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COLOUR-SPECIFIC RESPONSES OF THE GOLDFISH RETINAL GANGLION CELLS REVEALED BY CONE-ISOLATED VISUAL STIMULATION

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Three types of cones (long-wave, middle-wave and short-wave sensitive) in the goldfish retina determine its color vision observed in its behavior. However the most of retinal ganglion cells (GCs) projecting to the tectum opticum – motion detectors – seem to be colour blind. Nevertheless the connections of the ganglion cells (through the bipolar cells) with different spectral types of cones proved to be non-uniform. To examine these connections we use cone-isolated visual stimulation.

Earlier we showed that direction-selective GCs classified as ON-type cells according to the results of achromatic stimulation, respond to the movement of the stimuli selective for the long-wavelength (L) receptor as ON-type cells as well, but respond to the stimuli selective for the middle- and short-wave receptors (M, S) – as OFF-type cells. Orientation-selective GCs responding as ON-OFF cells to gray edges, respond to the coloured edges selective for L cones as ON-OFF cells as well, but respond as OFF-cells to the stimuli selective for M cones and as ON-cells to the stimuli selective for S cones. To explain this behaviour it was necessary to assume the presence of special types of bipolar cells in the retina, forming synapses of different signs with cones of different spectral types (Maximov et al., 2015).

The responses of sustained GCs to selective stimulation of color channels look even more complex. Some of the observed dark sustained GCs respond both to the stimuli exciting L cones and to the stimuli inhibiting L cones, and demonstrate complex colour interactions in the receptive field when stimulated with colours that excite (or inhibit) two spectral types of cones simultaneously. Thus the retinal circuitry underlying this interaction looks unclear and needs to be modelled.

The model is made in the form of a three-layer artificial neural network. An input layer consists of three receptors corresponding to the three spectral cone types of the goldfish. Neurons of the second layer (bipolar cells) are connected with all receptors by synaptic connections, the weights and signs of which can be arbitrarily chosen. In addition, each of the neurons of the second layer is given a certain potential corresponding to its state at the moment when no input signals come to it. The neuron of the third layer (a GC) is connected with second layer neurons by non-inverting rectifying synaptic contacts. The weights and signs of the synapses of the second layer neurons as well as their potentials are adjusted (manually or by iterative computations) to get the responses similar to those observed in the electrophysiological experiments.

The experiments with the model have shown that in most cases the responses of GCs to colour stimulation observed in the electrophysiological experiments can be explained by the model with two types of bipolar cells forming specific synaptic connections with cones of different spectral types.

Maximov, VV., Maximova, EM., Damjanović, I., Aliper, AT., & Maximov, PV. (2015). Color properties of the motion detectors projecting to the goldfish tectum: II. Selective stimulation of different chromatic types of cones. J. Integr. Neurosci., 14, 31-52.

Colour-specific responses of the goldfish retinal ganglion cells revealed by cone-isolated visual stimulation

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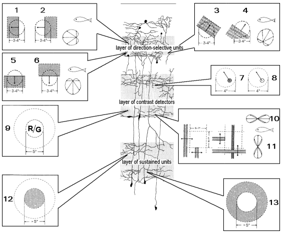
Introduction

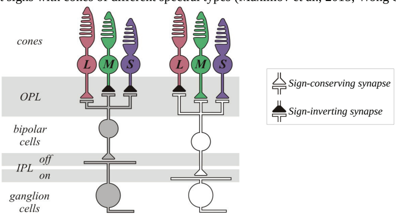
Three types of cones (long-wave, middle-wave and short-wave sensitive) in the goldfish retina determine its colour vision observed in its behaviour. Our experiments show that retinal ganglion cells (GCs) projecting to the tectum opticum are connected with all three types of cones.



1, 2 – ON- and OFF- direction-selective ganglion cells (DS GCs) of caudo-rostral preferred direction;
3, 4 – ON- and OFF- DS GCs of ventro-dorsal preferred direction;
5, 6 – ON- and OFF- DS GCs of dorso-ventral preferred direction;
7, 8 – black spot and white spot detectors;
9 – colour-opponent units (R/G type);
10, 11 – orientation-selective (OS) GCs – detectors of horizontal and vertical line;
12, 13 – dark sustained and light sustained units.

Stratification of retinal ganglion cells recorded from the goldfish tectum

Earlier we showed that direction-selective (DS) GCs classified as ON-type cells according to the results of achromatic stimulation, respond to the movement of the stimuli selective for the long-wavelength (L) receptor as ON-type cells as well, but respond to the stimuli selective for the middle- and short-wave receptors (M, S) – as OFF-type cells. To explain this feature it was necessary to assume the presence of special types of bipolar cells in the retina, forming synapses of different signs with cones of different spectral types (Maximov et al., 2015; Wong & Dowling, 2005).

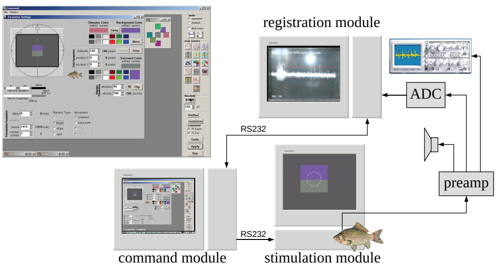


Putative schemes of colour-specific connections of the OFF (left) and ON (right) direction-selective cells

Methods

Experiment setup

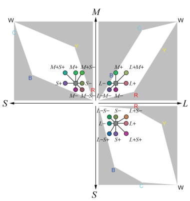
The experiment setup consists of three synchronized computer modules: (1) the registration module contains the ADC connected to the microelectrode through the amplifier; it serves for recording of the neuron responses, further visualization of them on the screen and storing the experimental data in the memory; (2) the stimulating module controls the stimulating monitor on which various visual stimuli are presented to the fish; (3) the command module serves for efficient manipulation of stimulation and recording parameters during the experiment and for additional real-time visualisation of the processed data (Maximov et al., 2010).



Selective and combined cone stimulation

To determine which cone types are involved in the functioning of a certain retinal ganglion cell type we designed special colours for stimulation. One of them was "grey" or "neutral" and usually served as a background on which the colour stimuli were presented. Six colours were calculated for selective, cone-isolated visual stimulation. Three of these colours (incremental colours) were 1.6 times more intense than the neutral colour for a given type of cones, and the intensity of the other three (decremental colours) was 1.6 times lower than the intensity of the "neutral" colour. The incremental colours are denoted as L+, M+ and S+, and the decremental colours, as L−, M− and S− for the long-wave, middle-wave and short-wave cones, respectively (Maximov et al., 2015).

To show the interactions between colour channels, the colour set was extended by the colours that simultaneously stimulated pairs of colour channels simultaneously, each stimulated colour channel being excited or suppressed. These colours are denoted as L+M+, L−M−, M+S+, M+S−, M−S−, L+S+, L−S+, L+S− and L−S− (Maximova et al., 2015). The positions of these colours in the physiologic colour space of the goldfish are demonstrated on the plot to the right.

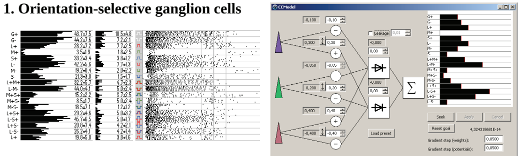


Later we extended the colour set by the "dark grey", which was 1.6 times less intense than "grey" for all three types of cones, and "light grey", which was 1.6 times more intense than "grey". We denoted these colours as G− and G+, correspondingly.

Results

The model is made in the form of a three-layer artificial neural network. An input layer consists of three receptors corresponding to the three spectral cone types of the goldfish. Neurons of the second layer (bipolar cells) are connected with all receptors by synaptic connections, the weights and signs of which can be arbitrarily chosen. In addition, each of the neurons of the second layer is given a certain potential corresponding to its state at the moment when no input signals come to it. The neuron of the third layer (a GC) is connected with second layer neurons by non-inverting rectifying synaptic contacts. The weights and signs of the synapses of the second layer neurons as well as their potentials are adjusted (manually or by computations) to get the responses similar to those observed in the electrophysiological experiments.

1. Orientation-selective ganglion cells

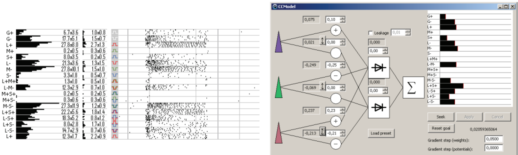


Experimental testing of colour interactions in the receptive field of a detector of horizontal line (left) and putative model of colour-specific connections of this unit matched by the program (right). Stimuli – coloured horizontal stripes flashing at the center of the unit's receptive field.

Despite the fact that OS GCs are ON/OFF-type cells, in most cases they proved to be insensitive to the incremental colour for middle-wave cones (M+). Most of the cells are insensitive to combined incremental stimulation of the middle-wave channel and decremental stimulation of the short-wave channel (M+S−). Detectors of horizontal and vertical lines do not differ in their colour properties.

2. Dark sustained units

Dark sustained units generate sustained spike discharge when the receptive field area is darker than the surround. The most intriguing feature of dark sustained units is their response to the colour stimulus incremental for the long-wave cones (L+).

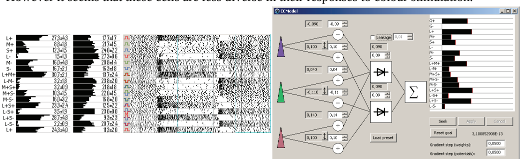


Experimental testing of colour interactions in the receptive field of a dark sustained unit (left) and putative model of colour-specific connections of this unit matched by the program (right)

GCs of this type differ from each other by the patterns of response to colour stimulation. Some cells respond with sustained discharge to some of the colours and with short spike bursts to other colours. Some cells respond with bursts to the stimulus switching off, and some cells do not. These facts suggest developing of a more complex model.

3. Light sustained units

Light sustained units respond when the receptive field area is brighter than the surround. We expected these cells to have the colour properties opposite to those of dark sustained units. However it seems that these cells are less diverse in their responses to colour stimulation.



Experimental testing of colour interactions in the receptive field of a light sustained unit (left) and putative model of colour-specific connections of this unit matched by the program (right)

Conclusion

Retinal GCs demonstrate complex and unexpected colour properties that can be revealed by cone-isolated colour stimulation. To understand putative connections of the GC with the cones of different spectral types the simple static network model was developed and tested. Experiments with the model have shown that:

1. In some cases the solution (the synaptic weights of connections) can be easily found, but sometimes it is difficult. It seems that the scheme with two bipolar cells with potential connections with cones of all types is not always sufficient for explaining the observed colour properties of the unit.
2. GCs sometimes respond with sustained discharge to one colour stimulus and with short bursts to another. To account for this feature the model components should possess temporal properties.

References

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