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# Information Processing in the Retina: Computer Model and Some Conclusions

VALERIJ BOŽKOV, TOMÁŠ RADIL-WEISS

A model of the mammalian retina constructed on the basis of electrophysiological data available is described. The input-output relationships are defined mathematically and equations suitable for described parameters of receptive fields are suggested. The model was realised by means of a LINC computer. The output activity of the model was computed for several basic patterns like square-grating of different spatial frequences, bars of different widths and edges. The spatial frequency response function of the model was also evaluated. Visual patterns used in psychophysiological experiments with humans have been tested by means of the model. It has been shown that output activity of the model fits the experimental results.

## 1. SOME PHYSIOLOGICAL CONSIDERATION

The visual system of vertebrates contains several information processing stages among which the retina is the lowest one. It is a highly complex neuronal net which does not only encode the visual image into nerve impulses but performs also a very strong preprocessing of it.

This means that activity in the retinal output is not simply related to the intensity of illumination falling on each retinal receptor but rather to specific properties of the visual image such as contrast at the borders and irregularities which contain a highest amount of information about the visual image [1].

This properties of retinal information processing can help us to understand some psychophysical phenomena like the Mach bands effect, simultaneous contrast and some kinds of optical illusions. Therefore modelling of these processes might contribute to our understanding of visual perception mechanism.

The morphological and physiological features of the retina could be schematized in the following simplified way: the retina of vertebrates is formed from three types of functional elements (neurons) arranged in three distinct layers, i.e. input detectors (or receptor units), connecting units (interneurons) and output units (Fig. 1). When

the receptor layer is stimulated by light pattern, series of electrical variations, called "action potentials" or "spikes" take place in its conducting nerve fibers. The frequency of these electrical events is related to the strength of the stimulus (the light intensity) and plays the role of internal code for further stages of information processing in the visual system.

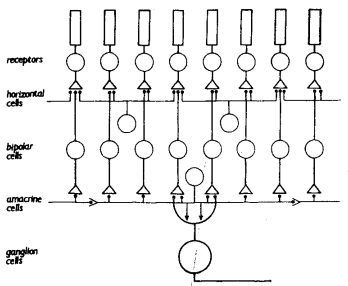


**Fig. 1.** Schematic representation of retinal layers.

So by means of the primary receptor process the continuous optical image of the external world is transformed into "discrete bioelectrical image" represented by the spatiotemporal distribution of action potentials over the huge amount of receptors.

Then by means of interneurons, called "bipolar cells", the messages from the receptors are transmitted to the ganglion cells, whose output fibers form the optic nerve, the sole output of the retina. Other interneurons, called "horizontal" and "amacrine" cells provide the lateral spreading of this information over the retina. This type of connections is important with respect to organization of receptive fields (see below).

The 150 millions retinal receptors converge to only 1 millions of ganglion cells, so that a single optic nerve fiber has connections with many bipolar cells which themselves are linked to many receptors. This convergence strongly reduces the amount of input information. In consequence, the area of retina over which a light stimulus may evoke a response in a single optic nerve fibre may be quite large. This region of the retina is called the receptive field of a ganglion cell. As the functional irganization of the receptive fields is concerned: the majority of them are arranged in two concentric regions, the center and the surround, both showing mutually antagonistic effects upon the ganglion cell impulse activity [2]. It is believed that the center and surround of the receptive fields represent functional units or response mechanisms, overlapping spatially (in the plan of receptor layer), but each having its own receptor representation [3].

If the geometry of stimulus is selected in such a way that both mechanisms are stimulated simultaneously, the ganglion cell receives excitatory signal from one mechanism at the onset of light and inhibitory from the other one. At the offset of light the mechanisms reverse their roles.

Moreover, it has been found, that the response of the ganglion cell to a combination of central and surround inputs equals more or less to the algebraic sum of the pure responses to the same inputs delivered separately. The last statement propose that, up to the ganglion cell, there is no interaction between both mechanisms and that the ganglion cell plays the role of a "summator" for excitatory and inhibitory signals [4; 5]. There are significant differences in the size of the receptive fields across the retina. It decreases gradually as one moves toward the centre of the retina, called fovea [6]. In the foveal region or very close to it the central region of the receptive field may be composed of just a single photoreceptor, while in the most peripheral regions its size may reach 2 angular degrees and even more.

It is also very important to note that over the whole retinal surface there is a strong overlapping of receptive fields [3].

The retinal properties, considered above, result in two fairly distinct from the functional point of view retinal regions: the central (foveal) and the peripheral one. The fovea is the regions of highest visual acuity through which sharp so called central vision is obtained. It is about 2 angular degrees out of a total range of vision which is about 180 degrees horizontally and 60 degrees vertically. All the rest of the retina provides so called peripheral vision and plays the role of an alerting system signalling that something has moved or changed in the visual field and giving its relative position.

On the basis of this information so called "saccidic" eye movements are carried out, bringing the retinal image of the object of interest into the region of the fovea. These scanning eye movements effectively compensate for the limited extent of foveal vision. In this way the information input from the eye to the brain is seriously reduced and matched to its information processing capacities.

## 2. DESCRIPTION OF THE MODEL

We shall abstract from the nature of all real coding processes (chemical and electrical) taking place in the retina and consider it as an abstract two-dimensional system of information processing, which can be fully described by its mathematical operator $\Omega$. Let $f(x, y)$ be a picture function describing the distribution of intensity over the input object plane and $g(x, y)$ the image function describing the distribution of the response amplitudes (given in relative units) over the plane of ganglion cells, which plays the role of output units of the retina.

Then the input-output relationship may be generally expressed

$$(1) \qquad g_{uv}(x, y) = \Omega\{T_{uv}[f(X, Y)]\} = \Omega\{f(X - u, Y - v)\} = \Omega\{f(x, y)\}\,,$$

where $f(x, y)$ is a picture function translated to the retinal coordinates, i.e. its projection to the receptor's plane of the retina ; $(u, v)$ are the coordinates of the projection of the fovea (playing the role of the origin – zero-point of the retinal coordinate system in the model) into the object's plane (Fig. 2). The point $(u, v)$ is usually called the fixation point of the eye upon the object. $T_{uv}$ is a "shifting operator" which we use here for emphasizing the role of scanning eye movements which shift the foveal projection (fixation point) over the object's plane and thereby move the object across the retinal surface. Thus for the same picture function but for various $(u, v)$

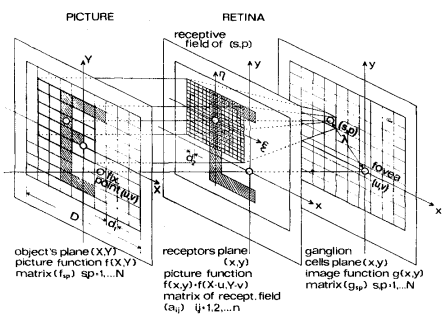


**Fig. 2.** Schematic representation of the model (for details see text).

we shall obtain different image functions because of functional nonhomogeneity of the retinal surface. Further we shall omit indexes $(u, v)$ for simplicity assuming that every output of the model is computed for particular fixation point, i.e. for a specific part of the retina. For all following discussions we assume that during the projection from object to receptors and to ganglion cells the geometry of the object does not change.

We also assume for sake of simplicity that the spaces of object, receptors and ganglion cells are continuous. We consider the same Cartesian coordinates for both receptors and ganglion cells.

We assume that any retinal cell $(x, y)$ is influenced by signals coming from photoreceptors – elementary areas of its receptive field and that each receptive field is organized into a circular central region with a concentric surround (Fig. 3a).

Fig. 3c shows schematically the functional organization of the receptive field of ganglion cell $(\sum)$ used in our model. Signals $e_i$ coming from all elementary areas (photoreceptors) which together constitute the central summating region $(\sum_c)$ are linearly summed, to provide one signal $u_c$ while signals from all elementary areas which constitute the surround summating region $(\sum_s)$ are separately linearly summed

to provide another signal $u_s$. Then the response of the ganglion cell $(g)$ is merely an algebraic sum of the two antagonistic signals $u_c$ and $u_s$.

We assume further that all ganglion cells have plus center and minus surround, i.e. we deal only with "on-center" and "off-surround" cells. We assume also that parameters of receptive field of ganglion cell depend upon its radial distance $\lambda$ from the fovea (Fig. 2). Taking into account all above considerations we can conclude that operator in Equation (1) is linear and nonhomogeneous (or not position invariant) and therefore may be expressed in the form

$$g(x, y) = \Omega\{f(x, y)\} = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} f(\xi, \eta)\, W(x, y, \xi, \eta)\, \mathrm{d}\xi\, \mathrm{d}\eta\,, \tag{2}$$

where $\xi$, $\eta$ are dummy variables and kernel $W(x, y, \xi, \eta)$ is usually called the point-spread function (the two-dimensional analog of the impulse function).

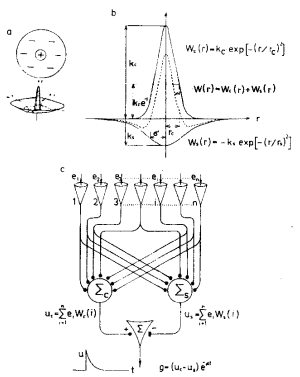


**Fig. 3.** a — geometry of the receptive field (of "on-center" type); b — sensitivy function of center and surround mechanism of receptive field; c — functional organization of the receptive field (for details see text).

In our model $W(x, y, \xi, \eta)$ plays the role of sensitivity function of the receptive field of ganglion cell $(x, y)$ which we assume to be the difference of two Gaussian-shaped sensitivity functions of central and surround mechanisms centritized in the same point (Fig. 3b).

$$\begin{aligned} W(x, y, \xi, \eta) &= W_c(x, y, \xi, \eta) - W_s(x, y, \xi, \eta) = \\ &= k_c(x, y) \exp\left[-(\xi^2 + \eta^2)/r_c^2(x, y)\right] - \\ &- k_s(x, y) \exp\left[-(\xi^3 + \eta^2)/r_s^2(x, y)\right], \end{aligned} \tag{3}$$

where $r_c$ and $r_s$ are the characteristic radii and $k_c$, $k_s$ are the maximum values of sensitivity functions of central and surround mechanisms respectively. We consider on the basis of the experimental data $k_c > k_s$.

Inserting (3) into (2) and taking into account the circular shape of the receptive field we shall obtain

$$g(x, y) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} f(\xi, \eta) \{k_c(\lambda) \exp [-(r/r_c(\lambda))^2] - k_s(\lambda) \exp [-(r/r_s(\lambda))^2]\} \, d\xi \, d\eta \,, \tag{4}$$

where

$$\lambda^2 = x^2 + y^2 \,, \tag{5}$$

$$r^2 = \xi^2 + \eta^2 \,. \tag{6}$$

To estimate $g(x, y)$ in Equation (4) the values of $r_c$, $r_s$, $k_c$, $k_s$ for the actual value of $\lambda$ have to be found.

In electrophysiological experiments, however, due to overlapping of central and surround mechanisms, the value of $r_c$ and $r_s$ can not be directly determined. Therefore the radius of center of receptive field is established as the distance $\sigma$ of the point of reversal of polarity of electrophysiological response from the geometrical center of the receptive field (Fig. 3b).

The relationship between $\sigma$ and $\lambda$ has been investigated in [6] and may be approximately represented as

$$\sigma(\lambda) = 0{\cdot}0137\lambda \,, \tag{7}$$

where $\sigma$ and $\lambda$ are expressed in angular degrees.

The relationship between $\sigma$ and $r_c$ (or $r_s$) may be derived from the equation

$$W_c(\lambda, r = \sigma) = W_s(\lambda, r = \sigma) \,, \tag{8}$$

or

$$k_c(\lambda) \exp [-(\sigma(\lambda)/r_c(\lambda))^2] = k_s(\lambda) \exp [-(\sigma(\lambda)/r_s(\lambda))^2] \,. \tag{9}$$

After the simple arrangement of Equation (9) we shall obtain

$$\ln \frac{k_c(\lambda)}{k_s(\lambda)} = \frac{\sigma^2(\lambda) [r_s^2(\lambda) - r_c^2(\lambda)]}{r_c^2(\lambda) \cdot r_s^2(\lambda)} \,. \tag{10}$$

Let us introduce following notations

$$c_1 = \frac{r_s(\lambda)}{r_c(\lambda)} \,, \tag{11}$$

$$c_2 = \frac{k_c(\lambda)}{k_s(\lambda)} \tag{12}$$

and assume $c_1$, $c_2$ to be independent of $\lambda$.

Considering (11) and (12), from (10) we shall obtain

$$r_c(\lambda) = \sigma(\lambda) \cdot \left( \frac{c_1^2 - 1}{c_1^2 \cdot \ln c_2} \right)^{1/2} \tag{13}$$

and considering (7) we eventually have

$$r_c(\lambda) \cong 0{\cdot}0137\lambda \left( \frac{c_1^2 - 1}{c_1^2 \ln c_2} \right)^{1/2} . \tag{14}$$

To find the exptession for $k_c$ let us write the equation describing the response of central summating mechanism when stimulated by uniform stimulus $f(x, y) = 1\,(-\infty < x, y < \infty)$

$$\int_{-\infty}^{\infty} \int_{-\infty}^{\infty} W_c(x, y)\, \mathrm{d}x\, \mathrm{d}y = a\,, \tag{15}$$

where $a$ is the amplitude of response.

Taking into account the circular form of the receptive field and its finite extent we may rewrite integral (15) in the form

$$I_c = \iint_S W_c(x, y)\, \mathrm{d}S = k_c \iint_S \exp\left[-(x^2 + y^2)/r_c^2\right] \mathrm{d}S\,, \tag{16}$$

where $S$ is area of the circle $x^2 + y^2 = d_c^2$ and $d_c$ is full radius of the central mechanism. To find $I_c$ we rewrite (16) in polar coordinates

$$I_c = k_c \int_0^{2\pi} \left( \int_0^{d_c} \exp\left(-r^2/r_c^2\right) r\, dr \right) d\Theta\,, \tag{17}$$

where $0 \leqq r \leqq d_c$ and $0 \leqq \Theta \leqq 2\pi$. Denoting integral in brackets as $I$ we may obtain

$$I = \frac{r_c^2}{2} \left[1 - \exp\left(-d_c^2/r_c^2\right)\right] . \tag{18}$$

Inserting (18) into (17) we have after simple computation

$$I_c = \pi k_c r_c^2 \left[1 - \exp\left(-d_c^2/r_c^2\right)\right] . \tag{19}$$

Considering $d_c = 2{\cdot}5r_c$ and taking into account that under this condition value in brackets is about 1 we definitively have

$$I_c \cong \pi k_c r_c^2 \tag{20}$$

and by analogy

$$I_s \cong \pi k_s r_s^2 . \tag{21}$$

Inserting (20) into (15) and considering $a = 1$ we shall obtain

$$k_c = \frac{1}{\pi r_c^2} . \tag{22}$$

When both centre and surround of the receptive field are simultaneously stimulated by the uniform stimulus, the ganglion cell is excited only weakly. This fact is caused by the perfect balance of central and surround mechanisms and may be expressed as

$$c_3 I_c = I_s \tag{23}$$

or

$$c_3 \pi k_c r_c^2 = \pi k_s r_s^2 , \tag{24}$$

where $c_3$ is usually called the coefficient of balance. The value of $c_3$ changes in a limited range (usually from 0·75 to 0·98) over the retinal surface [4].

We may obtain from (24)

$$c_3 = \frac{k_s r_s^2}{k_c r_c^2} , \tag{25}$$

or taking into account (11) and (12) we may write

$$c_2 = \frac{c_1^2}{c_3} . \tag{26}$$

In this way all the parameters of the receptive field may be computed from the expressions (26), (16), (13), (22), and (14) as well as $g(x, y)$ can be computed when the values of $c_1$ and $c_3$ are determined.

## 3. THE SPATIAL FREQUENCY RESPONSE FUNCTION (SFRF) OF THE MODEL

Let us consider a single ganglion cell when stimulated by the stationary sinusoidal grating of spatial frequency $v$, whose amplitude varies in $x$ direction only

$$f(x, y) = f_0(1 + \cos 2\pi v x) .$$

The SFRF of ganglion cell may be expressed as

$$H(v) = \mathcal{F}\{\omega(x)\} , \tag{27}$$

where $\mathcal{F}\{\cdot\}$ is the Fourier transform operator and $\omega(x)$ is so called line-spread function, describing the response of the ganglion cell to a strip of unit width at a distance $x$ from the centre of its receptive field.

Apparently $\omega(x)$ is a parametric integral

$$\omega(x) = 2\int_0^\infty W(x, y)\,\mathrm{d}y\,, \tag{28}$$

where $W(x, y)$ is the point-spread function of the receptive field.

Then the line-spread function of the central mechanism may be obtained

$$\omega_c(x) = 2k_c\int_0^\infty \exp\left[-(x^2 + y^2)/r_c^2\right]\mathrm{d}y = \sqrt{(\pi)}\,k_c r_c \exp\left(-x^2/r_c^2\right). \tag{29}$$

Finding in the same way $\omega_s(x)$ we may write

$$\omega(x) = \omega_c(x) - \omega_s(x) = \tag{30}$$
$$= \sqrt{(\pi)}\left[k_c r_c \exp\left(-x^2/r_c^2\right) - k_s r_s \exp\left(-x^2/r_s^2\right)\right].$$

Taking into account that $\omega_c(x)$ is an even function the SFRF of the central mechanism may be writen in the form

$$H_c(v) = 2\int_0^\infty \omega_c(x)\cos 2\pi v x\,\mathrm{d}x = \sqrt{(\pi)}\,k_c r_c\,2\int_0^\infty \exp\left(-x^2/r_c^2\right)\cos 2\pi v x\,\mathrm{d}x \tag{31}$$

Denoting integral in (31) as $I^*$ we may obtain

$$I^* = \frac{\sqrt{(\pi)}\,r_c}{2}\exp\left(-\pi^2 r_c^2 v^2\right). \tag{32}$$

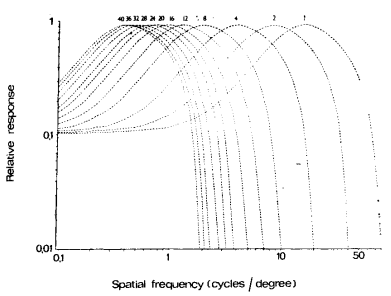


**Fig. 4.** Family of spatial frequency response functions at different distances from the fovea.

Inserting (32) into (31) we have

$$H_c(v) = \pi k_c r_c^2 \exp\left(-\pi^2 v^2 r_c^2\right). \tag{33}$$

Finding by analogy $H_s(v)$ and taking into consideration dependence of $r_c$, $k_c$, $r_s$, and $k_s$ on $\lambda$ we shall obtain the SFRT of the model

$$H(\lambda, v) = \pi\{k_c(\lambda)\, r_c^2(\lambda) \exp\left[-\pi^2\, r_c^2(\lambda)\, v^2\right] - \\ - k_s(\lambda)\, r_s^2(\lambda) \exp\left[-\pi^2\, r_s^2(\lambda)\, v^2\right]\}. \tag{34}$$

For concrete values of $c_1$ and $c_3$ the Equation (34) describes the family of curves whose position depends upon actual values of $r_c$, $k_c$, $r_s$ and $k_s$. Fig. 4 represents such family for $c_1 = 5$, $c_3 = 0{\cdot}8$ and for different $\lambda$, values of which are presented above each curve.

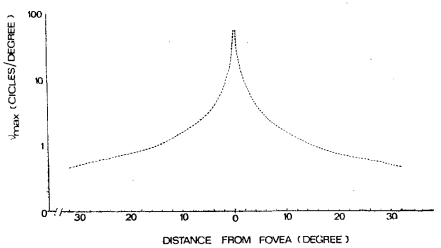


**Fig. 5.** Dependence of maxima of the spatial frequency response function on the distance from the fovea.

It may be seen from Fig. 4 that ganglion cells of the retina show band-pass type of response function whose maximum value displace very rapidly towards low frequencies as one goes from the fovea to the periphery (Fig. 5).

## 4. COMPUTER REALIZATION OF THE MODEL

The model described above has been realized by means of a LINC computer. Functions $f(x, y)$ and $g(x, y)$ have been represented by $96 \times 96$ (or $84 \times 84$) matrices $(f_{sp})$ and $(g_{sp})$ which correspond to digital picture function and digital image function respectively.

Matrix $(f_{sp})$ was binary-valued, i.e. could take only the two values 0 and 1 corresponding to "black" and "white" nature of input picture (i.e. no intermediate gray levels existed), whereas $(g_{sp})$ was a real-valued matrix with elements $-1 \leqq g_{sp} \leqq +1$.

The level of receptors was always represented by a single receptive field (binary-valued matrix $(a_{ij})$) belonging to the gangion cell $(s, p)$ the output activity of which was actually computed (see Fig. 2).



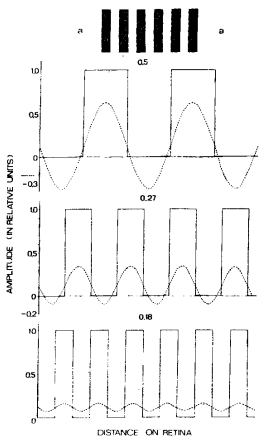


**Fig. 6.** Output of the model for square grating patterns of different spatial frequency. In the upper part — the actual is shown. The input (rectangular) and output activity of the model (in the same scale) for three different spatial frequencies are shown. Numbers represent relation of the width of grating to the diameter of receptive fields center.

To obtain approximately constant error of integral evaluation (Equation (4)) by summation the order $(n)$ of matrix $(a_{ij})$ (which represents the region of summation) was determined as the function of radius of receptive field actually represented by $(a_{ij})$

$$n = m \,.\, h\,, \tag{35}$$

where

$$m = \left(\left[\frac{r}{d}\right]\right), \tag{36}$$

and

$$h = \left[\frac{m + 10}{m}\right], \tag{37}$$

$r$ is the radius of central (or surround) mechanism, $d$ ($d_1$ in Fig. 2) is the angular size of element of digital picture function and $[x]$ denotes the greatest integer less than or equal to $x$.

The outputs of ganglion cells were iteratively computed and resulting digital image function ($g_{sp}$) was displayed on the oscilloscope of the LINC computer or

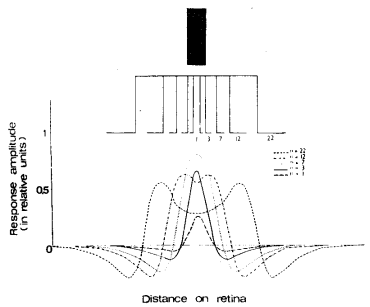


**Fig. 7.** Output of the model for bar patterns of five different widths. In the upper part the actual pattern is shown. The input (rectangular) and output activity of the model (in the same spatial scale) for five different widths are shown. Numbers represent the width of the bars expressed in number of elements of the matrix of digital input picture (the diameter of center of receptive field equating 11 elements).

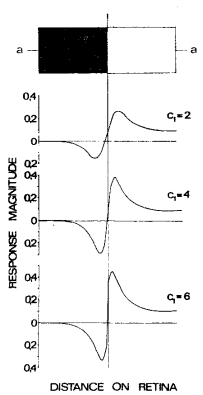


**Fig. 8.** Output of the model for edge (the actual pattern shown in the upper part of the figure) for different values of coefficient $c_1$ (see text).

printed by teletype. The output activity of the model for some basic input pattenrs (square-gratings of different spatial frequencies, bars of different widths and edge) are shown on the Fig. 6, 7, 8. 

During this and following computations we used values of input parameters: $c_1 = 5$, $c_3 = 0{\cdot}8$.

## 5. SOME PSYCHOPHYSIOLOGICAL CORRELATES OF THE MODEL

The model described may help to understand some psychophysiological phenomena:

a) *Distribution of eye fixations during searching pictures*

Using computer generated polygonal shapes as stimuli in pattern recognition experiments with eye movement recording we have found, that the density of eye fixations of our subjects is highest in the region of angles [7]. When the same figures are administered as input pictures in the model the maximal output activity is in

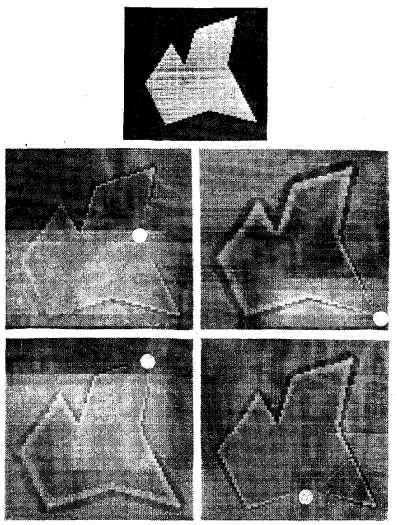

**Fig. 9.** Output activity of the model (map of excitation) on polygonal input shapes (see upper part of the figure) photographed from the CRT display of computer for four different "eye fixation points". Degree of gray corresponds to level of excitation of the ganglion cell layer of the model (i.e. as whiter as more excitation). The small discs represents the actual postition of fovea.

similar places (Fig. 9). It may be concluded that output of the retina might play certain role in control of the eye movements.

b) *The Müller-Lyer illusion*

It is well known that the length of two equal lines (Fig. 10 left) seems to be different. These patterns have been used as input pictures of the model. In case the line looks shorter the regions of highest output activity are shifted from its ends inward (Fig. 10 right). In opposite case they are shifted outward (not demonstrated in the figure for technical reasons). The distance of regions with maximal output activity could be related to the subjective measure of the length of the lines during perception.

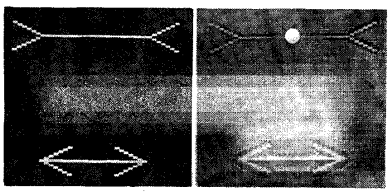

**Fig. 10.** Output activity of the model (map of excitation) on "Müller-Lyer" pattern. The actual input pattern shown left, the model output right. The small dics represents the actual position of fovea in the model. It can be seen from the graduation that maximal excitation in the arrow-shape pattern is shifted inward (for details see text).

c) *Fading of stabilized images*

When the nonmoving eye is fixed upon the middle of a pattern like a dimly illuminated disc the center region of the pattern is fading and it becomes surrounded by a dark ring gradually. The output activity of the model behave in a similar way when the same pattern is used as input (Fig. 11).

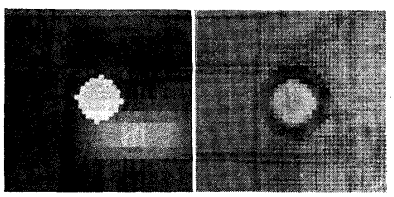

**Fig. 11.** Output activity of the model (map of excitation) — right, on a disc pattern (shown left). See text.

Both psychophysiological phenomena (*b*, *c*) described might be caused by the functional organization of the retinal receptive fields. 

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*Ing. Valerij Božkov, Doc. Dr. Tomáš Radil-Weiss, CSc., Fysiologický ústav ČSAV, (Institute of Physiology — Czechoslovak Academy of Sciences), Budějovická 1083, 142 20 Praha 4. Czechoslovakia.*