—Original—

Field adaptation in the horizontal cells

Rushtonian transformation

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Summary

In the presence of a steady ambient illuminance there occur two changes in the horizontal-cell incremental response; 1) The incremental sensitivity decreases which is Weber-Fechner like phenomena. 2) The response becomes faster. The response to a modulation around a mean is linear: This is a piecewise linearization. With the classical spot-annular experiment, a steady annulus of light increases the incremental sensitivity, makes the response faster, and linearizes the response. I propose to refer to the set of changes as the Rushtonian transformation which is an extension of Rushton's idea of field adaptation¹⁾.

Key words : retina, adaptation, sensitivity, kernel, white-noise

Introduction

One of the most important phenomenon in visual physiology is adaptation which has been the subject of numerous studies. The classical view on adaptation was summarized by Rushton in his 1962 Ferrier Lecture. In the paper, Rushton¹⁾ classified adaptation into two phases, bleaching and field adaptations. The bleaching adaptation, which is also known as the dark adaptation, is due to depletion of visual pigment and field adaptation, which is known as light adaptation, is related to the elevation of threshold in the presence of a brighter background.

Adaptation is a change in the sensitivity which must be quantified. In the long history of vision research, most widely used criteria for (quantitative) measure of sensitivity has been 'incremental sensitivity'. From incremental sensitivity should come the (modified) Weber-Fechner relationship which states that with increase in the magnitude of background illumination the threshold for test flash increases according to equation (1) :

$$\Delta I = A(1 + I/I_D) \dots \dots \dots (1)$$

where I is the background (or mean illuminance), I is the intensity of just detectable test flash, I_D is the intrinsic light and A is the absolute dark threshold. Rushton¹⁾, along with other investigators, argued that there must be a mechanism to produce such a function and he proposed an automatic gain control system based on Fuortes and Hodgkin's²⁾ original idea so that the incremental sensitivity decreased as the mean illuminance increased.

The neurons in the outer layer of the vertebrate retina produce only graded responses

which has no threshold. In 1966 Naka and Rushton³⁾ proposed that the relationship between the illuminance of step of light (given in dark) and the amplitude of the resulting response could be expressed by equation (2) :

$$\frac{V_0}{V_{\max}} = \frac{I_0}{I_0 + \sigma} \dots\dots\dots (2)$$

where I_0 is the illuminance of the flash given in dark, V_0 is the peak response amplitude, $V_{\max}$ is the response produced by a very bright flash, and σ is the illuminance of a flash to give a response of $1/2 V_{\max}$. The Weber-Fechner equation defines a neuron's threshold to some small change (usually for an increase in illuminance) from a steady mean illuminance whereas the Naka-Rushton equation defines a neuron's response to a step of light given in dark. The former, therefore, is the limited case of incremental (or AC) sensitivity and the later the absolute (or DC) sensitivity (Naka et al.⁴⁾). Note, however, that there is no time factor involved in both relationships. They are, therefore, applicable only to neurons whose responses do not change with time.

In 1957 Nobert Wiener⁵⁾ proposed to identify a system stimulating it with Gaussian white-noise and by computing a series of Wiener kernels. In a linear or quasi-linear system, the system's Wiener kernel is the impulse response. The response of a linear system to any stimulus (within the range of test stimulus) is predicted by the convolution integral (3) :

$$V(t) = \int_0^{\infty} h(\tau) L(t-\tau) d\tau \dots\dots\dots (3)$$

where $L(t)$ is the input, $V(t)$, the system's response and $h(\tau)$, the (first order) Wiener kernel or impulse response function. It can be seen from equation (3) that the Wiener kernel is a system's sensitivity and in the case of light stimulus it is a neuron's incremental sensitivity⁶⁾. In contrast with the threshold function which is applicable only to a specific stimulus magnitude (to produce a threshold response) sensitivity defined by the first order kernels is applicable to a large range of stimulus magnitude (within the limit of the magnitude of the test stimulus) and, in addition, the kernels define a system's frequency response.

By taking advantage of Wiener analysis I will describe what Rushton called field adaptation in horizontal cells. Further I will show that sensitivity (in a wider sense) of horizontal cells changes when the mean illuminance changes. Rushton's field adaptation represents only one facet of the many changes produced by mean illuminance and I propose to refer to the set of changes as the Rushtonian transformation.

Materials and methods

Biological : Materials used were 'eye-cup' preparation of channel catfish, *Ictalurus punctatus*. Recordings were made intracellularly from horizontal-cell somas. Both stimulus and response signals were stored on analog tape and digitized off-line onto the memory of a DEC VAX 11/780 computer. Analysis was performed using a signal analysis software system 'STAR' written by Numata, Ando and Sakuranaga.

Stimulus used was a large spot (referred to as a field) or a small spot of light of 0.4 mm in diameter whose illuminance was modulated by Gaussian white-noise signal. A steady annular illumination was also used (inner diameter, 0.45 mm and outer diameter, 3 mm) in conjunction with the spot stimulus. The mean illuminance (hence the 'depth of modulation') was controlled by a series of neutral density filters.

Analytical : A simplified experimental scheme is shown in **Fig. 1**. Illuminance of the light source (Sylvania R 1131 C glow tube) was modulated by white-noise signal. A series of neutral density filters equally attenuated the mean as well as the modulation of white-noise light so that the effect of added neutral density filter was to change the scale of the abscissa as shown in **Fig. 1 B**.

White-noise modulated white-noise signal can be written as :

$$L = L_0 + L(t) \dots\dots\dots (4)$$

in which L_0 is the mean and $L(t)$ is the white-noise modulation.

The horizontal-cell response evoked by white-noise stimulus can be written as :

$$V = V_0 + V(t) \dots\dots\dots (5)$$

in which V_0 is the mean hyperpolarization produced by L_0 and $V(t)$ is the dynamic voltage change produced by $L(t)$ as shown in **Fig. 3**. The relationship between L_0 and V_0 is the static (DC) sensitivity or gain as described by Naka-Rushton equation, and is plotted on the V_0 -log L_0 scale in **Fig. 2 B** and on (approximate) V_0 - L_0 scale is **Fig. 11**. The relationship between $L(t)$ and $V(t)$ is the dynamic (AC) sensitivity or gain which is defined by the (first order) Wiener kernel whose waveform as well as amplitude change with change in mean illuminance, L_0 . The kernel can be computed by crosscorrelating the input, $L(t)$ against $V(t)$ as in **Fig. 1 A** (Lee and Schetzen¹¹).

Definition of terms :

First-order kernel : First-order correlation between the light stimulus, $L(t)$, and the horizontal-cell response, $V(t)$, inversely weighted by the power of the stimulus. Note that

Fig. 1 Experimental scheme and white-noise stimulus. In A is shown a simplified experimental scheme. Input was white-noise modulated light attenuated by a series of neutral density filters. The light input was composed of two parts, a mean illuminance, L_0 , and a modulation around the mean, $L(t)$. Horizontal cell potentials were consisted of two parts, a mean hyperpolarization, V_0 , and a modulation around the mean, $V(t)$. $L(t)$ and $V(t)$ were stored on tape and digitized off-line. Crosscorrelation of $L(t)$ against $V(t)$ produced the first order kernel or impulse response in a linear system. In B is shown the time record of white-noise modulated light stimulus and its PDF. Neutral density filters in A changed the illuminance scale without changing the 'depth' of modulation. This is similar to the changes in visual scene whose mean illuminance changes according to times of a day or the season of the year.

the mean illuminance, L_0 , was subtracted. The kernel is a function of a time-lag between the stimulus and response, and is a general description of the best linear response to a Gaussian stimulus.

First-order model : The response of a cell to white-noise stimulus predicted by the first-order kernel as shown in equation (3).

Mean square error (MSE) : The mean square deviation of the predicted response from equation (3) from the recorded response to indicate the accuracy of the kernel's prediction and also to indicate the degree of nonlinearity in the response. The MSE is an index based on average response and does not necessarily indicate discrepancies point by point.

Probability density function (PDF) : This is the probability in which stimulus or response takes an amplitude within a infinitely narrow interval. The function is best approximated for stationary system by the amplitude histogram.

Exact algorithms for computing kernels, model response, power spectra, MSE, and PDF are published elsewhere (Sakuranaga and Naka⁸⁾).

Results

The relationship between the amplitude (illuminance) of stimulus and that of the response is shown in **Fig. 2** in which responses were evoked by steps of light given in dark. As the illuminance of stimulus was increased the amplitude of the response also increased. When the retina was moderately dark adapted a step input produced from the horizontal cells a response which was also step-like. In **Fig. 2** is also shown the relationship between the amplitude of the response and the illuminance of stimulus in V -log I plot which is the familiar form fitted by equation (2). The equation is applicable in this case because the response was step-like, i.e. the response amplitude did not change much with time or as long as the stimulus was maintained the membrane hyperpolarization was kept at a fixed level. The responses from the retina which was not dark adapted had an initial peak as seen in the records in **Figs. 3, 5, and 11**.

Fig. 2 The step-evoked horizontal cell response. Light stimulus was given in dark. Amplitudes of step-evoked responses were plotted against log I . Responses were evoked by lights of wavelength of 400, 500, 600, and 700 nm. Plots obtained at each wavelength were shifted laterally so that all points were superposed. V_{max} is the maximal amplitude of the step-evoked response.

The response produced by white-noise modulated stimulus is shown in **Fig. 3** in which A is the initial response to a step increase in the illuminance and B is when the response reached a steady state. V_0 was -35 mV as measured from the dark level of the horizontal cell membrane potential and p-p value of $V(t)$ was about 10 mV. Crosscorrelation performed between $I(t)$ and $V(t)$ produced the first-order kernel (**Fig. 6**, curve 2). Knowing the kernel and the stimulus, the response of the cell predicted by equation (3) is shown in **Fig. 3 B** (dotted line) and is superposed on the actual response (continuous trace). Except for a few deviations two traces matched showing that the kernel could predict the response with a high degree of precision; MSE was 5.5%. The power spectra of the stimulus, actual response (continuous line) and the predicted response (dotted line) are shown in **Fig. 4**. The two response power spectra were very similar confirming our observations made in **Fig. 3 B**. The analyses described so far were for the response obtained at a fixed mean illuminance of $0.2 \mu\text{W}/\text{cm}^2$.

Similar analyses on the responses obtained at different mean illuminances define the dynamics of incremental sensitivity. In **Fig. 5** are shown responses evoked by steps of light with illuminance attenuated by neutral density filters along with the PDFs of the responses obtained by white-noise stimulus having means similar to the amplitude of the step stimulus, L_0 . Note that the step-evoked responses by brighter stimuli had the initial peak as in **Fig. 3 A** and the steady level, V_0 , was reached after a few seconds. PDFs obtained at different mean illuminances were quite symmetrical suggesting that the responses produced by perturbation of a mean illuminance were linear. In **Fig. 6** are shown five kernels obtained at five mean illuminance levels using steps of 1 log unit. In A are shown the kernels plotted on the absolute scale and in B the kernels are normalized to compare the kernels' waveform. As the mean was increased, 1) the amplitude of the kernel was decreased monotonically, 2) the peak response times decreased, and 3) the width of the kernel became shorter. The kernel obtained with the brightest mean illuminance (trace 0), however, had a slightly longer peak response and had a broader width than the two kernels

Fig. 3 Time record of white-noise evoked response. Record A is the initial part of the response and record B is a part of the steady state response. The mean illuminance, I_0 , was $0.2 \mu\text{W}/\text{cm}^2$ and modulation is shown by $I(t)$. The mean hyperpolarization, V_0 , was 35 mV from the dark level and modulation is shown by $V(t)$. In B, $V(t)$ consists of 2 traces, the experimentally obtained response (solid line) and the response predicted by the (first-order) kernel (dashed line).

Fig. 4 Power spectra of the input, white-noise modulated light stimulus, of the actual response (continuous line) and of the response predicted by the first-order kernel (dashed line). The MSE of the predicted response was 5.6%.

Fig. 5 Responses produced by stimuli of various intensity. Responses were evoked either by a step of light given in dark or by white-noise modulated light whose mean illuminance was similar to the corresponding step stimulus. Illuminance of both stimuli was attenuated by a series of neutral density filters. Light signals were recorded before they were attenuated by the filters.

obtained by interposing 1 and 2 log neutral density filters (traces 1 and 2). The decrease in the kernel amplitude follows a Weber-Fechner-like relationship indicating that the incremental sensitivity decreased as the mean increased. Naka et al.⁴⁾ argued that the decrease was what one would expect if the incremental sensitivity is approximated by the local slope of the Naka-Rushton equation: this is graphically shown in **Fig. 11**. The second and third observations showed that the cell responded to faster inputs as the mean was increased. At a very bright mean illuminance the cell's response became slower again. Note here that the waveform of a kernel including its width is an indication of the cell's frequency

Fig. 6 The (first-order) kernels obtained at five mean illuminance levels. Traces marked 0 through 4 were obtained with mean illuminances of 20, 2, 0.2, 0.02, and 0.002 $\mu\text{W}/\text{cm}^2$. Absolute values of kernels were plotted in A and normalized kernels were plotted in B. When plotted as in A, the absolute value (the amplitude) of the kernels is the incremental sensitivity and the kernels' waveform shows the cell's frequency response at a mean illuminance.

used with a steady annulus having an inner diameter of 0.45 mm and an outer diameter of 4 mm. The test spot was introduced as a step or modulated by white-noise. In the figure the bar marked, 'SPOT', indicated the period of white-noise modulation. The stimulus, L_0 , produced a steady hyperpolarization, V_0 , and $L(t)$ produced small modulation, $V(t)$. The addition of a steady annulus, as indicated by the bar, 'STEADY ANN', produced larger V_0 and $V(t)$. The increase in the steady hyperpolarization is to be expected since the horizontal cells formed the S-space or lamina and hyperpolarization produced by an annulus of light is added to the steady hyperpolarization produced by the spot of light. The increase in $V(t)$ with a larger incremental response was not what one would have expected. The steady hyperpolarization produced by the annulus of light somehow increased the horizontal cell's incremental sensitivity. The set of kernels in **Fig. 8** marked 'S' was computed from the responses produced by the test spot alone and the set of kernels marked

Fig. 7 Time record of experiment to show the effects of a steady annular illumination on the white-noise response produced by a small spot of light. Steady annular stimulus produced 1) a larger hyperpolarization and 2) larger incremental response produced than by the spot input alone.

response.

So far I have described changes in the incremental sensitivity when the mean illuminance was changed. It has been shown that the geometry of stimulus modified the incremental threshold (Rushton¹¹). I have examined how the incremental sensitivity measured by a small spot of light was modified by the presence of a steady annulus of light. In **Fig. 7** is shown a record which summarizes my experimental procedure. A small test spot of light (diameter of 0.4 mm) was

'S/A' was computed from the responses obtained in the presence of a steady annulus of light. The presence of a steady annulus produced three changes in the kernels, 1) the amplitude increased, 2) the peak response time became shorter, and 3) the width became narrower. The first change indicated an increase in the incremental sensitivity while the second and third changes indicated that the cells responded to faster stimuli: these results were similar to the changes observed with an increase in the mean illuminance (Fig. 6).

Time records of the spot stimulus (upper trace) and response (lower trace) with their PDFs are shown in Fig. 9. Record A was with a spot of light alone and record B was with a steady annulus of light which displaced the mean hyperpolarization by 10 mV. As we have already observed in Figs. 7 and 8, the steady annulus of light increased the cell's response to white-noise modulation. Moreover, the response evoked by a spot of light alone was very nonlinear as seen from the large repolarizing peaks and the asymmetrical PDF. The response obtained with a steady annulus of light did not show any of such peaks and the PDF was symmetrical. Presence of an annulus of light linearized the response. This is shown in Fig. 10 in which power spectra of the responses in Fig.

9 (continuous lines) were computed together with the power spectra of the model response predicted by the kernels (dashed lines). The corner frequency of the response to the spot alone was about 2 to 3 Hz and the power spectrum of the predicted model differed somewhat from that of the actual model (MSE was 46.5%). The set for the spot with a steady annulus had a corner frequency of 10 Hz and the power spectra of the response and model matched quite well (MSE was 2.6%).

Fig. 8 Increase in the incremental sensitivity in the presence of a steady annular illumination. Records were from four horizontal cells. Traces marked S were for spot alone and those marked S/A were for the spot in the presence of a steady annulus of light.

Fig. 9 Time records of responses evoked by white-noise modulated spot of light without (A) and in the presence of a steady annulus (B). The steady annulus of light hyperpolarized the cell by 10 mV. PDFs of spot stimulus and responses are also shown. Note nonlinear response evoked by the spot alone.

Discussion

Adaptation is vital to the proper performance of our visual system and without adaptation the system must fail as often as does pictures taken by a camera without any exposure control. There are two aspects to adaptation, one is related to the bleaching of visual pigment and the other to changes in ambient illuminance. The bleaching adaptation, which takes place when light is scarce, has been studied mainly in the scotopic range (Dowling⁹, Rushton¹⁰). The other adaptation takes place when there is a steady (or abundant) light and is referred to as field adaptation : this adaptation was the main theme of this paper (Rushton¹¹).

Field adaptation is a decrease in (contrast or incremental) sensitivity in the presence of a steady illuminance, a

situation animals including us encounter in their daily vision (Shapley and Enroth-Cugell¹¹). The decrease in the (threshold) sensitivity is referred as the Weber-Fechner relationship.

The static sensitivity is related to the response amplitude produced by a step of light and the Naka-Rushton equation described the relationship between the amplitudes of stimulus and response. The static sensitivity can be defined only in the cells which produce sustained response although some authors applied the sensitivity to those cells which produced transient responses¹². Dynamic sensitivity, on the other hand, can be applied to any system which produces response to an input. In a linear system the dynamic sensitivity is defined by the system's impulse response which is the system's (first order) Wiener kernel.

There are two aspects in the field adaptation : one is the lateral shift of a V-log I curve and the other is the compression of the V-log I curve in the presence of a steady background. The former is a change without any real light as illustrated in **Fig. 1 B** in Naka¹³ : the dark potential of the horizontal cell does not change whereas the value of sigma changes as first shown by Naka and Rushton¹⁴ (signal horizontal cells receive is already scaled). The idea of lateral shift has been used by many authors to account for field adaptation^{15,16}. Changes in sensitivity by compression takes place in the presence of real light. And this is the mechanism some authors suggested for the Weber-Fechner relationship. The later is a change with light in a sense the horizontal cell is always hy-

Fig. 10 Power spectra of the spot evoked responses. Curves marked S were by spot of light alone and curves marked S/A were by the spot of light in the presence of a steady annular light. Continuous lines were for the actual responses and dashed lines were for the predicted responses from equation (3). Note that, in the presence of a steady annular illumination, the power spectra of the actual and predicted responses were almost identical whereas, with spot as the only stimulus, the power spectra of the actual and predicted responses were different. Therefore, response was nonlinear.

perpolarized to some degree (dictated by equation, 2) from the dark potential. There is a relationship between the two changes, namely that with an increase in the DC sensitivity (shift of V -log I curve toward increased DC sensitivity) the incremental sensitivity decreases. This was shown in **Fig. 6** in Naka et al⁽⁴⁾. In the figure they showed that as the retina was dark adapted, the steady hyperpolarization, V_0 , produced by a white-noise stimulus increased whereas the modulation, $V(t)$, decreased.

The decrease in the incremental sensitivity with an increase in the mean illuminance is due to the decreasing local slope of the V - I plot of the Naka-Rushton equation. One example is shown in **Fig. 11** in which responses from a horizontal cell were evoked by a series of flashed (given in dark) whose amplitude increased in an approximately linear fashion. The line which forms the crest of the response is the Naka-Rushton relationship on a linear I scale. The incremental response is produced by perturbation, Gaussian in this paper, of a mean illuminance. The incremental sensitivity is, therefore, related to the local slope of the curve and in the figure it can easily be seen that the local slope at a mean illuminance, b , is shallower than that at a dimmer mean illuminance, a . In this paper I have shown in addition that the incremental response around a mean illuminance was quite linear except for very dim or very bright range and that response dynamics changed with changes in the mean illuminance. This is piecewise linearization.

The incremental sensitivity is modified by the spatial distribution of light stimulus. A low sensitivity of a cell measured by a spot of light can markedly be increased by the presence of a steady annular light. As the test stimulus was 0.4 mm in diameter the increase excluded the possibility that the steady annulus of light changed the receptors themselves. Somehow the steady hyperpolarization produced by an annulus of light modified the receptor to horizontal cell transmission to increase the cell's incremental sensitivity. The negative feedback first postulated by Marmarelis and Naka⁽¹⁷⁾ is a possibility and this is the zeroth order effect as proposed by Krausz and Naka⁽¹⁸⁾. Similar increase in the spot-evoked incremental response was seen in the turtle horizontal cells⁽¹⁹⁾. This enhancement

Fig. 11 The horizontal cell responses evoked by a series of step stimuli whose illuminance increased approximately in a linear fashion. The crest of the response forms the Naka-Rushton relationship. Dark levels were for the light stimulus and the horizontal cell potential. See text for details.

must play very important role in photopic vision as in the natural environment no visual stimulus takes a form of a flashing solitary spot of light and if there is a spot of light it is always seen against an ambient illumination.

In conclusion I propose to refer to the set of changes seen in the incremental response as the Rushtonian transformation, changes which include many related phenomena. When Rushton wrote his Ferrier Lecture 1962 he could deal with only a facet of field adaptation, static stimulus-response relationship such as the Weber-Fechner law¹⁾. Now much richer aspects of the adaptation can be studied, analyzed, and appreciated. He wrote 'For light that is excluded cannot contribute to the signal; light that is caught and made to operate some parametric feed-back system could improve the detail of space-time discrimination and signal/noise reliability'. What I have describe in this paper is the improvement of time discrimination by the light which is caught. In this sense this paper is still within the limit of his Ferrier lecture.

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