SPECTRAL AND PATTERN RESPONSE IN THE RABBIT RETINA

JOHN C. ARMINGTON AND ALAN R. ADOLPH

SCHEPENS EYE RESEARCH INSTITUTE

The advantages of presenting sensory data in terms of stimulus variables are stressed. Spectral sensitivity plots of local electroretinograms and ganglion cell discharges from the dark-adapted rabbit retina illustrate the utility of using this kind of procedure. Spectral data agreed with the literature demonstrating two cone and one rod process in this animal. The spectral sensitivities of both the local electroretinogram and ganglion cell spikes were closely similar. Data pertaining to pattern vision may also be subjected to the same type of analysis and described in terms of stimulus variables.

Key words: pattern sensitivity, spectral sensitivity, electrophysiological response, vision, rabbits

The material in this paper may seem a bit afiel from the main themes of this festschrift, but in reality it has roots that extend back to 1952 when the Department of Experimental Psychology was just being set up under Joe Brady's direction in Building 80 at Walter Reed. At that time, one research effort was directed towards the electrophysiology of human vision, specifically towards problems of color vision. Features of this work were spectral measures of electroretinograms from normal and defective human eyes. The same procedures that were used then can be applied with some modification to other species and other response variables. As an example, Figure 1 shows spectral measures for ganglion cell spikes in the dark-adapted retina of the rabbit. It shows how the sensitivity of this retinal response changes with the wavelength (or color) of the stimulus. The rabbit eye is quite sensitive to short wavelength (blue) light and insensitive to long wavelength (red) light.

An important feature of this figure is the nature of the scales used along the two axes. Both are expressed in units that pertain to the stimulus. The abscissa is expressed in units of stimulus wavelength. The ordinate scale, also expressed in stimulus units, is plotted as log relative sensitivity; in other words, the logarithm of the reciprocal of the amount of light required to produce a constant response measure. Sensitivity is analogous to threshold. The use of such scales facilitates the comparison of electrophysiological data with those of other methods of investigation such as psychophysics, physics, or photochemistry, which often

use similar units. This is shown by the three smooth curves drawn between the experimental points. The one that has a maximum at 500 nm is the curve for visual purple. It has been identified in the rabbit retina. The other two are theoretical (Dartnall, 1953), but are also based on photochemical study. Together, the curves account fairly well for the electrophysiological results. Also, despite some differences in wavelength maxima, these results are in general agreement with previous research that points to two cone systems as well as a rod one in the rabbit retina (de Monasterio, 1978; Nuboer, van Nuys, & Wortel, 1983).

Fig. 1. Spectral sensitivity. Filled circles are for off bursts from ganglion cells. They have been fitted with smooth photochemical curves.

Address correspondence and reprint requests to John C. Armington, 20 Staniford Street, Boston, Massachusetts 02114.

Fig. 2. Spectral sensitivity plots for: A, on-ganglion cell bursts; B, off-ganglion cell bursts; C, on LERGs; and D, off LERGs. Error bars indicate 1 standard error of the mean.

Figure 2 is an illustration of how the relative spectral sensitivities of different retinal responses may be compared. Sensitivity data are presented for the following: A, maximum rate of *on* ganglion cell spikes; B, maximum rate of *off* ganglion cell spikes (i.e., a replot of the data shown in Figure 1); C, amplitudes of *on* local electroretinograms (LERGs); and D, amplitudes of *off* LERGs. Data have been

combined from several rabbits, with the error bars marking the standard error of the mean and with sensitivities equated at 520 nm. When the data are expressed in terms of sensitivity, all four of these visual-response measures are seen to convey nearly the same information. For the most part, the differences among the curves lie well within the limits set by the error bars.

Fig. 3. Sample recording: upper trace, stimulus marker; middle trace, on and off spike bursts; bottom trace, on and off LERGs.

The purpose of the present report is to show how sensitivity measures can be useful in studying elemental pattern vision in rabbits. In other words, an analysis similar to that used for investigating wavelength sensitivity may be useful in studying pattern vision electrophysiologically.

METHOD

Recording was performed using a modified version of equipment that has been described previously (Armington, 1974; Armington, Adolph, & Wu, 1991). Simultaneous recordings were made both of ganglion cell activity and of local electroretinograms from sites on everted, superfused rabbit retinas. The two signals were picked up with the same tungsten microelectrode and separated with band-pass filter circuits. Stimuli were presented with an

optical system that permitted control over a number of stimulus dimensions. The responses they produced were processed on a computer to produce averaged recordings of the sort shown in Figure 3. The recordings have three tracings, a stimulus marker (top), a peristimulus spike histogram (middle), and an averaged LERG (bottom). The timing is set so that stimulation occurs in the middle of the sweep. A 20- μ V calibration precedes the LERG record. The optical system, also under computer control, permitted delivery of drifting grating patterns of stripes or of spots of light of various diameters that were flashed to the retina. Stimulus intensity was controlled with neutral filtering. When no filters were in front of the stimulus beam, the stimulator provided a retinal illumination of 2,500 cd/m². It may be noted, in passing, that computers were in early use at Walter Reed.

The spike histogram of Figure 3 shows two bursts of activity, the first following the onset of the stimulus and the second, somewhat smaller, one following its offset. Sharp negative on and off potentials are seen in the LERG tracing. They are separated by a slower positive deflection.

RESULTS AND DISCUSSION

Perhaps the most common way to investigate pattern vision electrophysiologically is to present the eye with a grating pattern of alternate bright and dark stripes that drift (i.e., that move slowly and continuously across the retina). As the stripes pass over the local region from which recording is being performed, it receives sequential increases and decreases in

Fig. 5. Spike peristimulus histograms and LERGs produced by flashing spots of light covering a range of stimulus diameters.

Fig. 6. Representative intensity plots for on-spikes and simultaneous on LERGs in response to stimulus spots of three diameters.

illumination. Responses that depend on the size of the stripes as well as their rate of movement are produced. A typical result from this type of study is shown in Figure 4. Here, the peak rate in impulses per second for an on ganglion cell response is plotted against fundamental spatial frequency of a square wave

grating (i.e., the number of bright and dark stripe pairs occurring in a millimeter). It is seen that there is more response near a spatial frequency of 1 cycle per millimeter where a bright and dark pair of stripes is 1 mm wide. There is less stimulation and response for finer or coarser patterns.

Fig. 7. Relative displacements of intensity curves in log intensity units versus log stimulus area. Log relative intensity on the ordinate = $-\log$ sensitivity. On LERGs (open circles) and spike bursts (closed circles).

The peaking of response amplitudes at a spatial frequency near 1 cycle per millimeter (Figure 4) may be attributed to the center-surround structure of the elements generating the responses. For example, when the width of a bright stripe matches the inner diameter of an on-center receptive field, maximal response might be expected. Larger stripes extend into the inhibitory surround to reduce the vigor of the responses. Small stripes stimulate less of the excitatory center. Similar considerations apply to off-center fields. It was decided to test this idea directly with the simplest of all patterns, that of a single spot of light whose diameter could be changed as an experimental parameter.

Sample responses, obtained from 1 rabbit using stimuli of maximum available intensity and with a range of stimulus spot sizes, are shown in Figure 5. In the present case, the spike records reach a maximum rate at 250 μm and then drop off as the spot size increased. The waveform of the LERG goes through a complicated pattern of change, with a pair of negative deflections appearing in most cases.

It was decided to carry the analysis a step further. There are several reasons for going beyond a simple inspection of the records. First, an attempt towards quantification with graphs

having more useful scales along their axes is needed. Second, interpretation of the data may be limited unless possible effects of stimulus intensity are taken into account. The response measures may saturate at high intensities. Figure 1 has already demonstrated the utility of presenting spectral data on scales of sensitivity. A similar approach can be used in the case of data collected with stimulus spots.

Responses similar to those shown in Figure 5 were taken from another rabbit using a range of stimulus intensities as well as spot sizes. The peak amplitudes of the on spike-rate data and of the on negative potential of the LERG were measured. Then, plots were made of the relation between these measures and stimulus intensity. A sampling of these plots is shown for this rabbit in Figure 6. Stimuli were administered at (log) intensity values of 0.0, -0.6, -1.0, -1.6, -2.0, -2.6, -3.0, and -3.6, except in the regions marked with dashed lines where spacing was doubled for reasons of efficiency. A general pattern can be seen for both spike bursts and the LERG response, particularly when large stimulus areas are used. At first the response grows with intensity, but then it plateaus at high intensities. Thus, if response were plotted directly against stimulus size and if bright stimuli were used, the result would pertain only to saturation conditions. Although there are some differences in saturation levels, an important outcome is that as the size of the stimulus spot was changed, the plots appeared to be displaced along the intensity axis. This displacement is an indication of sensitivity. It was found in the present case that the greatest displacement to the left occurred when the spot size was 500 μm . This is the size to which this eye was most sensitive.

Although the data for 500 μm are not shown in Figure 6, their displacement can be determined from Figure 7. The ordinate in this figure, scaled in logarithmic units of relative intensity, is a direct indicator of the relative displacements of the intensity plots. Because sensitivity is the reciprocal of the intensity required to produce a fixed response characteristic, Figure 7 is a plot of relative sensitivity in logarithmic units against the logarithm of the retinal area of the stimulus spots. The five different areas for which displacements (intensities) are plotted correspond to spot diameters of 25 μm , 100 μm , 250 μm , 500 μm , and 1 mm. The data for both spikes and

LERGs rise linearly and with a slope of 45° until the spot is $500\ \mu\text{m}$ ($\log = 5.3$), in diameter, and then they fall off. This point marks the boundary between which summation in the central area of the retinal field is overtaken by inhibition from the immediately surrounding parts of the field.

The summation area seems to perform in accordance with a modified form of Ricco's law, which states that the product of stimulus area and intensity is constant (Woodworth & Schlosberg, 1954). This type of plot may then be useful for comparing psychophysical and electrophysiological data. What is needed now are appropriate behavioral data describing sensitivity to pattern in the rabbit.

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