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Functional Asymmetry of a Particular Type of Retinal Neurons in Apparent Symmetry of Its Morphology

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Abstract—Direction-selective neurons exist at different levels of the visual system in different vertebrates and invertebrates. In accordance with the name, such cells respond differently (asymmetrically) to different moving stimuli, depending on their direction. Contrast borders, stripes, spots which move in preferred direction cause a strong impulse discharge of the neuron, but the same stimuli moving in opposite direction ("0"-direction) do not cause response. Thus, these neurons are capable of recognition of the direction of stimulus movement. It is possible to use this in different forms of visual-based behavior.

Keywords: Neuron, retina, functional asymmetry, visible symmetry

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DIRECTION-SELECTIVE GANGLION CELLS OF RETINA

Essential processing of images of the outer world projected by optics of the eye on the photoreceptor surface is performed in the retina. Each of output neurons of the retina, i.e., ganglion cells (GC) of various morphophysiological types (more than two tens), sends specific description of the image to the visual centers of the brain (Roska and Werblin, 2001; Marc and Jones, 2002; Rockhill et al., 2002; Sun et al., 2002; Kong et al., 2005; Masland, 2012).

Each GC treats a small part of the image within its receptive field (RF), the receptor surface (from several to hundreds of receptors) connected with GC through bipolar cells, horizontal cells, and amacrine cells. Which features of the image (size of stimulus, sign of contrast, color, direction, rate of movements, etc.) "engage attention" of GC (character of image processing) is determined by its specific synaptic relationships with neurons of the previous levels, i.e., by the arrangement of its RF (Fig. 1). Transmission of signals of bipolar cells (ten types) and signals of various amacrine cells (more than 20 types) to dendrites of GC occurs in various strata of the inner plexiform layer (IPL) by means of a number of neurotransmitter mechanisms (Marc, 1986; Masland, 2001; Maximova, 2008).

In the retina of mammals (rabbits, mice), four physiological types of direction-selective ganglion cells (DSGCs) preferring temporonasal, dorsoventral, ventrodorsal, or nasotemporal directions of stimulus movements have been described. These are the so-called "fast" DSGCs, functioning in a wide speed range of stimulus movements (Barlow and Levick, 1965; Vaney, 1994; Weng et al., 2005). 1 Recently, the use of genetic methods allowed three new DSGCs types in mouse retina to be recognized (Rivlin-Etzion et al., 2011).

In fishes, turtles, and the Japanese quail, DSGCs distinguish three directions: temporonasal and two

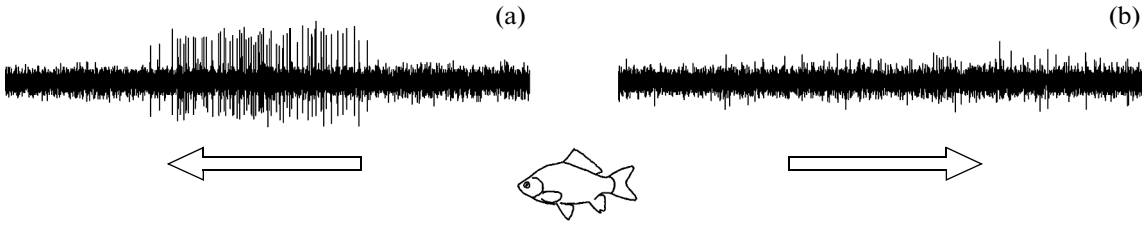

Fig. 1. Response of a direction-selective ganglion cell of the goldfish retina to the stimulus moving through its receptive field (recorded from axonal ends in the tectum): (a) stimulus moves in the preferable caudorostral direction; (b) absence of response to the stimulus moving in the rostrocaudal "0"-direction; arrows show the direction of stimulus motion relative to the fish.

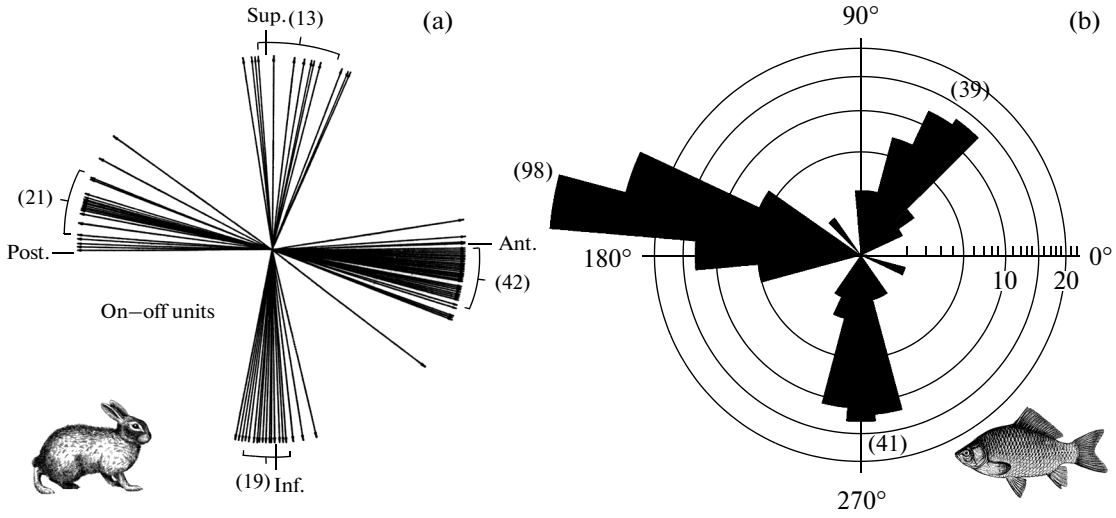

Fig. 2. Distribution of preferred directions of direction-selective cells of the retina: (a) rabbit (after Barlow et al., 1964) and (b) goldfish (original data) in the polar coordinates; figures in brackets show the number of cells with the given preferable direction.

other, differing from it by 120° (Fig. 2) (Jacobson and Gaze, 1964; Bowling, 1980; Uchiyama et al., 2000; Maximov et al., 2005a, 2005b).

In addition to "fast" DSGCs, animals representing all large taxa have the so-called "slow" DSGCs, which work within the range of small speeds of stimulus motion. "Slow" DSGCs are subdivided into three groups by the three preferable directions of motion of the stimulus, which are distinguished from each other by 120°, according to the planes of semicircular canals (Barlow et al., 1964; Giolli and Blanks, 2005; Sun et al., 2006; Yonehara et al., 2008, 2009).

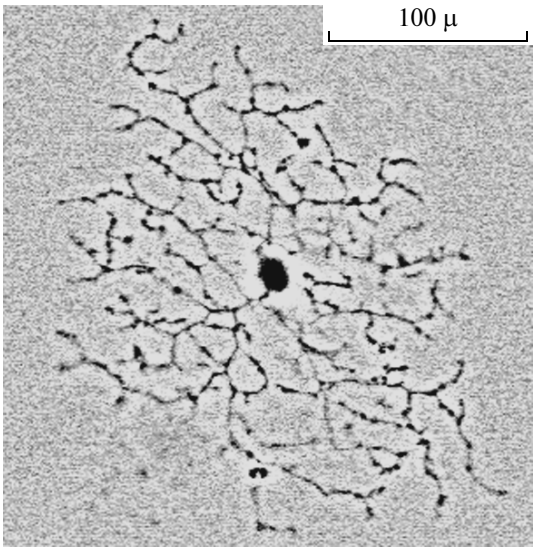

Fig. 3. Dendritic tree of a putative direction-selective ganglion cell of goldfish retina with a characteristic "lacy" structure, symmetrical relative to the cell body. Stained by DiI applied in a cut of the optic nerve. The image is inverted by the sign of contrast (after Maximova et al., 2006).

Since 1965, when DSGCs in rabbit retina were described for the first time (Barlow and Levick, 1965), several working teams tried to reveal the mechanism of generation of asymmetrical response of DSGCs by various techniques.

The shape of dendrites of DSGCs was the first to be tested for the role of the basis of asymmetrical responses of DSGCs, because physiological properties of ganglion cells are determined in many respects by the morphology of dendrites: the level of stratification, size and shape of dendritic tree, character of its branching, and cable properties. However, all of four types of "fast" DSGCs of rabbit (and other animals examined) differing in the preferable directions looked completely identical in dendrite crown structure, as they were stained intracellularly. Symmetrical relative to the cell body, "lacy" dendrites of "fast" DSGCs flatly branch in two narrow strata of IPL, where they are costratified with plexuses of the processes of on- and off-populations of starburst amacrine cells (O'Malley et al., 1992; Kittila and Massey, 1997; He et al., 1999; Dong et al., 2004; Maximova et al., 2006; Lee et al., 2010). Fields of the processes of starburst amacrine cells are also symmetrical relative to the cell body and almost identical in size to dendrite fields of DSGCs (Masland et al., 1984; Famiglietti, 1992; Dong et al., 2004).

In different animals, the morphology of these neurons is identical (Fig. 3). Thorough measurement of dendrite branching and calculation of primary, secondary, and tertiary dendrite processes in different sites of the dendrite field have not revealed any distinctions (correlations) in relation to preferable and "0"-directions in the receptive field of DSGCs. This

morphological symmetry astonished and nonplused researchers (Chen and Chiao, 2008).

Using pharmacological methods, it has been shown that asymmetrical response of DSGCs (inhibition of spike response, as stimulus moves in "0"-direction) is realized by γ-aminobutyric acid (GABA) (He et al., 1999). GABA releases just from dendrite varicosities of starburst amacrine cells (Yoshida et al., 2001).

During patch-clamp recording from DSGCs, it has been shown that just the spike output response is asymmetrical. Both EPSP and IPSP are present in the cell, as stimulus moves in both preferable and "0"-direction. In the first case, EPSP is greater than IPSP and spike response arises, while in the second case, IPSP is greater than EPSP and the threshold of spike generation is not reached (Fried et al., 2002).

Using the potential-dependent dye (method of functional calcium imaging), it has been shown that asymmetrical excitation in the retina initially appears in starburst amacrine cells. Excitation develops centrifugally from the cell body in one of sectors of dendritic tree and does not involve remaining part of the crown (Euler et al., 2002).

It remains obscure how this asymmetrical excitation of amacrine cells, which provides release of GABA, is selectively transmitted to dendrites of different types of DSGCs. The question is complicated by two facts: (1) fields of the processes of starburst amacrine cells strongly overlap and (2) the processes of starburst amacrine cells and dendrites of DSGCs with different preferable directions are not only costratified, but also cofasciculated (Famiglietti, 1992; Vaney, 1994; Dong et al., 2004).

Finally, new approach, i.e., combination of two-photon functional calcium imaging and SBEM (serial block-face electron microscopy), helped to understand the mechanism of asymmetrical response of "fast" DSGCs (Briggman et al., 2011).

Using the method of calcium imaging, 25 starburst amacrine cells and 25 DSGCs have been visualized within a site of 300 × 300 μm of living mouse retina. These DSGCs are represented by four groups, with the preference to one of four directions of stimulus motion, which are named "northern" (6 DSGCs), "eastern" (8 DSGCs), "southern" (7 DSGCs), and "western" (4 DSGCs). Based on the data of SBEM, "skeletons" of these 25 starburst amacrine cells and 25 DSGCs have been reconstructed. Contacts between the processes of six DSGCs and 25 amacrine cells were examined. Of 9260 contacts of the processes of amacrine cells and GCs, 831 were regarded as synapses. A mapping of these inhibitory synapses in sites of dendrites of DSGCs with different preferable directions has shown significant asymmetry in the number of synaptic contacts on dendrites. They were mostly clustered along "0"-direction of DSGCs. For example, the dendrite branches directed "to the north" of all of 25 amacrine cells formed synaptic contacts mostly on the dendrite branches of different DSGCs directed "to the southern" preferable direction. Each DSGC gives rise to particular directional selectivity, collecting mostly inputs of starburst amacrine cells that suppress excitation in "0"-direction, i.e., from the branches positioned along the "0"-direction. This confirms the idea that the inputs of starburst amacrine cells positioned in "0"-direction inhibit the generation of dendritic spikes of DSGCs, as the stimulus moves in "0"-direction.

The selective "wiring" of inhibitory synapses in a particular dendrite site of the DSGC is also evidenced by the results of experiments with simultaneous records of responses of pairs of DSGC–amacrine starburst cells (a total of 25 pairs), located at a distance of extended dendrite from each other. The inhibitory effect of GABA on the response of DSGCs caused by electric stimulation of the starburst amacrine cell was maximum in the pairs in which amacrine cells were positioned in "0"-direction of DSGCs. Inhibitory influence was absent in the case that amacrine cells were in the preferable direction from DSGCs and was insignificant, as relative positions were intermediate (Lee et al., 2010).

In electrophysiological experiments with fishes, the study of interaction of stimuli within RFs of DSGCs, which preferred one of three directions of stimulus motion, has shown that the zone of inhibitory interaction was observed on the "zero" side of DSGCs receptive field (Damjanović et al., 2009).

As mentioned above, in addition to the classical "fast" DSGCs with the properties described, projecting in the tectum opticum, mammals, fishes, and turtles have "slow" DSGCs projecting into the nucleus of accessory optic system. Morphological, immunochemical, and pharmacological studieshave shown that RFs of "slow" DSGCs are similar in structure to "fast" ones (Famiglietti, 1992; He and Masland, 1998; Dong et al., 2004).

Recent genetic studies have shown that, in addition to classical DSGCs with symmetrical dendritic arborization, "fast" DSGCs are represented by DSGCs with asymmetrical dendritic crowns, with their preferable direction coinciding with the vector of branching direction of the dendritic crown. In all other respects, they are similar to classical DSGCs (Rivlin-Etzion et al., 2011).

Development of directional selectivity

As a result of fine titanic work, the morphological basis of functional asymmetry was at last revealed. Each DSGCs subtype responds to motion along one of four axes in the visual field due the single type of synaptic inputs, which it receives. To reach such a remarkable degree of specificity of synaptic contacts (wiring specificity), visually identical DSGCss should differ at the molecular level (Kay et al., 2011). How-

ever, the question arises as to how the selectivity of synaptic contacts of segment of equally directed processes of many starburst amacrine cells with the counterparallel dendritic segments of DSGCs is provided in the course of development.

Usual keys, such as the level of dendritic stratification or neurotransmitter affinity or cell phenotypic identification could not be used in the process of determination of specific synaptic contacts (wiring specificity) between dendritic segments of starburst amacrine cells and counterparallel dendritic segments of DSGCs, because DSGCs with different preferences are costratified and cofasciculated.

In ontogeny, dendrites of retinal ganglion cells of different types behave differently. In some, the initially diffused dendrite branching throughout the IPL strata is gradually stratified in the course of development (Coombs et al., 2007). The change in its shape is influenced by acetylcholine waves in the retina and depends on early visual experience (Stacy and Wong, 2003). In others, including both "fast" and "slow" DSGCs, dendrites reach the final form rather early, by the moment of the establishment of photosensitivity and do not change in further development. Their axonal projections in the tectum opticum also remain unchangeable. Directional selectivity depends on neither acetylcholine waves in the retina nor early visual experience and is completely determined by the genetic program (Elstrott et al., 2008; Chen et al., 2009; Sun et al., 2011).

Optokinetic and optomotor reflexes of mice, which are connected with the activity of both rapid and slow DSGCs, arise in ontogeny by the moment of eye opening and are retained in the case of keeping under dark conditions (Yonehara et al., 2008, 2009).

In hutchling danio (aquarian fish *Danio rerio* L.) of 5–7 days after fertilization optokinetic and optomotor reflexes are already expressed (Portugues and Engert, 2009).

The study of 6-day-old danios using transgenic marker of calcium (Ca++) has shown that the tectum opticum already contains ordered projections of axonal terminals of DSGCs of three types (distinguished by the preferable direction: Nikolaou et al., 2012).

Electrophysiologically recorded responses of DSGCs from their axonal terminalia in the tectum opticum of adult fishes of different species have been investigated in detail (Maximov et al., 2005b; Maximov et al., 2007; Damjanović et al., 2012). Genetic (morphological) data obtained on 6-day-old hutchlings and electrophysiological data on adult fishes provide evidence of the constancy of projections of DSGCs with reference to both quantitative ratio of particular types of preferable directions and relative depth of recording responses selective to one of three directions of stimulus motion.

The tool of the selectivity of connection between cells of different levels of the visual system and spatial organization of the dendritic fields are adhesive molecules, such as JAM-B, Dasm-1, Dscam, Sidekick-1, Sidekick-2, SPIG 1, which are expressed at certain embryonic stages on cell membranes of the retina (Yamagata et al., 2006; Fuerst et al., 2008; Yamagata and Sanes, 2008; Yonehara et al., 2008, 2009; Maximova, 2009).

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