pattern of the fish OS GCs stimulated by paired stripes of opposite polarity? The present study was undertaken in order to check whether the stimulation of the fish OS GCs with paired stimuli of different sign of contrast will evoke facilitation, shown in the classical complex cells of the mammalian striate cortex, or it will demonstrate an inhibitory interaction, as in the computer model of the fish OS GCs.

2. Materials and Methods

2.1. *Experimental animals*

The data were collected from 24 cyprinid fishes *Carassius gibelio* (Bloch, 1782), which varied between 10 cm and 15 cm in standard body length (with weight from 35 g to 100 g). The fish were acquired from local suppliers (Moscow region) and maintained for several months in aerated fresh water aquaria at room temperature and natural daylight regime.

For electrophysiological experiments an immobilized fish was placed in a Plexiglas tank and fixed in natural position with perfusion of aerated water through its gills. The water level in the tank was maintained such that the eyes of the fish were under water but water was not poured into the brain. The fish looked on the monitor screen with its right eye through the transparent tank wall. Visual responses were recorded from a contralateral lobe of the tectum opticum. Surgical procedure was described in detail elsewhere (Damjanović *et al.*, 2009a).

2.2. *Visual stimulation*

Visual stimuli were presented to the fish on the computer-controlled 17″ CRT monitor LG Flatron 775FT from a distance of about 30 cm. From this distance, the screen occupied $43 \times 32^\circ$ of the fish visual field. To stimulate detectors of

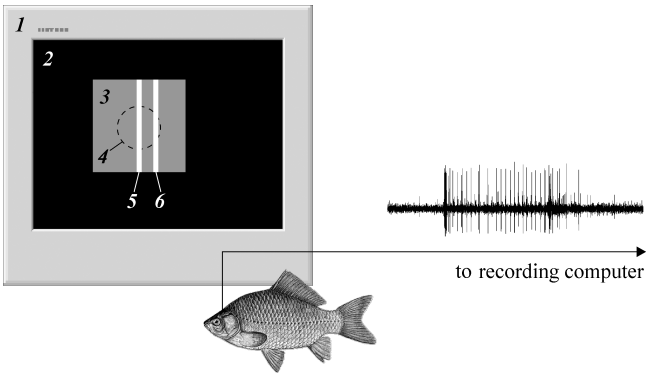

Fig. 1. A schematic view of the experimental paradigm. The appearance of the visual field in case, when two white stripes are presented on the gray background in black far surround: (1) stimulating monitor; (2) monitor screen; (3) stimulation area; (4) location of the RRF of the recorded unit; (5)−(6) central and peripheral stripe, respectively.

oriented lines, vertical or horizontal stripes were presented on the screen within a square area of stimulation with angular dimensions of $11 \times 11^{\circ}$. The stimulation area could be placed at arbitrary locations of the screen and was usually placed so that the receptive field of the recorded unit was located in its centre (Fig. 1).

Detectors of oriented lines in fish respond mainly to stripes of optimal orientation switching on and off, if their brightness changes mainly for the long-wavelength cones. Stripes contrasting to other classes of cones cause smaller and less unequivocal responses (Gačić *et al.*, 2009). Therefore, for definiteness, we varied the intensity of the stimuli only in respect of the long-wavelength cones. To do this, some gray colour of the stimulation area was chosen as a background, identical in all experiments. Its effective radiance for the long-wavelength cones was set at $14.2\,\mathrm{mW\ m^{-2}\,sr^{-1}}$. For stimulation by stripes, this background was replaced within the presented stripe by a combination of luminescence of three monitor phosphors, which differed in brightness from the background only "from the point of view" of long-wavelength cones and were similar in terms of medium- and short-wavelength ones. These differences could be either in the direction of increasing brightness (light stripes) or decreasing brightness (dark stripes). In both cases, the effective radiance differed by a factor of 1.6 from the background. Constant luminosity was maintained for the rest of the monitor screen outside the stimulation area. Colour of the rest of the screen was set neutral gray. Its brightness may vary from experiment to experiment, but kept constant during one experiment.

2.3. *Data acquisition*

Responses of OS GCs were recorded extracellularly from their axonal terminals in the tectal retinorecipient layer, beneath the superficial sublaminae of direction-selective units, using low impedance ($200 - 500\,\mathrm{K\Omega}$) recording electrodes made from metal-filled micropipette and tipped with a platinum cap of $2 - 10\,\mu\mathrm{m}$ in diameter (Gesteland *et al.*, 1959). The microelectrode was guided to a necessary tectal area under

visual control by means of a micromanipulator according to the retinotopic projection (Jacobson & Gaze, 1964). Experimental setup, used for amplifying, digitizing, storing and processing of the OS GC records, containing AC preamplifier (band pass 100−3.5 kHz), A/D converter (25 kHz sampling rate) and a system of three mutually connected and synchronized computer modules was described in detail elsewhere (Maximov *et al.*, 2005; Damjanović *et al.*, 2009a; Maximov & Maximov, 2010).

2.4. *Unit classification and RF characterization*

When a good orientation-selective unit was isolated and an approximate position of its RF was found, the first step was always to measure its polar diagram with contrast edges moving in 24 different directions across the RF. This confirmed the type of recorded unit and specified the size and location of its RF. The next step was to measure the RF by single stripes (horizontal ones for detectors of horizontal lines and vertical ones for detector of vertical lines) flashing in different parts of the presentation area in a quasi-random order. If the position and size of the RF, as measured by moving edges and flashing stripes, gave consistent results, a study of lateral interaction was started by means of special experimental procedure.

2.5. *Two-stripe interaction tool*

The experimental method used to reveal center/surround interaction inside the OS GC RF consisted of the stimulation of the unit by two stationary stripes of preferred orientation flashing simultaneously. In this method, the reference stimulus was always a light or dark stripe flashed in the center of the RF. The place and the brightness polarity (light or dark) of the second, peripheral stripe were quasi-randomly varied over different locations. The polarity of the central stripe, the width of stripes, their separation, the number of peripheral locations, and the time delay between separate trials were arguments of the corresponding automatic procedure. The procedure began with stimulation by the central stripe alone, followed with a series of paired presentations, and ended with the stimulation by the central stripe again, to ascertain the stability of the recording. The number of spikes in response to the flashes was counted during the first 500 ms after the onset of the stimuli. The responses for each configuration of the stimuli were averaged over six trials. The nature and magnitude of the effects of lateral stripes were estimated by the difference between mean number of spikes in response to stimulation by two stripes and mean number of spikes in response to reference stimulus alone. When the value of this difference was negative, the influence from the second stimulus was considered as "inhibitory". In the opposite case, the effect of the peripheral stripe was considered "excitatory".

3. Results

Four different combinations of paired stimuli were used in the present study of the influence of the surround by paired stripes: both stripes light, central light and

peripheral dark, central dark and peripheral light and both of them dark. The whole set of experimental data contained 184 of such series obtained in single unit recordings from 43 OS GCs, comprising 27 detectors of horizontal lines and 16 detectors of vertical lines. For each series, independent histogram was calculated, showing the dependence of the unit response on the position of peripheral stimulus. Results were mapped considering the position of the second peripheral stripe. Bars in the histograms represented the difference between the number of spikes in response to stimulation by two stripes and the number of spikes in response to the reference stimulus alone. All histograms proved to be quite diverse, which can be attributed to individual differences in the recorded units, to a different strength of inhibitory processes in the retina and, may be, to a physiological state of the fish. In addition, the form of histograms depends on the method of stimulation: the width of the stimulating stripes, the location of the reference stripe within the RRF etc. Nevertheless, in all this array of data, the following pattern could be seen. When the peripheral stimulus flashed near the central stripe, the responses to the simultaneous stimulation were summed non-linearly, while remote lateral stripes more often provided an inhibitory effect rather than an excitatory one. No difference between the detectors of horizontal and vertical edges in this respect was found.

Three typical experiments with a central light stimulus are shown in Fig. 2. As the series were combined in pairs according to the polarity of the central stripe by procedure, whereas lateral stimuli were presented with both polarities in a single experiment (see Methods), it is possible to compare the results for lateral stripes of different polarity obtained almost at the same time. Two corresponding histograms for each unit are shown for comparison in Fig. 2: for light lateral stimuli (top row) and for dark lateral stimuli (bottom row). One can see in the histograms that almost all remote bars are pointing down, indicating reduction of the unit responses to paired stimulation compared with the stimulation of the central stripe alone. This demonstrates the inhibitory influence of the surround in case when light stripe is fixed in the center, irrespective of the sign of contrast of the peripheral stimulus.

On the other hand, stimulation with dark stimulus fixed in the center gave some discrepant results. While stimulation with paired stripes of the same sign of contrast revealed mainly inhibitory influences of the remote surround as in the cases when light stripe is fixed in the center, paired stimuli of the opposite polarity with the dark stimulus fixed in the center evoked an unusual excitatory effect in some recordings. Figure 3 shows the experimental data obtained in three OS GCs stimulated alternately by pairs of dark stimuli (bottom row of histograms) and paired stripes of the opposite polarity with dark central and light peripheral stripes (top row of histograms). The bottom row of histograms illustrates inhibitory influences of the remote dark stripes. In the case of paired stimuli of the opposite polarity (top row), remote light lateral stripes evoked similar inhibitory effect in units (a) and (b), as in the bottom row in this figure, or in all histograms of Fig. 2, whereas in the cell (c) light lateral stripes had clear excitatory effect — increased the response to the dark central stimulus. Thus, the horizontal edge detector shown in Fig. 2(c) and

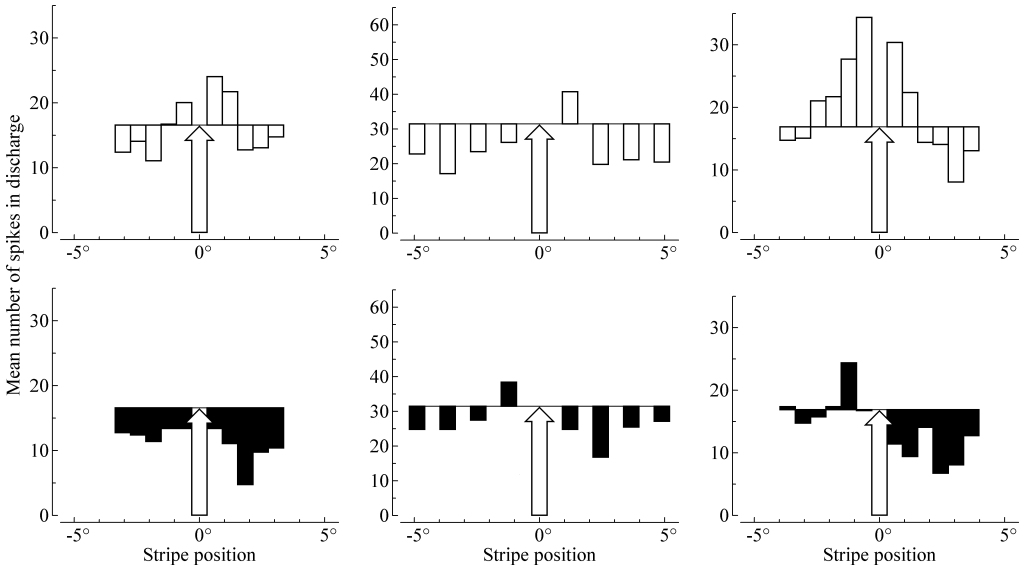

Fig. 2. Results obtained in three retinal OS GCs by means of paired stripes with the light stimulus fixed in the center. All three units were detectors of horizontal lines, the diameters of their RRF, as previously measured by moving edges and flashing stripes, were 2.5° (Fig. 2(a)), 3.2° (Fig. 2(b)) and 4.1° (Fig. 2(c)). White upward arrows indicate the magnitude of the unit response to stimulation with a central reference stripe presented alone. This value determines the position of baseline in each histogram. Each bar, directed upwards or downwards from these lines represents the difference in the response produced by adding the second peripheral stripe at each position. The upper row of histograms corresponds to the two-stripe interaction experiments in which stripes were of the same polarity (both of them light). The bottom row represents the results obtained when the same units were stimulated by paired stripes of the opposite polarity (central light and peripheral dark). Widths of histogram bars in Fig. 2 correspond to the widths of stimuli. Note the convention of the figures that the differences produced by adding light peripheral stimuli are indicated by open bars while the differences evoked by dark peripheral stimuli are indicated by black bars.

Fig. 3(c) has demonstrated inhibitory effect of remote lateral stripes in three of the four combinations of polarities of stimuli, but in one combination showed excitatory effect.

Obtained results were subjected to statistical analysis in order to evaluate effects recorded in response to different combinations of paired stimuli. The analysis tested the number of bars of histograms evidenced in favor of the mutual excitation or inhibition in each variant of the experiments in the case of remote lateral stripes. Bars satisfying the following two conditions were selected. First, corresponding lateral stimuli had to lie far enough — more than 1°20′ from the RRF center. Second, the differences in the magnitude of response to paired stimulation and to reference stimulus alone was supposed to exceed 20%. Corresponding areas are marked in gray in Fig. 3(c). The statistical analysis of the data confirmed presence of the inhibitory surround in majority of experimental conditions. Resulting ratios of excitatory and inhibitory peripheral stripes calculated for all four combinations of paired stimuli are presented in Table 1. Proportion of inhibitory lateral stimuli was significantly higher

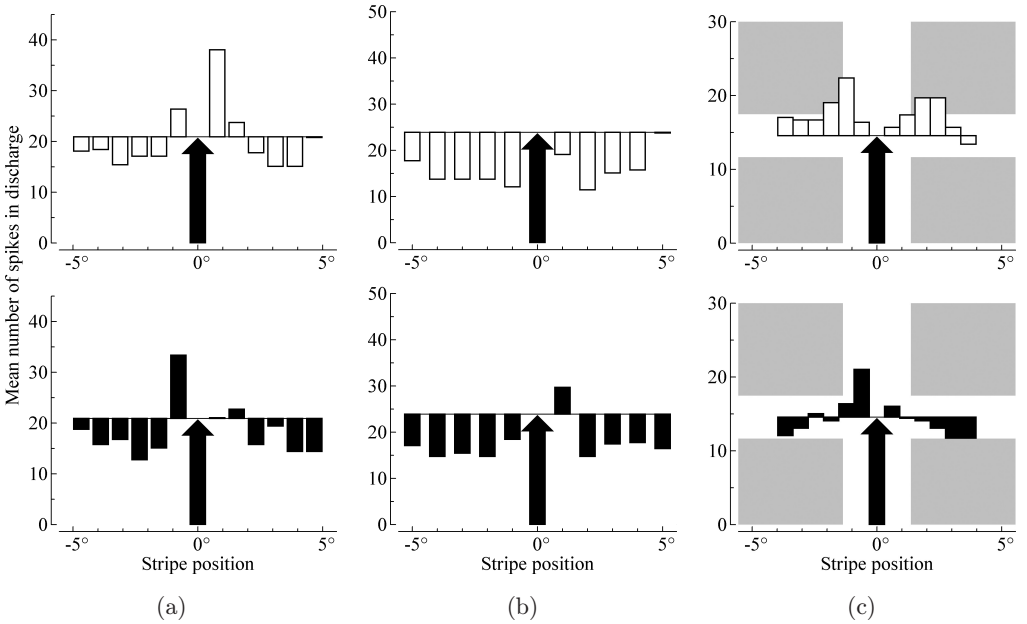

Fig. 3. Results obtained in three retinal OS GCs by means of paired stripes with the dark stimulus fixed in the center. (a) Detector of horizontal lines with the diameter of its RRF equal to 3.5°. (b) Detector of vertical lines with RRF of 5.2°. (c) Detector of horizontal lines with RRF of 4.1° — the same unit, which is shown in Fig. 2(c). Black upward arrows indicate the magnitude of the unit response to stimulation with a central reference stripe presented alone. Other designations are the same as in Fig. 2. Gray squares in histograms at (c) mark limitations used to select data for further statistical analysis (for detailed explanation see text).

Table 1. Ratios of excitatory and inhibitory influences of the remote peripheral stripes registered for different combinations of paired stimuli.

Central stripe	Lateral stripe	
	Light excitation:inhibition	Dark excitation:inhibition
Light	**14:124**	**7:115**
Dark	**107:93**	**35:157**

in three cases that corresponded to the situations when central stripe was light or when peripheral stripe was dark. But in the case with dark central and light peripheral stripes, excitatory and inhibitory influences of the lateral stimuli were distributed in approximately equal amounts.

4. Discussion

The method for mapping RF by two flashing stripes uses central reference stimulus, which evokes certain excitation in the cell. This excitation can be increased or

reduced by the influence of the second (peripheral) stimulus presented at the other locations within the RF. Strong evidences for lateral inhibitory influences in the fish OS GC RF were already given in our former study (Damjanović *et al.*, 2009b). In experiments with stimulation by two stripes of the same sign of contrast (both of them light, or both dark), the inhibitory influences of the lateral stripe were always initiated inside the RRF area. The results of the study suggested that the OS GC RF in fish appears to be functionally divided into small subunits sensitive to the appropriately oriented stimuli, and that these subunits should be influenced by inhibition from other subunits, extending far beyond the limits of the RRF (Maximov, 2010). Morphological substrate of the subunits could be retinal bipolar cells, and the inhibitory effects could be carried out within the inner synaptic layer by some type of amacrine cells. In the experiments of the present study, OS GCs were stimulated alternately either by stripes of equal brightness or by stimuli of opposite polarity (light and dark ones) in order to elucidate if the interaction between paired stripes depends on the polarity of stimuli or just their spatial locations. Obtained results testify that fish retinal OS GCs respond to paired stripes always in the same manner in three combinations of paired stimuli — when both stimuli are of the same polarity (either light or dark) or when the stripes are of the opposite polarity, but with the light central and dark peripheral stimuli. In all these cases, inhibitory influences of the remote surround were revealed, whereas the stimulation with the dark stripe in the center and the light one at the periphery revealed that the effect of light peripheral stimulus is not always straightforward. It was shown that besides inhibition, bright periphery can sometimes facilitate the response to the central dark stripe. An explanation may consist of the fact that in addition to the inhibitory interaction between the subunits, there is also an opposite effect of the periphery.

One of the possible mechanisms underlying the excitatory effect of bright surround in the retina is associated with horizontal cells. In 1967, already Byzov showed that the electric polarization of horizontal cells in the turtle retina affects the magnitude of the light-induced local electroretinogram (ERG). The hyperpolarization increased the ERG, while depolarization decreased it. On this basis, Byzov formulated an idea of horizontal cells as regulators of synaptic transmission from receptors to subsequent neurons (Byzov, 1967). Later, Maximova showed that such a polarization of horizontal cells in a similar way changes responses of the retinal outputs — the ganglion cells (Maximova, 1969). A comparable magnitude natural polarization of horizontal cells arises from stimulation of a substantial part of the RF of cells with light, e.g., with a steady annular illumination. This implies that the change in lighting at the far periphery of the RF can affect the signal flow in the central part of the RF. Accordingly, at the level of bipolar cells, Werblin showed that their responses can be augmented by a bright annular surround in the mudpuppy retina (Werblin, 1974). A corresponding phenomenon was discovered independently by researchers working not at the level of isolated retina, but with whole animals. In fish and frogs, responses of different detectors to stimuli presented in black annular surround decrease, but increase in white surround (Zenkin, Pigarev, personal communication).

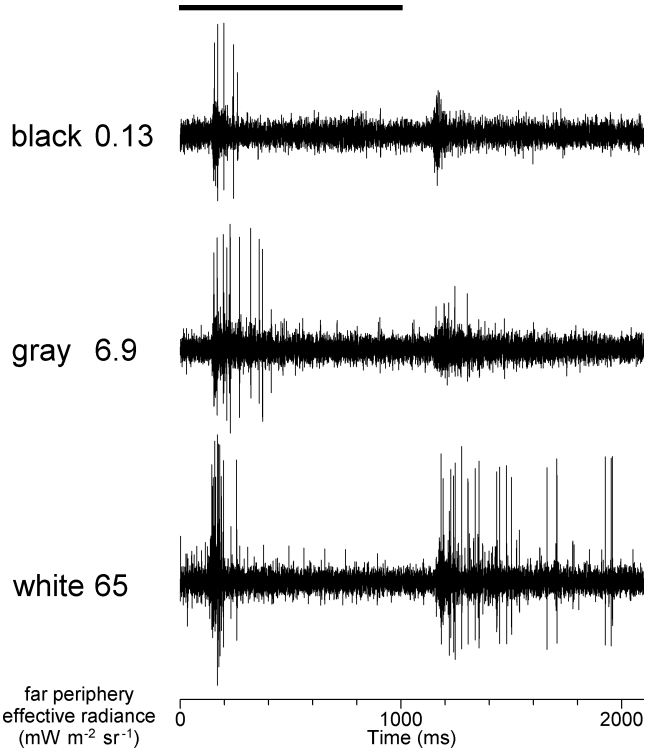

Fig. 4. Influences of different levels of steady illumination of the far periphery of the OS GC on the response evoked in the center of the cell RRF. Responses of a detector of horizontal lines to a narrow black horizontal stripe (about half a degree in width) flashed in the center of the RRF in the presence of differently illuminated far surround. Duration of the stimuli was 1 s (marked by horizontal bar above records). Stimulus intensity "from the point of view" of long-wavelength cones (effective radiance for the long-wavelength cones) was 0.13 mW m^{-2} sr^{-1}. Background intensity of the stimulation area was set at 14.5 mW m^{-2} sr^{-1}. Intensities of different far surrounds are given to the left of the corresponding spike discharges.

Figure 4 demonstrates this effect in a detector of horizontal lines stimulated by a narrow black horizontal stripe flashing in the center of the RRF in the presence of differently illuminated surrounds. The surround of the cell was illuminated from the part of monitor screen located beyond the central stimulation area (Fig. 1). Constant luminosity maintained on this part of monitor screen could be varied during the experimental procedure. The top row of Fig. 4 shows a spike discharge of the unit in response to the stripe in a black surround. This unit did not respond by a sustained discharge to the stripe, and in these conditions gave only a weak transient response to its onset. When increasing the brightness of the surround (gray), the number of spikes in the response increased. In the white surround, the number of spikes in response to the stimulus onset increased further, the discharge became more compact, and a response to the stimulus offset appeared; this was absent in case of dark surrounds. So, one can see that the gradual increase of surround illumination evoked facilitation of the OS GC responses.

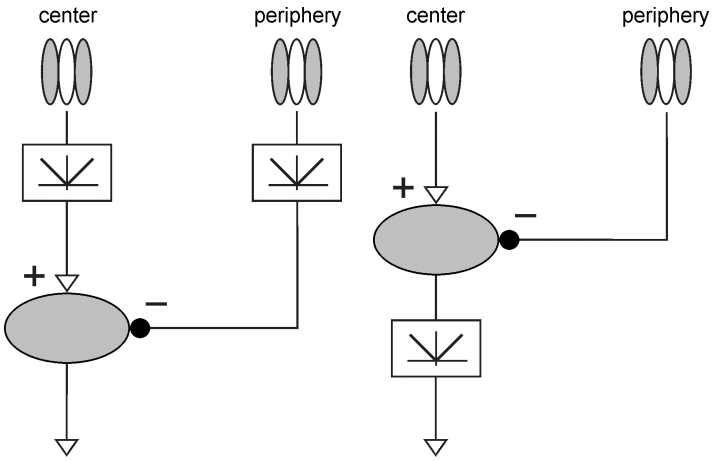

Fig. 5. Two schemes of lateral interaction of signals that exhibit different behavior in experiments with the paired presentation of stripes of opposite sign of contrast. It is assumed that the signals from the subunits have different signs depending on the polarity of applied stimuli, and the total inhibitory signal from the surround assumed to be summed from subunits over a large area (not shown). The excitatory (+) and inhibitory (−) signals from the central and peripheral subunits of the receptive field meet in the site of opponent interaction. The two schemes vary in the position of full-wave rectifiers, indicated by rectangles.

Thus, in addition to lateral inhibition between the subunits of the RF of retinal OS GCs at the level of the inner synaptic layer, there is a mechanism of facilitatory influence of lateral light stimuli realized within the outer synaptic layer of the retina, which can mask the effect of inhibition. This may explain the ambiguous results of the experiments with the light stripe at the periphery (Fig. 3) in which the effects should have been generated by simultaneous activation of at least two independent peripheral mechanisms, exhibiting opponent effects on the main central response.

If we disregard the lateral influence through the horizontal cells, the circuitry providing distinctive features of lateral interaction in our experiments can be represented schematically as in Fig. 5(a). The ON-OFF nature of the OS GC response implies that a full-wave rectifier is inserted in some place of the scheme. In the scheme of Fig. 5(a), it is placed at the output of subunits, providing the same inhibitory effect of peripheral stripes regardless of the sign of their contrast.

Long before our experiments, the same experimental procedure with paired stripes was applied to cat complex cells located in the striate cortex (Movshon *et al.*, 1978). Obtained results expressed evident dependence of two-stripe interrelations on the polarity of stimuli. When the paired stripes were equal, peripheral stimulus always antagonized the response to the central stripe. On the other hand, when paired stimuli were of the opposite polarity, facilitation from the lateral stripe was permanently recorded. These properties will conform to a network in which a full-wave rectifier is placed after the site of opponent interaction of signals (Fig. 5(b)). Thus, it should be emphasized that the discrepancy of our results obtained in fish OS GCs

with those reported for cat complex cells by Movshon *et al.* (1978) testify about considerably different RF organizations between the two cell types. The difference in mechanisms may be due to the different functions of these cells, which should be reflected in marked differences in responses to some important stimuli other than paired stripes. In particular, upon presentation of periodic gratings consisting of alternating light and dark stripes, the total inhibitory signal from the surround, summed over a large area after a full-wave rectification, is strong in the circuit (Fig. 5(a)). As a result, retinal orientation-selective units must respond poorly to gratings. On the contrary, in the circuit (Fig. 5(b)) unrectified signals of different polarities from light and dark stripes cancel each other, and the total inhibitory signal from the surround is weak. A weaker lateral inhibition may contribute to a better tuning to spatial frequency filtering in the visual cortex.

Horizontal edge detectors were first discovered in the pigeon (Maturana & Frenk, 1963). The presence of such detectors in birds was quite understandable as the horizon is an important feature for the visual orientation in flight. Later, such detectors were found in pike (Zenkin & Pigarev, 1969) and trout (Galand & Liège, 1975), and the question arose of their role in the visual system of animals never seeing the horizon. We described the detectors of horizontal edges in many other fish species (Maximova *et al.*, 1971) and subsequently found similar detectors with opposite (vertical) preferred orientation (Maximova *et al.*, 1973). A comparison of physiological properties of these two types of detectors of oriented lines has shown that they do not differ in any other properties, except for their preferred orientation (Maximova & Maximov, 1981). Surprisingly, in the rabbit retina, recent studies of the synaptic mechanisms generating orientation selectivity show distinct differences at least in the synaptic circuitry of the two cell types, which seems to have no effect on their physiological properties except for the preferred orientation (Venkataramani & Taylor, 2010).

While the properties of the detectors of oriented lines are rather well investigated, their function is obscure. Are they specific feature detectors, i.e., do they detect some behaviorally relevant key stimuli of environment, just as the ⟨bug detectors⟩ in the frog retina (Barlow, 1953; Lettvin *et al.*, 1959) detect dark spots, or they are only some basic elements of preliminary image processing? When detecting different features such as horizontal and vertical orientations, why are the detectors of oriented lines so identical in their physiological properties? Why in this case they terminate at the same place of the tectum and may be converge to the same neurons? Judging from the symmetry of their properties and the place of their projections in the tectum, these units should be considered rather as universal filters of preprocessing, that we encounter, for example, in the mammalian cortex. But if so, why, in each point of the fish visual field, are there only two preferred orientations detected and not a continuum as in mammalian cortical complex cells?

In sum, the general pattern of interactions between the centre and surround in the RF of the fish OS GCs was that the influence of the remote peripheral stripe was inhibitory, regardless of the polarity of each stripe. The fact that in some cases white

lateral stripes act otherwise, may be attributed to an additional opposite influence acting on another retinal level. The discrepancy between the results for the fish OS GCs and those reported for the complex cells of the mammalian striate cortex may indicate essentially different RF organizations in the two cell types and essential difference in their functions in vision.

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