Transformation of color signal in human retina

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Abstract

Nowadays it is obvious that human eye has a very difficult structure and our vision system is so complicated. In this work, we look into the details of transformation of color signal in human retina. Firstly, we review the human visual system. We start from some biological ideas and definitions and then, we look into the details of structure of human retina. Secondly, we consider in details a Multi – Stage Color model, represented the process of transformation of color signal in retina. Then we construct an artificial neural network (ANN), based on this model. This ANN calculates the results of transformation of color signal after each retina's level. Also, ANN constructed so, that can be changed. It is possible to add or remove some new elements in any layer, add or remove a layer, and make new connections between any elements of neural network. Finally, we make a few experiments using this network.

Chapter 1

Introduction

Life, from beginning to end, is uninterrupted process of receiving, processing and appraisal information. Information arrives from environment. On basis of this information we decide to do something or to disregard it.

Center of information's treatment is brain. But brain itself can't hear, see and feel any sensations. Organs of sense are sources of information for brain. One of sense's organs is eye.

The eye is striking organ with very difficult structure and therefore it has composite function. It can detect differences between luminosity, differ small details, perceive color, form, size, character of surface, movement, glimmer and pass information about it to the brain such that human feel and after that assimilate outside world from nearest environment to farther stars.

Because our vision system is so complicated, eye is a subject of great number of structural, anatomical, functional and physiological inquiries. Many scientists make important contributions to this field of science. Among them, there are Russell L. and Karen K. De Valois. They propose a Multi-Stage Color Model, which represents the process of transformation and recognition of color signal.

Some words about why we dwelled on this model. The first models of color vision were essentially simple one-stage models. There are at least three good reasons why this was so. First, there are valid scientific justifications for developing as simple theories as possible. Secondly, various complexities of vision with which we are now acquainted were not then well understood. Thirdly, most problems were considered individually, in isolation from other visual processes. If any specific problem is examined in isolation, it is often possible to find a one-stage solution to it, and this is what happened in the case of early theoretical formulations of various aspects of vision. However, visual system does not have the luxury of solving just one specific problem at a time. Rather, it must work towards the solution of many specific problems simultaneously, especially in the early stages of processing. Moreover, the solution of one problem must not entail steps, which prevent the later solution of other problems.

Furthermore, the visual system has many sharp constraints in terms of the types of algorithm that can be implemented, the distances over which interactions can take place, and so forth. Finally, there is the special constraint in the early stages of the visual system that all information must be passed through the bottleneck of the optic nerve (De Valois & De Valois, 1998).

Both of classic theories of color vision in the 19 century, those of Helmholtz (1867) and of Hering (1878), were, as first formulated; essentially one-stage models which accounted for only small and largely nonoverlapping fractions of the facts. That these two theories for so long coexisted in opposition to each other was primarily due to the fact that their adherents argued from different sets of findings, from color-mixing experiments on the one hand and perceptual observations on the other. Although there were several proposals of two-stage models that joined these supposedly-opposing ideas (e.g. Donders, 1881; von Kries, 1905), they were not taken very seriously, primarily because the field was long dominated by those whose primary interest lay in questions that are primarily determined at the receptor level.

Jameson and Hurvich (1955, 1956) quantitatively formulated a two-stage model. Soon after then physiological evidence from primates (De Valois, Smith, Kitai & Karoly,1958; De Valois, 1965; De Valois, Abramov & Jacobs, 1966; Wiesel & Hubel, 1966) and fish (Svaetichin & MacNichol, 1958) provided firm evidence for the actual existence of spectrally-opponent cells in the visual path way. Since that time, some version of a two-stage model encompassing three cone types combined in a later opponent organization has become the accepted dogma in color vision, the Standard Model (e.g. Guth, Donley & Marrocco, 1969; Ingling & Tsou, 1977; Boynton, 1979; Guth, Massof & Benzchawel, 1980).

The authors of Multi-Stage Color Model (Russell L. De Valois & Karen K. De Valois) in accord with Hering's suggestions, when the Zeitgeist at the time was strongly apposed to the notion, the earliest recordings revealed a discrepancy between the Hering – Hurvich – Jameson opponent perceptual channels and the response characteristics of opponent cells in the macaque lateral geniculate nucleus (LGN). Thus authors noted, "the good agreement between recording and psychophysical data breaks down at the short wavelengths" and suggested that "it may indicate that the blue system is amplified in effect at some cortical level" (De Valois *et al.*, 1966). Later investigators also found

the same discrepancy, with different stimulation techniques (Derrington, Krauskopf & Lennie, 1984; Kaplan, Lee & Shapley, 1990), and made the same point. Recently De Valois & De Valois suggests a third stage to reconcile this discrepancy.

There are other factors besides the discrepancy between the characteristics of monkey LGN opponent cells and perceptual color space led us to consider a multi-stage color model. One is that, because of the spatial arrangement of their inputs from different cone types, most LGN cells respond to both color and luminance variations, and confound them. As shown by Wiesel and Hubel (1966), most opponent cells in the parvocellular LGN layers appear to have input in the RF center from one cone type, and in the surround from a different cone type. Such cells have sometimes been incorrectly characterized (e.g. Lennie & D'Zmura, 1988) as having a receptive field (RF) that is both spatially and chromatically opponent. However such a cell should be considered to have not one but two different RF organization, one for luminance and the over one for color (De Valois & De Valois, 1975). A cell with an excitatory L-cone center and an inhibitory M-cone surround, for instance, will have a center-surround antagonism for luminance variations, since intensity changes will drive both L and M cones in the same directions and they feed into the LGN cell in opposite directions. An equiluminant color change, however, will drive the L and M cones in *opposite* directions and thus produce a center-surround synergy. One would thus predict not only that such an LGN cell would fire to both luminance and color changes (thus confounding these perceptually very different variables) but that it would have different spatial and temporal tuning characteristics for the two. These predictions have been verified (De Valois, Snodderly, Yund & Hepler, 1977). Thus a second goal for Multi-Stage Color Model is to provide, at a third processing stage, for the unconfounding of color and luminance.

A third goal for Multi-Stage Color Model is to incorporate recent information on retinal anatomy and to explore the extent to which essentially random connectivity (as suggested by the anatomy) might result in a sensible color organization.

Finally, much recent anatomical evidence confirms the extreme paucity of S cones. The Standard Model has one color system (the RG system) based on the outputs of the L and M cones, some 90-95% of the cone population, whereas the whole YB system is centered on just the remaining 5-10% of the cones, the S cones. Such an imbalance seems inherently implausible, and one of the considerations that led De

Valois and De Valois to model was that of attempting to arrive at a more balance arrangement between the inputs to the red-green and the yellow-blue color systems. One can reasonably argue that the preponderance of L and M cones reflects the fact that these cone types alone are used for luminance detection. However, with current color models, this still leaves one with either an imbalance between the two chromatic systems of the spectrally – opponent information from L and M cones contributes to color vision.

At first part of work, we will give target setting: biologic ideas and definitions, introduction of Multi-Stage Color Model and definitions of neuron network. Second part will be devoted the Multi Stage Color Model. Finally, we will present an artificial neural network, which supposed to learn some new about of the retina works. So, the aims of this work are as follows:

- Learn how Multi Stage Color Model woks.
- Construct a simple network that will be represents the works of De Valois and De Valois model. Using this net, we could know how color signal is transformed after every layer of Multi Stage Color Model (we could know the correct output after each layer).
- Use Multi Stage Color Model as a framework in order to build an artificial neural network that describes how color signal is transformed after getting it to the retina. The stages in this network have to be represented in a way that enables testing of the output at each intermediate level according to the Multi Stage Color Model predictors. Also this neuron network have to be build so, that it can be changed (the unknown defines anatomical representation can be studied and added to the network during in the course of learning process).

Chapter 2

Human visual system

Human's visual perception begins from visual image (visual image is image, which human can perceive).

It is possible to compare optics of eye with optics of camera, although this comparison vastly simplifies situation. Each element of eye plays important role in the act of vision. Figure 1 shows the basic elements of the eye.



Figure 1 The anatomy of the human eye (Peter K. Kaiser & Robert M. Boynton, 1996)

The basic optical element of eye is cornea. Cornea bends the light rays, which proceed farther, across the pupil – the aperture at the center of the iris (iris is the colored part of the eye which surrounds the pupil). The pupil and iris work like diaphragm of camera. Then the light rays bend by the lens, and proceed further, on the retina. The lens can change its optical power (focal length), just as camera sharpens the image. Figure 2 and figure 3 shows what the lens does.



Figure2 Refraction of lens (case when object is far away) (Peter K. Kaiser & Robert M. Boynton, 1996)

If the object is far away, the lens is kind of skinny, and if the object is nearby, so the lens becomes fatter by adjusting its focal length.



Figure 3 Refraction of lens (case when object is nearby) (Peter K. Kaiser & Robert M. Boynton, 1996)

The retina is light sensitive tissue which lie inside of the eyeball and which works like a photosensitive film in the camera. Retina covers about 65 percent of eye's interior surface. The central part of the retina (about 10 percents) is called macula – small sensitive area of the retina, which provides central vision. This area contains the most part of the cone type of photosensitive cells. Cones provide the eye's color sensitivity. All cones can be divided into "red" cones (64%), "green" cones (32%), and blue cones (4%) (K. Kaiser & M. Boynton, 1996) Distal part of the retina mainly is responsible of the spatial vision and vision at the low light levels and contains photosensitive cells, which are called "rods". The rods are more numerous of the photoreceptors, some 120 million, and are more sensitive than the cones. However, they are not sensitive to color. They are responsible for our dark-adapted vision. Receptors (photosensitive cells rods and cones), bipolar and ganglion cells are the most important neural cells (neurons) in the retina, which pass visual information. Each of ganglion cells can collect information from many receptors, possibly from few hundreds receptors. Figure 4 represents the basic layers of the retina.

A neural impulse goes across the optical nerve to the brain where the visual picture is formed. Optical nerve connects the retina to the lateral geniculate layer (LGN), which is in the middle of the brain. The LGN consists of six layers; three of the layers receive input from same side of the eye and other three from the opposite side of the eye. The bottoms two of layers are the magnocellular layers, these layers work for non-color vision processing. The other four layers are the parvocellular layers which are very important for color vision.



Figure 4 Schematic diagram of structure of retina (Peter K. Kaiser & Robert M. Boynton, 1996)

Just in retina and higher parts of brain with help of chemical and electrical processes information about color, size, movement and other spatial and temporal descriptions of representation to synthesize with the same, that is kept at memory. This information provides visual perception.

Chapter 3

Proposed color processing model

The Multi-Stage Color Model (Russell L. De Valois & Karen K. De Valois, 1993) lies at heart of this work. This model reproduces the process of absorption and transformation color signal from the moment of getting signal to retina to the moment of passing signal in optical nerve, which transmit signal into the brain. Wavelength and luminosity are the basic properties of the signal.

The main property of this model is that it consists of three layers; therefore, we can trace what happen with signal after passing each layer. And as far as our aim is to try to construct an artificial neural network (ANN), it so important to know how the signal is transformed after passing each layer (we have to know it for the training of ANN). So, we can build ANN for each layer and then combine them.

The Multi-Stage Color Model consists of three layers:

- 1. The layer where incoming signal is filtered.
- 2. The layer where opponent signals are formed.
- 3. The layer where signals are summed.

Consider now in detail the organization of each layer.

3.1 First stage of the model

At this layer special photosensitive cells (cones) make a filtering process of incoming signal. There are three types of photosensitive cells. S – cones absorb signal with wavelength from 370nm to 530nm. M – cones absorb signal with wavelength from 400nm to 650nm. L – cones absorb signal with wavelength from 400nm to 700 nm. The maximum absorbances are in 420nm, 540nm, 560nm respectively. Figure 5 shows the absorption curvse (Smith-Pokorny, 1975).

S – cones can now be distinguished anatomically, and constitute only some 2-10% of the cone population, depending on eccentricity, in human retina (Ahnelt, Kolb & Pflug, 1987; Curcio, Allen, Sloan, Lerea, Hurley, Klock & Milan, 1991). One can not provide similar exact information on L and M cones, but one may assume that there are two times

more L – cones from M – cones. Therefore the proportions between the cell populations are L:M:S = 10:5:1.



Figure 5 Absorption curves for the three pigments (Smith-Pokorny (1975) function)

Also note that S – cones are regularly arranged, but L – cones and M – cones are randomly arranged, so, as a result there are clumps of L-cones and less constantly clumps of M-cones.

There are a lot of cones in the retina (around 7 million), but for understanding mechanism of interaction between cells in the retina it is enough to consider their minimum set.

The process of filtration happens in the following way, each of the cones absorb all signal, but pass only part, which agrees with admission diapason. Following formula describes the process of filtration for each type of cells as a function of (i):

$$y_i = y_i * k_i$$
 (i = 370, 380, ... 670), (1)

Where k_i is maximal luminosity, which can absorb, for a given i (we take values from table 1 in Appendix), and y_i is the luminosity of incoming signal, for a given i.

3.2 Second stage of the model

There are two synaptic levels in the retina: the receptor – horizontal cell – bipolar synapse and bipolar – amacrine cell – ganglion cell synapse (Russell L. De Valois & Karen K. De Valois, 1993).

The first assumption of this stage is the presence of two different types of bipolar cells (according to anatomical evidence) which picking up from the cones: midget bipolar (and then midget ganglion cells) which (in the central part of the retina: $5 - 10^{\circ}$ (Curcio & Allen, 1990)) connect just a single cone and diffuse bipolar which connect with a group of neighboring L-cones and M-cones (Boycott & Dowling, 1969).

The anatomical evidence indicates that in the periphery L and M-midget bipolar contacts with more than one cone and they do not differentiate the M-cones from L cones (Mariani, 1984b). The S-midget bipolar in the periphery also contacts with more than one cone, but they connect only with S-cones, not with L or M-cones (Mariani 1984a).

Both midget bipolar and diffuse bipolar have two type cells of contacts with receptor: one invaginating and one flat midget bipolar. When light changes one (invaginating type of contact) depolarizing to increments and other (flat midget bipolar) to decrements. The midget bipolar contacts with midget ganglion cells connect to the parvocellular geniculate layer. The diffuse bipolar contacts with parasol ganglion cells connect to the magnocellular LGN layer (Russell L. De Valois & Karen K. De Valois, 1993).

Each of the cones is also connected with four horizontal cells, which picks up from a number of surrounding cones (Boycott & Sperling, 1987). The anatomical evidence indicates that the horizontal cells connect to all cones in the region (Dacheux & Ravila, 1990). Assuming this, horizontal cells would produce the LMS signal and for each wavelength (i) we will have own LMS_i signal. Horizontal cells are summing the signals from all cones in the region:

$$LMS_i = L_i + M_i + S_i$$
 (i = 370, 380, ... 670), (2)

Where LMS_i is the signal, which horizontal cells produced, L_i is signal, which L – cones filtered, M_i is the signal, which M – cones filtered, S_i is the signal, which S – cones filtered.

Because the number of the surrounding cones are 16, so the LMS signal will be calculate follows:

We have 16 cones for the center signal too. Thus the formulas for calculation of the opponent signals are:

for direct input
$$\begin{cases}
L_{0i}^{+} = 16 \bullet L_{i} - LMS_{i} \\
M_{0i}^{+} = 16 \bullet M_{i} - LMS_{i} \\
S_{0i}^{+} = 16 \bullet S_{i} - LMS_{i}
\end{cases}$$
(3)

for indirect input
$$\begin{cases} L_{0i}^{-} = -16 \bullet L_{i} + LMS_{i} \\ M_{0i}^{-} = -16 \bullet M_{i} + LMS_{i} \\ S_{0i}^{-} = -16 \bullet S_{i} + LMS_{i} \end{cases}$$
(4)

The cell, which has L – cone center input receive the antagonistic input only from M – cones and vice versa.

3.3 Third stage of the model

On the third layer signal from the midget bipolar cells across the amacrine cells pass to the ganglion cells, and ganglion cells make sum of all incoming signals and then transmit this sum, by optic nerve, to the brain. Let's make the following table of symbols:

 L_0^+ is L_0 , L_0^- is (-L₀); M_0^+ is M_0 , M_0^- is (-M₀); S_0^+ is S_0 , S_0^- is (-S₀).

Figures 6 and 7 show how the model separates color and luminance (De Valois & De Valois, 1975). These regions of a set of cones are called receptive fields (RF). As figure 5 shows cell L_0 (L - M) has an excitatory center and inhibitory surround RF in response to

luminance increment. In other way, L_0 has a uniformly excitatory RF when color change to long wavelength. The cell M_0 has inhibitory center and excitatory surround RF for luminance increment, but M_0 has uniform excitatory RF for color change towards long wavelengths (like the cell L_0).



Figure 6 Distinguishing cone input maps from receptive fields (after De Valois & De Valois, 1975). An LGN opponent cell with one cone type feeding into the center and another into the surround has not one, but two different RFs. An L₀ cell has an excitatory center and inhibitory surround (top) for luminance increments, but a uniform excitatory RF for color shift towards long wavelengths

Figure 7 shows what happens when we combine the outputs of different cell types (for example $L_0 - M_0$).



Figure 7 Combining stage 2 units in different ways at stage 3 would separate color and intensity information (De Valois & De Valois, 1993)

Since, the intensities of L_0 and M_0 are opposite their responses to intensity changes cancel each over. Their responses to color changes sum since their color RFs are the same. The results for other combinations are: $L_0 + M_0$ sums luminance and cancel color; Mo – Lo sums color and cancel luminance; $M_0 + L_0$ sums luminance and cancel color (Lennie & D'Zmura, 1988).

Now consider the chromatic axis rotation. Figure 8 shows a simple diagram of a color axis rotation.



Figure 8 The S-opponent units are added to or subtracted from the L_0 and M_0 difference signals to produce the proposed perceptual color system at stage 3 (De Valois & De Valois, 1993)

The outputs of the S_0 opponent cells (doubled in weights) are added (or subtracted from) to $M_0 - L_0$ and $L_0 - M_0$ cells and we get four perceptual color systems which give red – green and yellow – blue axes of the perceptual color space. Adding S_0 (solid line) to $M_0 - L_0$ results blue and subtracting S_0 from it (dashed line) results green. If S_0 is added to $L_0 - M_0$ results red and subtracting results yellow. In this stage the proportions of $L_0:M_0:S_0$ are 10:5:2 (Russell L. De Valois & Karen K. De Valois, 1993).

Figure 9 shows the complete diagram for the third stage. This diagram includes color and intensity information when the second stage units sums in different combinations. In the horizontal rows we add together cells with same luminance RFs but different color RFs (sum luminance and cancel color). In the vertical columns we sum cells with different luminance RFs but with same color RFs (cancel luminance and sum color). This diagram is final result for the third stage and for Multi-Stage Color Model.



Figure 9 A complete diagram of the proposed stage 3, combining the features outlined in Figs 7 and 8 (De Valois & De Valois, 1993)

Chapter 4

Artificial neural network

4.1 General principles of artificial neural networks (Robert Callan, 1999)

The aim of our work is construction of a neural network, which realizes Multi – Stage Color Model. This chapter explains the basic ideas of neural network's theory.

Artificial neural network it is a set of *elements*, which connects in some way. These elements, which also are called neurons or nodes, are simple processors. They combine the incoming signal and calculate an output signal. Element can pass significance of output signal of other elements by connections. Depending on the value of weighting coefficient the signal, which element passes on the weight, intensifies or weakens. Figure 10 shows an element of ANN.



Figure 10 Element of ANN (Robert Callan, 1999)

Artificial neural networks are systems of parallel computing. They consist of large number of simple processors, which interact between each other. Usually these processors are very simple. Each processor of ANN works with signal, which it sends periodically to the other processors. But when we join processors in to the same network this locally simple network is capable to realizes quite difficult tasks.

The most types of neuron networks have a set of total characteristics, which we can present with help of the following abstractions:

> Quantity of simple processors Structure of connections The rule of expansion of signals in the network The rule of combining of incoming signals

The rule of computation of activation signal The learning rule, which corrects the weights of connections

Let us consider these characteristics in more detail:

• Quantity of simple processors

Each processor is connected with a set of input and output connections. By input connections signals from other elements of the ANN come to this element and by output connections signals from this element pass to the other elements. Some of ANN's elements are designed for getting signals from environment (that is why they are called entering elements) while some of them, which are used to output the results of computing to the environment (that is why these elements are called exit elements).



Figure 11 Multi – layer perceptron (Robert Callan, 1999)

• Structure of connections

Structure of connections reflects how elements of ANN are joined together. Each connection is defined by three parameters: by element, from which this connection issues; by element towards to which this connection direct; and by number (usually it is real number), which indicate weighting coefficient (i.e. weight of the connection). Negative value of weight corresponds to suppression the activity of corresponding element. Positive value corresponds to intensification its activity. Absolute value of weighting coefficient characterizes strength of connection.

Usually, structure of connections is presented in a form of weighting matrix W. At this matrix each element w_{ij} presents the value of the weighting coefficient coming from

element i to element j. For description the structure of connections one can use not only one, but several weighting matrices (if the elements of network are grouped together).

• The rule of expansion of signal in the network

Each concrete model of neural network supposes availability of certain rule. By this rule renovation of network elements station takes place (i.e. it is the rule of rearrangement incoming signals and computations outgoing signal). Also this rule defines how signal will be sent.

• The rule of combining of incoming signals.

Rather often incoming signals of the element are combined by summing the values of weighting coefficients:

$$u_{j} = \sum_{\substack{i=1\\j=1}}^{m} x_{i} * w_{ij}$$
 (5)

Where u_j is result of rearrangement j element's entry, x_i is output of element i, n is number of equipped connections, w_{ij} is connection's weight between element i and element j.

Also other forms of rearrangement incoming signals are used. One of oftenencountered method is to review square of difference between the value of connection's strength and value of transmitted signal for each incoming connections of a particular element, which after that are summarized.

• The rule of activation signal

For all elements we need a rule of exit value's computation, which is supposed to pass to other elements or to environment. This rule is called *activation function* and corresponding exit value is called *activity* of corresponding elements. Activity can be represented by arbitrary appearance of certain real value or by real value from limited interval of values (for example from interval [0, 1]). Also, it can be represented by certain value from specified intermittent set of values (for example [0, 1] or [-1, 1]). At the entry of activation function is a value of combined input of element. Below there are examples of different activation functions are given.

Identical function:

Identical function means that value of activity (signal, which is sent to other elements) turns out equal rearrangement entry exactly.



Figure 12 Plot of Identical function

Threshold function:

Threshold function confines activity by 1 or 0. It is depends upon value of rearrangement entry in comparison with certain threshold value θ .

$$f(u) = \begin{cases} 1, & \text{if } u_j \ge \theta \\ 0, & \text{if } u_j < \theta \end{cases}$$



Figure 13 Plot of Threshold function

Piecewise-linear function:

$$f(u) = \begin{cases} 1, & \text{if } u_j \le a_2 \\ u, & \text{if } a_1 \le u_j \le a_2 \\ 0, & \text{if } u_j < a_1 \end{cases}$$



Figure 14 Plot of Piecewise-linear function

Sigmoid function:

This is most useful form of function. Outgoing values of this function continuously fill diapason from 0 to 1. For example following logical function:



Figure 15 Plot of Sigmoid funciton

• The learning rule, which corrects the weights of connections

The main feature of neuron networks is that they suppose presence rules with help of which network can be programmed automatically. The aim of learning is to change values of weights to get in result necessary characteristics of network's behavior.

Typical form of learning is *error-correction learning*. In that case, for each set of data which is given in the process of learning to network's entry, there is a well – known corresponding outgoing set. Usually, at the beginning of learning weighting coefficients are determined by casual way equally to small values. That is way at first appearance of learning sample's network it is very improbable that network can execute right output.

Differences between what we desired to have (correct output) and what we have (real output) is error, which can be used to correct the weights. Widrow-Hoff rule (delta-rule) is an example of rule of error's correction:

$$\Delta w = \imath * \delta * x$$

Where x is signal, which comes to outgoing element, η is learning rate (real number >0), δ is error calculated by the following ways:

$$\delta = t - y$$

Where y is real output, and t is desired output. New weighting coefficients are calculated by following form:

$$w = w + \Delta w$$

In the course of learning process weighting coefficients are given to input set by set and as a result of their working weighting coefficient are corrected until for all incoming sets errors will be a bit smaller then some sufficiently small value. In the end of learning process the network is tested on sets, which wasn't used in the learning.

4.2 Construction of an artificial neural network according to the Multi – Stage Color Model

In this chapter we consider how to build a neural network for each layer of Multi – Stage Color model. These will be nets, which show transformation of incoming signal from moment of getting it to the retina to the moment of passing signal to the optical nerve, but these nets will be not determine the luminosity of color signal.

Now we build neuron network for the first layer of Multi-Stage Color Model. Figure 16 shows how ANN for first layer looks in diagram.



Figure 16 ANN for the first layer of Multi Stage Color Model

The light is absorbed by the cones and each cone starts to make a filtering process for the incoming signal. The output for this layer is:

$$u_{ij} = x_i \bullet w_{ij}$$
 (i=1,2, ... 31) (5)
(j=1,2, ...16)

Where u_{ij} is element of column U_j (U_j is a column of values of signal filtered by cone j), x_i is value of strength of the incoming signal (i shows for which wavelength we calculate u_{ij}), w_{ij} is weight from node i to node j.

Matrix W₁ is a matrix of weights for first layer. This matrix is given by:

 $B = \begin{bmatrix} 0 & 0 & 0.35 & 0.35 & 0.34 & 0.34 & 0.35 & 0.38 & 0.42 & 0.49 & 0.56 & 0.67 & 0.78 & 0.88 \\ 0.95 & 0.99 & 0.99 & 0.93 & 0.82 & 0.67 & 0.53 & 0.4 & 0.29 & 0.2 & 0.14 & 0.09 & 0.06 & 0.04 & 0 & 0 \end{bmatrix}^{T}$

 $A = \begin{bmatrix} 0 & 0 & 0.36 & 0.36 & 0.33 & 0.3 & 0.29 & 0.28 & 0.3 & 0.34 & 0.39 & 0.47 & 0.55 & 0.63 \\ 0.73 & 0.83 & 0.91 & 0.96 & 0.99 & 0.98 & 0.93 & 0.85 & 0.74 & 0.61 & 0.47 & 0.34 & 0.24 & 0.16 \\ 0.105 & 0.068 \end{bmatrix}^{T}$

and the numerical values even taken in table 1 (Appendix).

After the filtering process signals go to the second layer. On the second layer signals from each cone transfer to the horizontal cells and also to the midget bipolar cells. Figure 17 shows the schematic form of neuron network for the second layer.



Figure 17 ANN for the second layer of the Multi Stage Color Model

Horizontal cells sum all the incoming signals. So, matrix W_2 is a matrix of weights between cones and horizontal cells. All values of elements of this matrix will be equal to 1.

	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
W –	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
$w_2 =$	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Also in this layer signals from cones transfer to the midget bipolar cells (each midget bipolar cell contacts only with one cone cell). Midget bipolar cells produce the "opponent" signals. In other words they excite or inhibit signals Excite and inhibit takes plase as follows: if signals, originating from M – cones keep the maximum value of strength midget bipolar cells excite these signals and inhibit signals, originating from L – cones, and vice versa. Signals, originating from S – cones be have as follows: if the value of strength of signal is more than 0 then midget bipolar cells excite these signals. Equations (3) and (4) describe inhibition and exciting processes.

Weights between cones and midget bipolar cells are equal to 16 if midget bipolar cells excite signals or –16 if midget bipolar cells inhibit signals. Thus:

$$W_{21} = diag[\pm 16]$$

W₂₁ is a matrix of weights between cones and midget bipolar cells.

Weights between horizontal cells and midget bipolar cells will be equal -1 if midget bipolar cells excite signals, originating from cones or 1 if midget bipolar cells inhibit signals, originating from cones. W₂₂ is a matrix of weights between horizontal cells and midget bipolar cells.

On the third layer signals from midget bipolar cells across amacrine cells propagate to the ganglion cells. Figure 18 shows the schematic form of neural network for third layer.



Figure 18 ANN for the third layer of Multi Stage Color Model

Unfortunately it is still a question what really amacrine cells do. But we just assume that amacrine cells sum all incoming signals (signals, which came from midget bipolar cells) and pass result of the sum to the ganglion cell. Also, we assume that our neuron network will contain two amacrine cells. Amacrine cell A_1 gets signal from midget bipolar cell, which connects with S-cone, and from midget bipolar cells, which connect with M-cones. Amacrine cell A_2 also gets signals from midget bipolar cell, which connects with S – cones, and get signal from midget bipolar cells, which connect with L – cones. Matrix W_{31} it is a matrix of weights between midget bipolar cells and amacrine cells:

Ganglion cell makes sum of all incoming signals and pass this sum to the optic nerve. We assume that weights between amacrine cells and ganglion cell are all equal to 1. Thus:

$$W_{32} = \begin{bmatrix} 1 & 1 & 1 \end{bmatrix}$$

Figure 19 shows the result of joining of artificial neural networks, which we constructed for each layer.



Figure 19 ANN for the Multi – Stage Color Model

Chapter 5

Experimental part

This part considers the results of experiment, given by our neural network. Figure 20 shows signal, which we have used as incoming signal. Table 2 (Appendix) contains more accurate values of the incoming signal.



Figure 20 Curve of incoming signal

As explained above, on the first layer cones make a filtering process for the input signal. S – cone makes filtering process according to:

$$u_{ij} = x_i \bullet w_{ij}$$
 (i = 1,2, ... 31)
(j = 1)

Where u_{ij} is an element of U_j , U_j is a column vector containing the signals filtered by S – cones, x_i is a strength (luminosity) of the input signal, and w_{ij} is the weight between the nodes i and S – cone cell. Note that only one S – cone is included to the model.

Figure 21 shows signal, which is filtered by S-cone cell. Table 3 (Appendix) contains more accurate values of this signal.



Figure 21 The response function of the first stage unit (S - cone)

M - cones make a filtering process also by the same scheme:

$$u_{ij} = x_i \bullet w_{ij}$$
 (i = 1,2, ... 31)
(j = 1,2, ... 5)

Where u_{ij} is an element of U_j , U_j is column vector containing the signals filtered by M – cone, x_i is the strength (luminosity) of the input signal, and w_{ij} is the weight between the node i and M – cone cell. Note that only five M – cone cells are included to the model.



Figure 22 The response function of the first stage units (M – cones)

Figure 22 shows signal, which is filtered by M-cone cells. Table 4 (Appendix) contains more exact values of this signal.

For L-cone cells situation also is the same. We use again form (5):

$$u_{ij} = x_i \bullet w_{ij}$$
 (i = 1,2, ... 31)
(j = 1,2, ... 16)

Where u_{ij} is an element of U_j , U_j is column vector containing the signals filtered by L – cone, x_i is the strength (luminosity) of the input signal, and w_{ij} is the weight between the node i and L – cone cell. Note that only ten L – cone cells are included to the model.

Figure 23 shows signal, which is filtered by L – cone cells. Table 5 (Appendix) contains more accurate values of this signal.



Figure 23 The response function of the first stage units (L-cones)

On the second stage signals from cones propagate to the horizontal cells and to the midget bipolar cells. Horizontal cells sum all incoming signals and produce LMS signal (form (2')). Figure 24 shows this LMS signal. Table 6 (Appendix) shows the values of LMS signal.



Figure 24 The response function of the second stage units (horizontal cells)

Also on the second layer midget bipolar cells produce "opponent" signal, i.e., midget bipolar cells excite or inhibit signals, which originated from cones. Firstly, bipolar cells define which from signals (now we consider only the signals, which came from M – cone cells and from L – cone cells) contain the highest value of absorption. From table 7 (Appendix) we can see that signals, which came from L – cone cells contain the biggest value, therefore midget bipolar cells will excite signals, which came from L-cone cells and:

$$L_{0ii}^+ = 16 \bullet L_i - LMS_i$$

Where L_{0ij}^{+} is a signal after exciting, i shows for which wavelength midget bipolar cell number j makes exciting, L_i is the signal from L-cone cell, and LMS_i is signal, which is produced by horizontal. Figure 25 shows the result of exciting. Table 8 (Appendix) contains values of this signal.



Figure 25 The response function of the proposed cone-opponent type L₀

Correspondingly, midget bipolar cells, which get signal from M-cone cells, will inhibit these signals as:

$$M_{0ii}^- = -16 \bullet M_i + LMS_i$$

Where M_{0ij}^{-} is the inhibited signal, M_i is the signal, filtered by M – cone cells, and LMS_i is the signal, produced by horizontal cells. Figure 26 shows the inhibited signal. Table 9 (Appendix) contains values of inhibiting signal.



Figure 26 The response function of the proposed cone-opponent type M₀

We assume that midget bipolar cells excite any non – zero signal from S – cones and inhibit zero – signals. In our experiment percent of absorption is 0.345; therefore midget bipolar cells excite the signal:

$$S_{0ii}^+ = 16 \bullet S_i - LMS_i$$

Where S_{0ij}^+ is the excited signal, M_i is signal, which is filtered by M – cone cells, and LMS_i is signal, produced by horizontal cells. Figure 27 shows the signal. Table 10 (Appendix) contains values of this signal.



Figure 27 The response function of the cone-opponent type S₀

On the third layer signals from midget bipolar cells propagate to the amacrine cells. In our neuron network there are two amacrine cells. They just sum signals, which originated from the midget bipolar cells, and pass the results to the ganglion cell. Consider an amacrine cell A_1 . It sums signals from 6 midget bipolar cells (5 signals from midget bipolar cells which connect M – cones and 1 signal from the midget bipolar cell which connects a single S – cone). Thus:

$$Sum_{A_1} = S_{oj}^+ + \sum_{i=1}^{n=5} M_{0i}^-$$

Where M_{0i}^{-} is signal which midget bipolar cell i receives from M-cone cell inhibits it, S_{0j}^{+} is signal which midget bipolar cell j receives from S-cone cell and excited it. Figure 28 shows the result of this summation and table 11 (Appendix) contains the values of summation.



Figure 28 The response function of the third stage unit

The same situation happens with amacrine cell A_2 . It sums signals from 11 midget bipolar cells. The result of this summation is:

$$Sum_{A_2} = S_{0j}^+ + \sum_{i=1}^{n=10} L_{0i}^+$$

Where L_{0i}^+ is signal which midget bipolar cell i receives from M – cone cell and inhibits it, S_{0j}^+ is signal which midget bipolar cell j receives from S – cone cell and excited it.



Figure 29 The response function of the third stage unit

Figure 29 shows result of this summation and table 12 (Appendix) contains values of the summation. Figure 30 shows the transformed color signal which ganglion cell pas to the optic nerve and table 13 (Appendix) contains values of this signal.



Figure 30 The response function of the third stage unit

We considered in detail what kind of transformation takes place with signal on each layer. Let's consider how the network detects the color of an incoming signal. As shown in figure 9 all incoming signals divide into four color classes: blue, green, yellow, red.

5.1 Transformation of blue color signal

All signals, which belong to this color class have maximum value of luminosity in M - cones area and also they have some non - zero values in S - cones area (figure 31).



Figure 31 Curve of incoming signal

Basing on this rule we build the teaching process for our network. The results of teaching process are as follows:

Matrices W_1 and W_2 will remain unchanged. W_{21} (matrix of weights between cones and midget bipolar cells) is a diagonal matrix with the following elements on diagonal:

$W_{21} = \begin{bmatrix} 16 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & $																	
$W_{21} = \left[\begin{array}{cccccccccccccccccccccccccccccccccccc$		16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
$W_{21} = \left[\begin{array}{cccccccccccccccccccccccccccccccccccc$		0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0
$W_{21} = \begin{bmatrix} 0 & 0 & 0 & -16 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & $		0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0
$W_{21} = \begin{bmatrix} 0 & 0 & 0 & 0 & -16 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & $		0	0	0	-16	0	0	0	0	0	0	0	0	0	0	0	0
$W_{21} = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 16 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & $		0	0	0	0	-16	0	0	0	0	0	0	0	0	0	0	0
$W_{21} = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 16 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & $		0	0	0	0	0	16	0	0	0	0	0	0	0	0	0	0
$W_{21} = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 16 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & $		0	0	0	0	0	0	16	0	0	0	0	0	0	0	0	0
$w_{21} = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & -16 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 &$	117	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0
$\begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & -16 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0$	$W_{21} =$	0	0	0	0	0	0	0	0	-16	0	0	0	0	0	0	0
$\begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 $		0	0	0	0	0	0	0	0	0	-16	0	0	0	0	0	0
$\begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 $		0	0	0	0	0	0	0	0	0	0	-16	0	0	0	0	0
$\begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 $		0	0	0	0	0	0	0	0	0	0	0	-16	0	0	0	0
$\begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 $		0	0	0	0	0	0	0	0	0	0	0	0	-16	0	0	0
$\begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 $		0	0	0	0	0	0	0	0	0	0	0	0	0	-16	0	0
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	-16	0
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-16

On the second layer the matrix W_{22} (the matrix of weights between horizontal cells and midget bipolar cells) is:

On the third layer we have two matrices of weights: W_{31} and W_{32} (matrices of weights between amacrine cells and ganglion cell). Matrix W_{31} represents the weights between midget bipolar cells and amacrine cells, as follows:

Matrix W_{32} includes the weights between amacrine cells and ganglion cell and it will always remain constant. The result of transformation of blue color is shown in figure 32.



Figure 32 The response function of the third stage unit

One can see from this picture that the signal from S-cone (S₀) is added to $M_0 - L_0$ cell to give blue.

5.2 Transformation of green color signal

Signals from this color class have maximum value of luminosity in the M – cones area (figure 33).



Figure 33 Curve of incoming signal

Teaching process is as follows:

Matrices W_1 , W_2 and W_3 forming the first, second and third layer respectively always remain constant. Matrices W_{21} and W_{22} behave as in the case for blue color. Matrix W_{31} is as follows:

The result of transformation of green color signal by ganglion cell is shown on figure 34. We can see that blue part of incoming signal is subtracted from $M_0 - L_0$ cell to represent green.



Figure 34 The response function of the third stage unit

5.3 Transformation of yellow color signal



Yellow color signals have maximum value of luminosity in the L – cones area (figure 35).

Figure 35 Curve of incoming signal

Teaching process is as follows:

Matrices W_1 , W_2 and W_3 forming the first, second and third layer respectively always remain constant. Matrix W_{21} is diagonal matrix:

	[16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0]
	0	-16	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	-16	0	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	-16	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	-16	0	0	0	0	0	0	0	0	0
117	0	0	0	0	0	0	0	-16	0	0	0	0	0	0	0	0
$W_{21} =$	0	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	16	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	16	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16

Matrix W_{22} is as follows:

Matrix W_{31} behave as in the case for green color.

The result of transformation of yellow color signal by ganglion cell is shown on figure 36. The blue part of the incoming signal is subtracted from $L_0 - M_0$ cell to give yellow.



Figure 36 The response function of the third stage unit

5.4 Transformation of red color signal

Red color signals have maximum value of luminosity in L-cones area and also these signals have some values in S-cones area (figure 37).



Figure 37 Curve of incoming signal (red color)

Teaching process is as follows:

Matrices W_1 , W_2 and W_3 forming the first, second and third layer respectively always remain constant. Matrices W_{21} and W_{22} behave as in the case for yellow color. Matrix W_{31} behave as in the case for blue color. The result of transformation of re color signal by ganglion cell is shown on figure 38. The blue part of incoming signal is added to $L_0 - M_0$ to represent red color.



Figure 38 The response function of the third stage unit

Chapter 6

Discussion and conclusion

In this work we have and analyzed the process of human color vision. In the first part we started from biological background, then we considered the human's visual system, which consists from several layers. Further, we considered and studied the Multi-Stage Color Model of Russel L. De Valois and Karen K. De Valois, which represents a novel model for color vision. Then we reviewed some general principles of artificial neural networks and constructed an artificial neural network (ANN). In the experimental part we conducted several experiments using our ANN.

The main reason why we chose this model is that it has several layers and due to this fact we were able to know the results of color signal transformation not only in the end of way, but also each layer.

We conclude that at ANN shows the transformation of color signal in the retina. In other words it is a simple model of human retina. The stages in ANN were constructed in such a way that it enables testing of the output at each intermediate level according to the Multi-Stage Color Model predictors. Also the ANN were built so that it might be changed (the unknown defines anatomical representation can be studied and added to the network during in the course of learning process).

In the experimental part we conducted a few experiments with different colors. We imported different color signals to ANN and studied what kind of transformation takes place after each layer. The results of these experiments were following. The results after every stage were like Multi-Stage Color Model predicted. Our ANN is able to divide all incoming color signals into for color classes: Red, Yellow, Green, and Blue.

However, this ANN isn't able to define the luminosity of the incoming signal. Also in the first layer we have used only one type of the photosensitive cells – cone cells, but in real life also the rod cells take part to the visual process.

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Appendix

Wavelength $\lambda(nm)$	Luminosity							
	S-cones	M-cones	L-cones					
370	0.59	0	0					
380	0.67	0	0					
390	0.76	0	0					
400	0.88	0.35	0.36					
410	0.96	0.35	0.36					
420	1	0.34	0.33					
430	0.96	0.34	0.3					
440	0.86	0.35	0.29					
450	0.68	0.38	0.28					
460	0.5	0.42	0.3					
470	0.36	0.49	0.34					
480	0.25	0. 56	0.39					
490	0.18	0.67	0.47					
500	0.12	0.78	0.55					
510	0.08	0.88	0.63					
520	0.05	0.95	0.73					
530	0.03	0.99	0.83					
540	0	0.99	0.91					
550	0	0.93	0.96					
560	0	0.82	0.99					
570	0	0.67	0.98					
580	0	0.53	0.93					
590	0	0.4	0.85					
600	0	0.29	0.74					
610	0	0.2	0.61					
620	0	0.14	0.47					
630	0	0.09	0.34					
640	0	0.06	0.24					
650	0	0.04	0.16					
660	0	0	0.105					
670	0	0	0.068					

Table1 Relative Spectral Absorbtances of Human Cones Measured by Bowmaker and Dartnall (1980)

Wavelength	Value				
370	0				
380	0				
390	0				
400	0,36				
410	0,36				
420	0,33				
430	0,3				
440	0,29				
450	0,28				
460	0,3				
470	0,34				
480	0,39				
490	0,47				
500	0,55				
510	0,63				
520	0,73				
530	0,83				
540	0,91				
550	0,96				
560	0,99				
570	0,98				
580	0,93				
590	0,85				
600	0,74				
610	0,61				
620	0,47				
630	0,34				
640	0,24				
650	0,16				
660	0,1				
670	0,06				

Table 2 The values of input signal

Table 3 The values of the response function of the first stage unti (signal from Scone)

	/
Wavelength	Value
370	0
380	0
390	0
400	0,32
410	0,34
420	0,33
430	0,29
440	0,25
450	0,19
460	0,15
470	0,12
480	0,09
490	0,08
500	0,06
510	0,05
520	0,03
530	0,02
540	0
550	0
560	0
570	0
580	0
590	0
600	0
610	0
620	0
630	0
640	0
650	0
660	0
670	0

Table 4 The values of the response function of the first stage unit (signal from Mcones)

cones)							
Wavelength	Value						
370	0						
380	0						
390	0						
400	0,13						
410	0,13						
420	0,11						
430	0,1						
440	0,1						
450	0,1						
460	0,13						
470	0,17						
480	0,22						
490	0,31						
500	0,43						
510	0,55						
520	0,69						
530	0,82						
540	0,9						
550	0,89						
560	0,81						
570	0,66						
580	0,49						
590	0,34						
600	0,21						
610	0,12						
620	0,06						
630	0,03						
640	0,01						
650	0,006						
660	0						
670	0						

Table 5 The values of the response function of the first stage unit (signal from Lcones)

	,				
Wavelength	Value				
370	0				
380	0				
390	0				
400	0,13				
410	0,13				
420	0,1				
430	0,09				
440	0,08				
450	0,07				
460	0,09				
470	0,11				
480	0,15				
490	0,22				
500	0,3				
510	0,39				
520	0,53				
530	0,69				
540	0,83				
550	0,92				
560	0,98				
570	0,96				
580	0,86				
590	0,72				
600	0,55				
610	0,37				
620	0,22				
630	0,11				
640	0,06				
650	0,03				
660	0,01				
670	0,004				

Table 6 The values of the response function of the second ctage unit (signal from horizontal cells)

Wavelength	Value				
370	0				
380	0				
390	0				
400	0,58				
410	0,6				
420	0,54				
430	0,48				
440	0,43				
450	0,36				
460	0,37				
470	0,4				
480	0,46				
490	0,61				
500	0,79				
510	0,99				
520	1,25				
530	1,53				
540	1,73				
550	1,81				
560	1,79				
570	1,62				
580	1,35				
590	1,06				
600	0,76				
610	0,49				
620	0,28				
630	0,14				
640	0,07				
650	0,03				
660	0,01				
670	0,004				

Table 8 The values of the response function of the second stage unit (signal from midget bipolar cells which connect with L-cones)

winen connect						
Wavelength	Value					
370	0					
380	0					
390	0					
400	0,02					
410	0,02					
420	-0,02					
430	-0,07					
440	-0,1					
450	-0,17					
460	-0,21					
470	-0,3					
480	-0,39					
490	-0,56					
500	-0,76					
510	-0,94					
520	-0,96					
530	-0,79					
540	-0,43					
550	0,17					
560	1					
570	1,82					
580	2,23					
590	2,29					
600	1,99					
610	1,5					
620	0,93					
630	0,51					
640	0,26					
650	0,11					
660	0,06					
670	0,02					

Wavelength λ(nm)	Percent of absorption of	Percent of absorption of incoming signal for M	Percent of absorption of
	cone cell	cone cells	cone cells
370	0	0	0
380	0	0	0
390	0	0	0
400	0,32	0,13	0,13
410	0,34	0,13	0,13
420	0,33	0,11	0,1
430	0,29	0,1	0,09
440	0,25	0,1	0,08
450	0,19	0,1	0,07
460	0,15	0,13	0,09
470	0,12	0,17	0,11
480	0,09	0,22	0,15
490	0,08	0,31	0,22
500	0,06	0,43	0,3
510	0,05	0,55	0,39
520	0,03	0,69	0,53
530	0,02	0,82	0,69
540	0	0,9	0,83
550	0	0,89	0,92
560	0	0,81	0,98
570	0	0,66	0,96
580	0	0,49	0,86
590	0	0,34	0,72
600	0	0,21	0,55
610	0	0,12	0,37
620	0	0,06	0,22
630	0	0,03	0,11
640	0	0,01	0,06
650	0	0,006	0,03
660	0	0	0,01
670	0	0	0,004

Table 7 Values of response functions of secont stage units

Table 9 The values of the response function of the second stage unit (signal from midget bipolars which connect with M-cones)

connect with Mi-cones)	
Wavelength	Value
370	0
380	0
390	0
400	0,23
410	0,25
420	0,28
430	0,06
440	-0,02
450	-0,19
460	-0,33
470	-0,55
480	-0,78
490	-1,17
500	-1,63
510	-2,08
520	-2,26
530	-2,12
540	-1,63
550	-0,6
560	0,87
570	2,38
580	3,22
590	3,48
600	3,11
610	2,38
620	1,48
630	0,82
640	0,42
650	0,18
660	0,1
670	0,04

Table 10 The values of the response function of the second stage unit (signal from midget bipolars which connect with S-cone)

Wavelength	Value
370	0
380	0
390	0
400	2,83
410	3,25
420	3,3
430	2,9
440	2,39
450	1,54
460	0,72
470	-0,15
480	-1,15
490	-2,51
500	-4,18
510	-5,98
520	-8,25
530	-10,62
540	-12,78
550	-13,68
560	-13,86
570	-12,88
580	-11,11
590	-8,92
600	-6,55
610	-4,33
620	-2,53
630	-1,3
640	-0,64
650	-0,29
660	-0,1
670	-0,04

Table 11 The values of the
response function of the
third stage unit (signal from
amacrine cell A_1)

amaci me cen A ₁)		
Wavelength	Value	
370	0	
380	0	
390	0	
400	3,06	
410	3,5	
420	3,58	
430	2,96	
440	2,37	
450	1,35	
460	0,39	
470	-0,7	
480	-1,93	
490	-3,68	
500	-5,81	
510	-8,06	
520	-10,51	
530	-12,74	
540	-14,41	
550	-14,28	
560	-12,99	
570	-10,5	
580	-7,89	
590	-5,44	
600	-3,44	
610	-1,95	
620	-1,05	
630	-0,48	
640	-0,22	
650	-0,11	
660	0	
670	0	

Table 12 The values of the response function of the third stage unit (signal from amacrine cell A₂)

	=/
Wavelength	Value
370	0
380	0
390	0
400	2,85
410	3,27
420	3,28
430	2,83
440	2,29
450	1,37
460	0,51
470	-0,45
480	-1,54
490	-3,07
500	-4,94
510	-6,92
520	-9,21
530	-11,41
540	-13,21
550	-13,51
560	-12,86
570	-11,06
580	-8,88
590	-6,63
600	-4,56
610	-2,83
620	-1,6
630	-0,79
640	-0,38
650	-0,18
660	-0,04
670	-0,02

$\begin{array}{c c c c c c c c c c c c c c c c c c c $	wavelength	value
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	370	0
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	380	0
4007 410 8 420 7,33 430 5,43 440 3,61 450 0,42 460 -2,4 470 -6,14 480 -10,19 490 -16,52 500 -24,09 510 -31,81 520 -37,45 530 -39,84 540 -38,08 550 -28,65 560 -13,27 570 4,26 580 16,22 590 22,52 600 22,45 610 18,24 620 11,66 630 6,58 640 3,38 650 1,5 660 0,95 670 0,36	390	0
$\begin{array}{c cccc} 410 & 8 \\ 420 & 7,33 \\ 430 & 5,43 \\ 440 & 3,61 \\ 450 & 0,42 \\ 460 & -2,4 \\ 470 & -6,14 \\ 480 & -10,19 \\ 490 & -16,52 \\ 500 & -24,09 \\ 510 & -31,81 \\ 520 & -37,45 \\ 530 & -39,84 \\ 540 & -38,08 \\ 550 & -28,65 \\ 560 & -13,27 \\ 570 & 4,26 \\ 580 & 16,22 \\ 590 & 22,52 \\ 600 & 22,45 \\ 610 & 18,24 \\ 620 & 11,66 \\ 630 & 6,58 \\ 640 & 3,38 \\ 650 & 1,5 \\ 660 & 0,95 \\ 670 & 0,36 \\ \end{array}$	400	7
$\begin{array}{c cccc} 420 & 7,33 \\ \hline 430 & 5,43 \\ \hline 440 & 3,61 \\ \hline 450 & 0,42 \\ \hline 460 & -2,4 \\ \hline 470 & -6,14 \\ \hline 480 & -10,19 \\ \hline 490 & -16,52 \\ \hline 500 & -24,09 \\ \hline 510 & -31,81 \\ \hline 520 & -37,45 \\ \hline 530 & -39,84 \\ \hline 540 & -38,08 \\ \hline 550 & -28,65 \\ \hline 560 & -13,27 \\ \hline 570 & 4,26 \\ \hline 580 & 16,22 \\ \hline 590 & 22,52 \\ \hline 600 & 22,45 \\ \hline 610 & 18,24 \\ \hline 620 & 11,66 \\ \hline 630 & 6,58 \\ \hline 640 & 3,38 \\ \hline 650 & 1,5 \\ \hline 660 & 0,95 \\ \hline 670 & 0,36 \\ \end{array}$	410	8
$\begin{array}{c ccccc} 430 & 5,43 \\ 440 & 3,61 \\ 450 & 0,42 \\ 460 & -2,4 \\ 470 & -6,14 \\ 480 & -10,19 \\ 490 & -16,52 \\ 500 & -24,09 \\ 510 & -31,81 \\ 520 & -37,45 \\ 530 & -39,84 \\ 540 & -38,08 \\ 550 & -28,65 \\ 560 & -13,27 \\ 570 & 4,26 \\ 580 & 16,22 \\ 590 & 22,52 \\ 600 & 22,45 \\ 610 & 18,24 \\ 620 & 11,66 \\ 630 & 6,58 \\ 640 & 3,38 \\ 650 & 1,5 \\ 660 & 0,95 \\ 670 & 0,36 \\ \end{array}$	420	7,33
$\begin{array}{c ccccc} 440 & 3,61 \\ 450 & 0,42 \\ 460 & -2,4 \\ 470 & -6,14 \\ 480 & -10,19 \\ 490 & -16,52 \\ 500 & -24,09 \\ 510 & -31,81 \\ 520 & -37,45 \\ 530 & -39,84 \\ 540 & -38,08 \\ 550 & -28,65 \\ 560 & -13,27 \\ 570 & 4,26 \\ 580 & 16,22 \\ 590 & 22,52 \\ 600 & 22,45 \\ 610 & 18,24 \\ 620 & 11,66 \\ 630 & 6,58 \\ 640 & 3,38 \\ 650 & 1,5 \\ 660 & 0,95 \\ 670 & 0,36 \\ \end{array}$	430	5,43
$\begin{array}{c ccccc} 450 & 0,42 \\ \hline 460 & -2,4 \\ \hline 470 & -6,14 \\ \hline 480 & -10,19 \\ \hline 490 & -16,52 \\ \hline 500 & -24,09 \\ \hline 510 & -31,81 \\ \hline 520 & -37,45 \\ \hline 530 & -39,84 \\ \hline 540 & -38,08 \\ \hline 550 & -28,65 \\ \hline 560 & -13,27 \\ \hline 570 & 4,26 \\ \hline 580 & 16,22 \\ \hline 590 & 22,52 \\ \hline 600 & 22,45 \\ \hline 610 & 18,24 \\ \hline 620 & 11,66 \\ \hline 630 & 6,58 \\ \hline 640 & 3,38 \\ \hline 650 & 1,5 \\ \hline 660 & 0,95 \\ \hline 670 & 0,36 \\ \end{array}$	440	3,61
$\begin{array}{c ccccc} 460 & -2,4 \\ \hline 470 & -6,14 \\ \hline 480 & -10,19 \\ \hline 490 & -16,52 \\ \hline 500 & -24,09 \\ \hline 510 & -31,81 \\ \hline 520 & -37,45 \\ \hline 530 & -39,84 \\ \hline 540 & -38,08 \\ \hline 550 & -28,65 \\ \hline 560 & -13,27 \\ \hline 570 & 4,26 \\ \hline 580 & 16,22 \\ \hline 590 & 22,52 \\ \hline 600 & 22,45 \\ \hline 610 & 18,24 \\ \hline 620 & 11,66 \\ \hline 630 & 6,58 \\ \hline 640 & 3,38 \\ \hline 650 & 1,5 \\ \hline 660 & 0,95 \\ \hline 670 & 0,36 \\ \end{array}$	450	0,42
$\begin{array}{c ccccc} 470 & -6,14 \\ \hline 480 & -10,19 \\ \hline 490 & -16,52 \\ \hline 500 & -24,09 \\ \hline 510 & -31,81 \\ \hline 520 & -37,45 \\ \hline 530 & -39,84 \\ \hline 540 & -38,08 \\ \hline 550 & -28,65 \\ \hline 560 & -13,27 \\ \hline 570 & 4,26 \\ \hline 580 & 16,22 \\ \hline 590 & 22,52 \\ \hline 600 & 22,45 \\ \hline 610 & 18,24 \\ \hline 620 & 11,66 \\ \hline 630 & 6,58 \\ \hline 640 & 3,38 \\ \hline 650 & 1,5 \\ \hline 660 & 0,95 \\ \hline 670 & 0,36 \\ \end{array}$	460	-2,4
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	470	-6,14
$\begin{array}{c cccc} 490 & -16,52 \\ 500 & -24,09 \\ 510 & -31,81 \\ 520 & -37,45 \\ 530 & -39,84 \\ 540 & -38,08 \\ 550 & -28,65 \\ 560 & -13,27 \\ 570 & 4,26 \\ 580 & 16,22 \\ 590 & 22,52 \\ 600 & 22,45 \\ 610 & 18,24 \\ 620 & 11,66 \\ 630 & 6,58 \\ 640 & 3,38 \\ 650 & 1,5 \\ 660 & 0,95 \\ 670 & 0,36 \\ \end{array}$	480	-10,19
$\begin{array}{c ccccc} 500 & -24,09 \\ 510 & -31,81 \\ 520 & -37,45 \\ 530 & -39,84 \\ 540 & -38,08 \\ 550 & -28,65 \\ 560 & -13,27 \\ 570 & 4,26 \\ 580 & 16,22 \\ 590 & 22,52 \\ 600 & 22,45 \\ 610 & 18,24 \\ 620 & 11,66 \\ 630 & 6,58 \\ 640 & 3,38 \\ 650 & 1,5 \\ 660 & 0,95 \\ 670 & 0,36 \\ \end{array}$	490	-16,52
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	500	-24,09
$\begin{array}{c cccc} 520 & -37,45 \\ \hline 530 & -39,84 \\ \hline 540 & -38,08 \\ \hline 550 & -28,65 \\ \hline 560 & -13,27 \\ \hline 570 & 4,26 \\ \hline 580 & 16,22 \\ \hline 590 & 22,52 \\ \hline 600 & 22,45 \\ \hline 610 & 18,24 \\ \hline 620 & 11,66 \\ \hline 630 & 6,58 \\ \hline 640 & 3,38 \\ \hline 650 & 1,5 \\ \hline 660 & 0,95 \\ \hline 670 & 0,36 \\ \end{array}$	510	-31,81
$\begin{array}{c cccc} 530 & -39,84 \\ \hline 540 & -38,08 \\ \hline 550 & -28,65 \\ \hline 560 & -13,27 \\ \hline 570 & 4,26 \\ \hline 580 & 16,22 \\ \hline 590 & 22,52 \\ \hline 600 & 22,45 \\ \hline 610 & 18,24 \\ \hline 620 & 11,66 \\ \hline 630 & 6,58 \\ \hline 640 & 3,38 \\ \hline 650 & 1,5 \\ \hline 660 & 0,95 \\ \hline 670 & 0,36 \\ \end{array}$	520	-37,45
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	530	-39,84
$\begin{array}{c ccc} 550 & -28,65 \\ \hline 560 & -13,27 \\ \hline 570 & 4,26 \\ \hline 580 & 16,22 \\ \hline 590 & 22,52 \\ \hline 600 & 22,45 \\ \hline 610 & 18,24 \\ \hline 620 & 11,66 \\ \hline 630 & 6,58 \\ \hline 640 & 3,38 \\ \hline 650 & 1,5 \\ \hline 660 & 0,95 \\ \hline 670 & 0,36 \\ \end{array}$	540	-38,08
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	550	-28,65
$\begin{array}{c cccc} 570 & 4,26 \\ \hline 580 & 16,22 \\ \hline 590 & 22,52 \\ \hline 600 & 22,45 \\ \hline 610 & 18,24 \\ \hline 620 & 11,66 \\ \hline 630 & 6,58 \\ \hline 640 & 3,38 \\ \hline 650 & 1,5 \\ \hline 660 & 0,95 \\ \hline 670 & 0,36 \\ \end{array}$	560	-13,27
580 16,22 590 22,52 600 22,45 610 18,24 620 11,66 630 6,58 640 3,38 650 1,5 660 0,95 670 0,36	570	4,26
590 22,52 600 22,45 610 18,24 620 11,66 630 6,58 640 3,38 650 1,5 660 0,95 670 0,36	580	16,22
600 22,45 610 18,24 620 11,66 630 6,58 640 3,38 650 1,5 660 0,95 670 0,36	590	22,52
610 18,24 620 11,66 630 6,58 640 3,38 650 1,5 660 0,95 670 0,36	600	22,45
620 11,66 630 6,58 640 3,38 650 1,5 660 0,95 670 0,36	610	18,24
630 6,58 640 3,38 650 1,5 660 0,95 670 0,36	620	11,66
640 3,38 650 1,5 660 0,95 670 0,36	630	6,58
650 1,5 660 0,95 670 0,36	640	3,38
660 0,95 670 0,36	650	1,5
670 0,36	660	0,95
	670	0,36

 Wavelength
 Value