Information processing in the outer retina of fish
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Summary

Visual perception starts in the retina with the transduction of light into neuronal signals. Light can be considered to be visual information. The retina has evolved such that it can process and code this information efficiently, before it sends it to the brain. To achieve this, the retina consists of multiple layers of neurons, which can be subdivided in many different types, each with their own specific function regarding the process of coding visual information. The research described in this thesis focuses on the first steps of this process, which starts with the absorption of photons by visual pigments in so-called photoreceptors. This absorption leads to a conformational change of the visual pigment, which sets off a biochemical chain reaction, which ultimately results in a hyperpolarization of the voltage over the photoreceptor membrane. Photoreceptors communicate with bipolar cells and horizontal cells by releasing neurotransmitter molecules at a signal junction called a synapse. Bipolar cells and horizontal cells express receptors at the synapse, which bind the released neurotransmitter, which consequently leads to polarization of these cell types. Bipolar cells subsequently communicate with ganglion cells, whereas horizontal cell provide inhibitory feedback to photoreceptors.

Processing of visual information is complicated by the large range of light intensities occurring naturally. In a single visual scene the difference in intensity can be thousand fold, whereas the difference between day and night can be more than trillion fold. The retina possesses various mechanism to remain sensitive over this entire range. For instance, there are two types of photoreceptors: rods and cones. Rods are very sensitive to light and are responsible for vision at low light intensities. Cones are less sensitive to light and are involved in vision during the day. By using two photoreceptors with different sensitivities the retina can remain responsive over the entire range of light intensities the occurring during a day-night-cycle.

The retina of fish, used in this thesis, has a number of different cone types. These cones differ functionally in the way they respond to different colors of light. This so-called spectral coding forms the basis of color vision. In chapter 2, a description can be found of the spectral coding of four different cone types of the zebrafish. Based on the responses of these cones,
predictions are made regarding the composition of the visual pigments they
contain. Knowledge of the spectral sensitivities of zebrafish cones is
important for future research in the field of visual neuroscience, in which
this organism is becoming increasingly popular.

A visual scene contains a large amount of redundant temporal, spatial, and
spectral information. This redundant information is brought about by the
structure of everyday visual scenes: relatively large areas of more or less
equal color and intensities, alternated with abrupt transitions to others
colors and intensities. Transmitting all this information would be a very
inefficient way of information processing. Therefore, various processes are
present in the retina which diminish the amount of redundant information.
In the remaining chapters of this thesis, retinal mechanism are studied,
which contribute to this optimization process.

In chapter 3, the responses of cones to a so-called natural stimulus are
studied in the goldfish retina. Such natural stimuli are characterized by a
skewed distribution of occurring light intensities. De vast part of the
stimulus consists of light with a low intensity alternated with brief peeks of
light with a high intensity. However, the cone response to this stimulus
display a more normal distribution. This means that the skewed distribution
of stimulus intensities is redistributed into a normal response distribution.
This way the available response levels of cones is more optimally utilized.
The light responses of cones are also used to validate a mathematical cone
model. This model consists of several equations, which describe the
biophysical processes underlying the light response of photoreceptors. A
number of these equations are of nonlinear nature. This model turns out to
give a better description of cone responses to a natural stimulus than
conventional linear and logarithmic models.

The goldfish retina contains different types of horizontal cells. Horizontal
cells are excited by neighboring photoreceptors. Thus, the response size of
horizontal cell are a measure for the average global light intensity of a part
of the retina, whereas the response of a photoreceptor reports the local light
intensity. Because horizontal cells provide inhibitory feedback to
photoreceptors, by which they are excited, the signal ultimately transmitted
to bipolar cells is the difference between the global light intensity, as sensed
by horizontal cells, and the local light intensity, as sensed by
photoreceptors. In contrast to the different cone-types, not only the
response size of horizontal cells, but also the direction of the response,
depends on the color of the stimulus. Monophasic horizontal cells hyperpolarize of the entire stimulus spectrum, but biphasic horizontal cells only hyperpolarize to blue light and depolarize to red light, and triphasic horizontal cells hyperpolarize to blue and red light, and depolarize to green light. The response patterns are caused by the selective contacts, which horizontal cells make with the different cone-types and the feedback form horizontal cells to cones. In chapter 4, a natural stimulus is used to evaluate the visual information processing in monophasic and biphasic horizontal cells. Like cones, horizontal cells display a redistribution of light intensities over their response range, but no further optimization can be seen relative to cones. Because horizontal cells pool the signal of several photoreceptors, considerable improvement of the so-called signal-to-noise ratio does occur.

In chapter 5, the influence of two different cone chloride currents on the size of feedback from horizontal cells is described. Both activation of the GABA-induced chloride current as well as the calcium-dependent chloride current lead to a reduction of the size of this feedback. This effect is explained by means of a model of the synapse between photoreceptors and horizontal cells. Although, both currents regulate the size of feedback it is proposed that this occurs relatively slowly and globally in the case of the GABA-induced chloride current, whereas this happens rapidly and locally in the case of the calcium-dependent chloride current. Possibly, the GABA-dependent chloride current is involved in modulating the size of feedback during the day-night-cycle, and the calcium-dependent chloride current regulates the balance between excitation and inhibition in one adaptive state.

Finally, the main findings are recapitulated and discussed in chapter 6.