Receptive-Field Structure of Direction-Selective Ganglion Cells Projecting to the Goldfish Tectum

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ABSTRACT: The receptive field of a direction-selective unit of any type consists of an excitatory center that 3º– 5º in size, a near inhibitory surround and a far surround upon which illumination exerts an influence for both spontaneous activity and specific cell response.

KEYWORDS: direction-selective neurons; receptive field; lateral inhibition; ganglion cells; amacrine cells; horizontal cells; tectum opticum; goldfish

The receptive-field (RF) structure of direction-selective ganglion cells (DS GCs) is determined by specific retinal circuits including connections with various interneurons in the outer plexiform (OPL) and the inner plexiform (IPL) layers, the RF center being determined by direct pathways from receptors through bipolar cells within the dendritic field of the GC.

In our electrophysiological experiments with extracellular recordings from axon terminals of DS GCs in the goldfish tectum, sizes of the RF center of the cells were evaluated in four ways: (1) a rough estimate as a product of the duration of spike train in response to contrast edges moving across the RF in preferred direction and the velocity of the movement; (2) more precisely, RF can be outlined with edges moving in many different directions, provided the temporal delay in the network is known; (3) tracing by small contrast spot moving on several parallel tracks allows to estimate the RF width by the number of spikes along each track and the RF length by the duration of spike train; when tracing in two mutually orthogonal directions (at 45° to the preferred one), the method permits calculation of a value for the delay from the same experiment; (4) since DS GCs respond well to "on" or "off" of small stationary spots, it is possible to use the canonical method of RF mapping with a flashing spot.

All methods gave consistent results. Centers of the RF amounted to 3º– 5º in all types of DS GCs.

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Stimulation of the RF surround does not excite DS GCs (by definition), but it is possible to demonstrate its influence on the cell spike responses. So, spots moving at the near surround in preferred direction or stationary flashing spots inhibit spontaneous activity of DS GCs (white spots in the case of ON-units and "flashed" black ones in the case of OFF-units). Movement of a stimuli in preferred direction at the near surround also exerts inhibitory effect on a specific central response. As a result, a DS GCs response to a moving stripe (extending with its flanks to the near surround) is appreciably weaker than one to a small spot moving within the bounds of the RF center. A more far surround turned out to be effective also, but its influence can be demonstrated only by massive stimulation. So, an illumination of the whole far surround, beyond the area three times as much as the RF center (or 400 μm from the RF center on retinal surface), as a rule inhibits a central response but enhances spontaneous activity independently on the type of DS GCs. This means that the influence of the far surround on the activity of DS GCs is similar to the influence of the near one in the case of OFF-units and opposite to it in the case of ON-units.

It is hypothesized that the direct pathway from cones to DS GCs in the fish retina are realized through Cajal's "giant bipolars destined for rods" of ON and OFF types, which receive synapses (besides rods) from principal, red-sensitive components of double cones, just as it is necessary for the red sensitivity of the DS GCs. These bipolars are known to be color-opponent and thereby can account for the color-opponency of the DS GCs. Apparently the color-opponency is realized in the OPL by a feedback from horizontal cells to cones. The same cells can also be responsible for influence of a far surround. Cellular mechanisms underlying the directional selectivity and effects of the near surround are less clear. A functional model with asymmetric lagged inhibition explains our data on velocity responses of the DS GCs. Therefore one can suppose that some unknown inhibitory amacrine cells (presumably GABAergic) distributed in two (ON and OFF) strata of the IPL are involved in organization of directional selectivity.

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