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## COLOUR AND SPATIAL PROPERTIES OF DETECTORS OF ORIENTED LINES IN THE FISH RETINA

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'Detectors of horizon' were first discovered in pigeons, and their possible function in the visual orientation in flight has been discussed. Later such detectors were found in pike and trout, and the question arises of their role in the visual system of animals never seeing the horizon. We described the detectors of horizontal edge in many other fish species and subsequently found similar detectors with opposite (vertical) preferred orientation.

The response of ganglion cells was recorded extracellularly from their axon terminals in *tectum opticum* of the curarized fish, placed in a transparent Plexiglas tank with perfusion of a physiological solution across its gills. There is a retinotopic projection in *tectum opticum*. Axons of different cell type terminate at different depths forming layers with specific features. The same stratification of specialized units can be found in all species investigated:

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i) directional selective units of both ON- and OFF-type with the preferred direction of movement from tail to nose, ii) similar units with the opposite preferred direction, iii) units sensitive to moving contrast, like the 'bug detectors' in frogs, iv) units responding by sustained discharges. Detectors of the oriented lines selectively sensitive to contrast moving or stationary bars and edges of proper orientation, similar to the cortical 'complex' units of mammals, are recorded in a very thin sublayer between contrast sensitive and spontaneously active units. Only two types of these detectors with preferred orientation orthogonal to each other can be found in any visual field of the fish. In the lateral visual field the orientations are vertical and horizontal. These two types are identical in their features. Their receptive fields, measured by moving or stationary bars of proper orientation (or by means of inhibition of firing by the bar oriented normally to the preferred orientation) are rectangular in shape and of  $5-7^\circ$  in size. The sign of the contrast and the direction of movement of the stimuli are of no importance. The possible divergence of stimulus orientation from the optimal one, still evoking the response, is  $45^\circ$ , so that the diagram of orientation tuning is '8'-shaped. Detectors of oriented lines are shown to be driven by red sensitive cones only. They are silent when a diffuse light switches on and off, while the light spot evokes a small response.

While the properties of the detectors of oriented light are rather well investigated, their functional meaning is obscure. Are they specific detectors, i.e. do they detect some key stimuli of environment, or are they only some elements of preliminary processing? Why are the detectors of oriented light identical in their physiological properties when detecting such different features as horizontal and vertical orientations? If they are elements of a preliminary processing, why in each point of the fish visual field are there only two preferred orientations detected and not a continuum as in the mammal system of cortical 'complex' cells?

*Key words:* fish retina, ganglion cells, oriented lines, receptive field

'Detectors of horizon' were first discovered in pigeons (Maturana and Frenk, 1963), and their possible function in the visual orientation in flight was discussed. Later such detectors were found in pike (Zenkin and Pigarev, 1969) and trout (Liege and Galand, 1971), and the question arises of their role in the visual system of animals never seeing the horizon. We described the detectors of horizontal edge in many other fish species (Maximova *et al.*, 1971) and subsequently found similar detectors with an opposite (vertical) preferred orientation (Maximova *et al.*, 1973). A comparison of physiological properties of these two types of detectors of oriented lines was presented in the article by Maximova and Maximov (1981). Here we discuss the colour and spatial properties of their receptive fields.

The response of the ganglion cells was recorded extracellularly from their axon terminals in the *tectum opticum* of the curarized fish, placed in a transparent Plexiglas tank and constantly perfused with physiological saline through the gills. There is a retinotopic projection in the *tectum opticum*. Axons of different cell types terminate at different depths forming layers with specific features. In all the species investigated the same stratification of specialized units can be found:

- directional selective units both ON- and OFF-types with preferred direction of movement from tail to nose;
- similar units with the opposite preferred direction;
- units sensitive to moving contrast (like the 'bug detectors' in the frog retina);
- units responding by sustained discharges.

Detectors of the oriented lines (DOLs) selectively sensitive to contrast moving or stationary bars and edges of proper orientation, similar to the cortical 'complex' units of mammals, are recorded in a very thin sublayer between contrast sensitive and spontaneously active units.

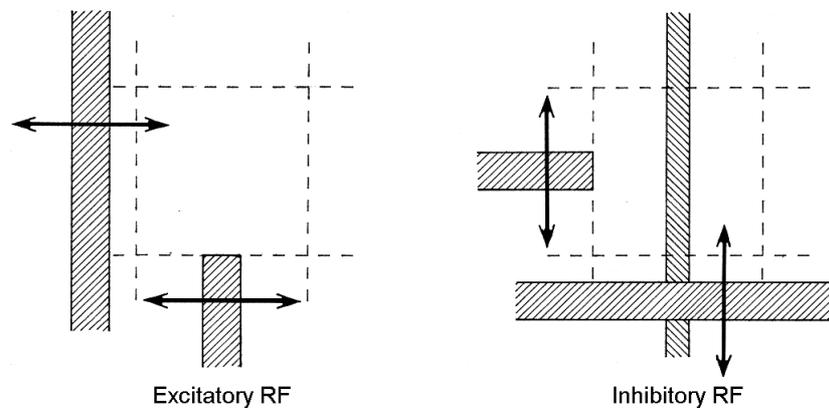


Fig.1. The mapping of the receptive field of a detector of vertical lines. Left: determination of limits (borders) of the excitatory receptive field by means of stimuli (vertical contrast stripes) evoking a unit response. Only stimuli for determination of the left and lower borders are represented. The right and upper borders are determined in a similar manner. Right: the mapping of the inhibitory receptive field using stimuli (horizontal stripes) inhibiting sustained unit responses to the stationary vertical stripe presented in the centre of its receptive field. Dotted lines indicate borders of the receptive field.

A detailed investigation of DOLs was performed in crucian carp *Carassius carassius*. Only two types of these detectors with preferred orientation orthogonal to each other can be found in any visual field of the fish. These two types of DOLs are identical in their features. They do not respond to switching on and off of diffuse light, while the light spot evokes a small response. The sign of contrast and the direction of movement of properly oriented stimuli are of no importance. Their excitatory receptive fields, measured using stationary or moving bars of proper orientation are rectangular in shape and of  $5-7^\circ$  in size (Fig.1, left). The inhibitory receptive field borders may be mapped by means of inhibition of firing by bars oriented normally to the properly oriented bar (Fig.1, right). Thus, determined excitatory and inhibitory receptive field borders coincide completely. The possible divergence of stimulus orientation from the optimal one, still evoking the response, is  $45^\circ$ , so that the diagram of orientation tuning is '8'-shaped. Not only the stripes of proper orientation, but also some stimuli of a more complex configuration can evoke the detector response, if possessing elements of proper orientation. Figure 2-1 shows some stationary stimuli exciting vertical line detectors. After a  $90^\circ$  rotation these stimuli will excite detectors of horizontal lines.

Stimuli presented in Fig.2-2 are ineffective for both types of DOLs, because they have in their configuration elements inhibiting responses of any detector. This mutual inhibition of orthogonal orientations is so strong that it is impossible to construct any stationary stimulus exciting both types of detectors simultaneously.

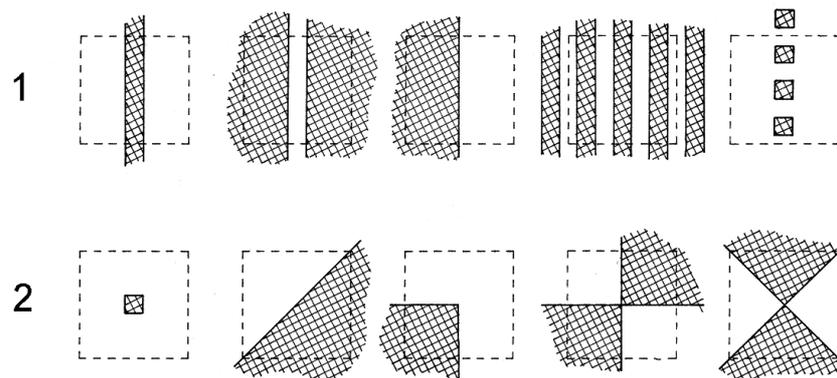


Fig.2 Different stationary stimuli that evoke (1) and do not evoke (2) responses of the detectors of vertical lines. The same stimuli as in (1) rotated by  $90^\circ$  excite the detectors of horizontal lines. Dotted squares indicate the positions of the receptive field.

Axon terminals of DOLs with reciprocally normal preferred stimuli orientations are packed so closely in the *tectum opticum* that it is possible sometimes to record their responses simultaneously, with the same microelectrode. In these cases the unit responses are discernible one from another by spike amplitude only. We succeeded with one position of the microelectrode to record 15 pairs of these elements in different visual fields of the fish. In such recordings, the change of stimulus orientation to the orthogonal orientation resulted in the replacement of the firing of one unit (e.g. detector of horizontal line) by the firing of another unit (detector of vertical line). The positions of the receptive fields of both units coincided.

Fish are known to possess colour vision. Spectral sensitivities of their cones are well known (Harosi, 1976). There are colour opponent cells at different levels of the fish visual system. But the majority of ganglion cells having their axon terminals in *tectum opticum* (e.g., the directionally selective units) are colour blind. To determine colour properties of DOLs we performed a series of experiments using the method of so called paper colorimetry (Maximov *et al.*, 1985). The appropriate stimuli represented by coloured papers were presented to DOLs in the presence of different gray and coloured backgrounds. The reflectance spectra of all papers and backgrounds were measured beforehand. To specify their colours in terms of the fish vision, relative excitation of their cone mechanisms were determined under given illumination. We found several groups of stimuli indistinguishable by DOLs. For example, stimuli number 47 (having a "beet" colour for a human observer), number 226 (green) and number 228 (turquoise) have been found to be indistinguishable from background number 188 (gray) and from each other. As shown in Fig.3 (left), differing in the blue-green region of the spectrum, these papers have similar reflectances (about 20%) in the red region, where only red sensitive cones are active. Estimated values of

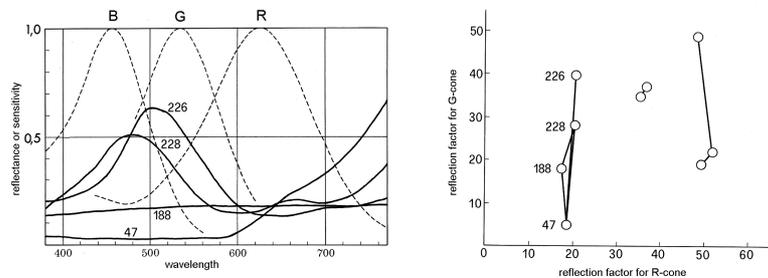


Fig.3 Colour properties of the detectors of oriented lines. Left: Spectral and colour properties of the stimuli: dotted lines - spectral sensitivities of cones (R,G,B) in Cyprinidae; solid lines - spectral reflectances of four painted papers, indistinguishable from each other by detectors of oriented lines. All papers equally reflect approximately 20% of light to the red-sensitive cones, but were different from the point of view of blue- and green-sensitive ones. For a human observer the papers have "beet" (47), gray (188), green (226) and turquoise (228) colours. Right: colours of the stimuli in a dichromatic colour space of red- and green-sensitive cones. Circles indicate positions of colours of light reflected from different painted papers under incandescent lamp illumination. Solid lines join the stimuli indistinguishable by detectors of oriented lines.

excitation of each type of cones demonstrate that all four indistinguishable stimuli excite equally red-sensitive cones, while the excitation of green-sensitive cones differs dramatically, almost 10-fold (Fig.3 right). Similar differences in excitation values existed also for the blue-sensitive cones (not shown in the Fig.3). Besides this group of four indistinguishable colours, two more similar groups are presented in the same graph. They are more light for the red-sensitive cones reflecting about 35% and 50% of an incident light in this region of the spectrum. At the same time, coloured stimuli that excited red sensitive cones to different extents, being similar to green and/or blue sensitive cones were discriminated by DOLs. Therefore we can conclude that DOLs are driven by red sensitive cones only. As we have mentioned above, almost all detectors projected into the *tectum* possess the same features. The only exception is a rare type of colour opponent units found in the layer of units sensitive to moving contrast (Maximova *et al.*, 1973).

While the properties of the DOLs are rather well investigated, their function is obscure. Are they specific detectors, *i.e.* do they detect some key stimuli of the environment, or are they some elements of preliminary processing? When detecting such different features as horizontal and vertical orientations, why are the DOLs identical in their physiological properties? Why do they, in this case, terminate in the same place of the *tectum* and may converge perhaps to the same neuron? This situation would be more natural for elements of some preliminary processing occurring, 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 the mammalian cortical 'complex' cells?

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