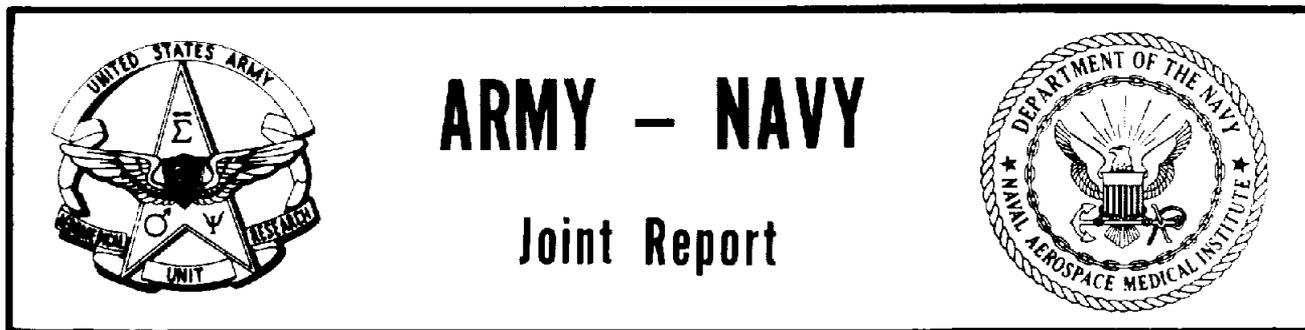


ROD-CONE INTERACTION IN S-POTENTIALS FROM CAT RETINA

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## SUMMARY PAGE \*

### THE PROBLEM

Rod-cone interaction in cat S-potentials was studied by analyzing the effect of wavelength and intensity upon the form of dark-adapted responses.

### FINDINGS

Flashes of white light, increasing in intensity, produced responses that increased in amplitude over at least a 6.0-log range. At low intensities, responses were of the rod type and thresholds were well within the scotopic range. At higher intensities the form changed and came to resemble the cone type.

Relatively monochromatic flashes also produced responses that seemed to originate from the excitation of both receptor types as a function of the wavelength and intensity of the flash. This assumption was supported by calculating spectral sensitivity curves for specific response characteristics. In addition, changes in form as a function of intensity could now be interpreted.

Thus, in response to blue flashes (433 nm) the peaking of the S-potential at  $\sim 2.5$  log above threshold and the increase in duration at  $\sim 3.0$  log above threshold originated from the rods. The cone response remained relatively more rectangular, even at the highest intensities, but also increased in duration at the maximum intensity. In response to white light and colored flashes the cone response seemed in some way to add to the changing rod response as intensity increased.

The V-Log I curves with blue flashes showed that the rod response (initial peak voltage) reached a ceiling at  $\sim 3.5$  log above threshold, while the maintained response rose less steeply and leveled off at a lower intensity. Both ceilings were obscured by the cone contribution. With orange flashes no ceiling occurred and the slope was considerably steeper, resembling the slope of V-Log I curves following strong bleaches. It suggested that the cone function rises more steeply than the rod.

The hypothesis that the rod and cone contributions added, received support from dual-flash experiments. Cone and rod responses to brief orange and blue lights of moderate intensity, separated in time, added together across a complete range of intervals.

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\*The findings in this report are not to be construed as an official Department of the Army position, unless so designated by other authorized documents.

The animals used in this study were handled in accordance with the "Principles of Laboratory Animal Care" established by the Committee on the Guide for Laboratory Animal Resources, National Academy of Sciences-National Research Council.

## INTRODUCTION

In a previous paper (14) S-potentials in the area centralis of cat retina were shown to receive contributions from both the rods and cones, but the nature of the interaction between these inputs was not specified. A preliminary examination of the data with this question in mind suggested algebraic addition of the rod and cone components as the simplest explanation for the records. Proper study of their interaction, however, required that the rods and cones be excited separately at first and then jointly; but this was extremely difficult to do in the cat's area centralis. Instead, I undertook a comprehensive survey of the responses to lights of different colors and intensities to determine if any were incompatible with algebraic addition. No clear disagreement with the hypothesis was found, and under one set of conditions, in which known rod and cone excitations were superposed, clear support was obtained.

The preparation and maintenance of the cat, recording technique from the intact eye, and conditions of stimulation have been described in previous publications (13, 16). Additional information with regard to the study of S-potentials was presented in the previous paper (14).

## RESULTS

### WHITE LIGHT

Figure 1 presents a sequence of dark-adapted responses to white light (color temp, 2850°K) through a 6.7-log intensity range. At threshold (0.0) flash intensity was quite low (0.5 log td. scotopic) and the long "on" and "off" latencies suggested a rod response (14). Latencies remained long ( $\geq 50$  msec), and the response grew uniformly through a 2.0-log intensity increment. At much higher intensities (5.5), however, both latencies were short ( $< 25$  msec), and the responses were of the cone type (14) except that the potential did not immediately return to the baseline.

Since the scotopic and photopic mechanisms are maximally sensitive in dark-adapted retinae, it is not surprising to find them both represented in response to white light. But are they combined in the response, added together in some way, or is there competition between them? In the transition phase from the rod to the cone response (Figure 1, 2.0 to 3.5) several complex changes of form occurred. An initial peak was acquired (a), and a short-latency decay-phase suddenly appeared (b), increased in size, and was followed by a second decay-phase which increased in latency as the intensity increased (c). It will be shown that these changes originate from alterations of the rod response at high intensities relative to threshold, and the apparent addition to it of the cone response.

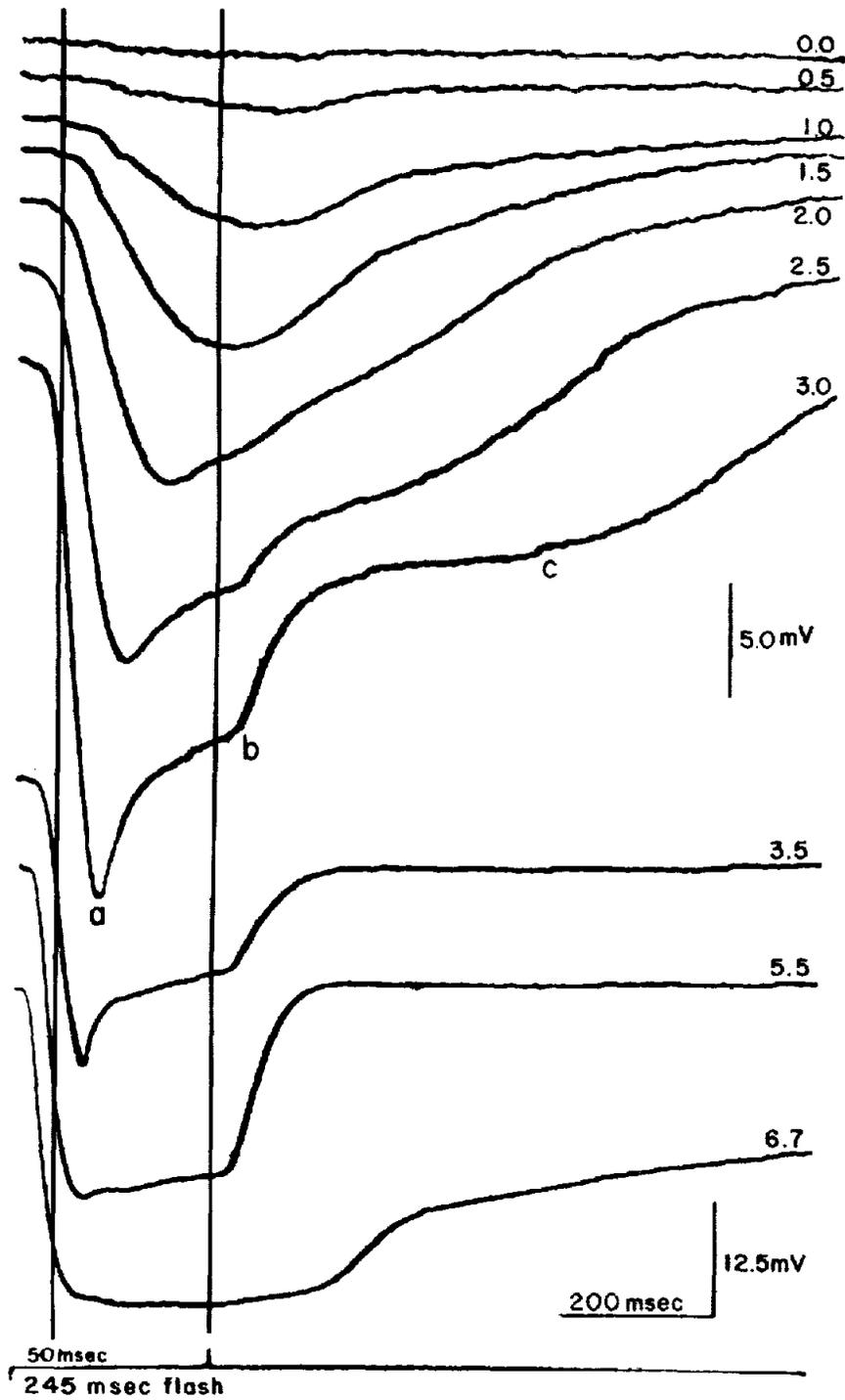


Figure 1

Intensity sequence in response to white light (color temp. 2850°K) in a dark-adapted retina. The intensity of a 245-msec flash was increased in log steps as indicated in the right margin (in this and all other figures). Flash diam 2.00 mm. Note that the last three responses were photographed at a lower amplification. Negative responses in this figure and all others are displayed downward.

## MONOCHROMATIC LIGHT

Flashes of light having discrete wavelength maxima are more apt to isolate the rod and cone components because of their different spectral sensitivities. Figure 2A presents brief intensity sequences at three wavelength maxima across the spectrum (433, 550, 666 nm) in a retina adapted to dim red light. Response form differed strikingly as a function of wavelength. Blue responses (433 nm) peaked and decayed in two phases as intensity increased, while red responses (666 nm) remained rectangular and decayed abruptly in one phase. The responses to a green-yellow light (550 nm) were intermediate in form. These differences could be assigned to the scotopic and photopic mechanisms by calculating the spectral sensitivity of two response characteristics, the initial peak voltage and the maintained voltage (Figure 2C). At the identical criterion voltage (5 mV) the maximum sensitivity of the initial peak was at 500 nm (●) while the maintained response (■) shifted to a photopic maxima at 550 nm. Therefore, peaking of the response was a rod effect, and at a moderate voltage (5 mV) the cones had already contributed to the maintained voltage in this dimly light-adapted retina. At a higher criterion (10 mV) cone excitation was more pronounced, as evidenced by a shift to 550 nm (▲) for maximum sensitivity of the initial peak. With stronger light adaptation the rod response diminished, responses to blue flashes approached the cone form (Figure 2B, 433 nm), and the spectral sensitivity of both the initial peak and maintained voltages at the 5-mV criterion were at 550 nm.

It was not possible to evoke completely isolated rod or cone responses over a large intensity range ( $\geq 3.5$  log) in dark-adapted retinae. Each S-unit (with five exceptions, see below) had sufficiently prominent contributions from both receptors so that even widely separated monochromatic flashes excited both components. For example, an orange flash (615 nm) had sufficient quanta absorbed by rods so that the threshold response exhibited the rod form (Figure 3). In fact, responses to blue (433 nm) and orange lights (615 nm) were of the rod type and almost identical until about 1.2 log above threshold. More intense 615-nm flashes suddenly shortened both the "on" and "off" latencies, but the latencies of equivalent 433-nm responses remained long ( $\geq 50$  msec). At higher intensities the 615-nm response retained the rectangular form and abrupt "off" latency, while the 433-nm response peaked (3.2, 3.8), and the latency of decay increased while the rate of decay decreased (3.8). The vast majority of S-potentials in the area centralis behaved in a similar way; 433-nm responses began to increase in duration at  $\sim 3.0$  log above threshold, but peaked at a lower intensity (0.4 to 0.6 log). Note in Figure 3 the onset of the abrupt decay at a high intensity (3.8) and the shift to a short "on" latency (3.2, 3.8) in the 433-nm response, implying that the cone component now was contributing to the response.

The increase in latency of decay can be more clearly seen in Figure 4, a similar series at a shorter flash duration (245 msec). Observe that at relatively high intensities (2.3 to 2.9), the increase in duration of the 433-nm responses produced a long-latency decay-phase, and it was the rod response which increased in duration because the long-latency decay-phase had its maximum sensitivity at 500 nm (not illustrated). The

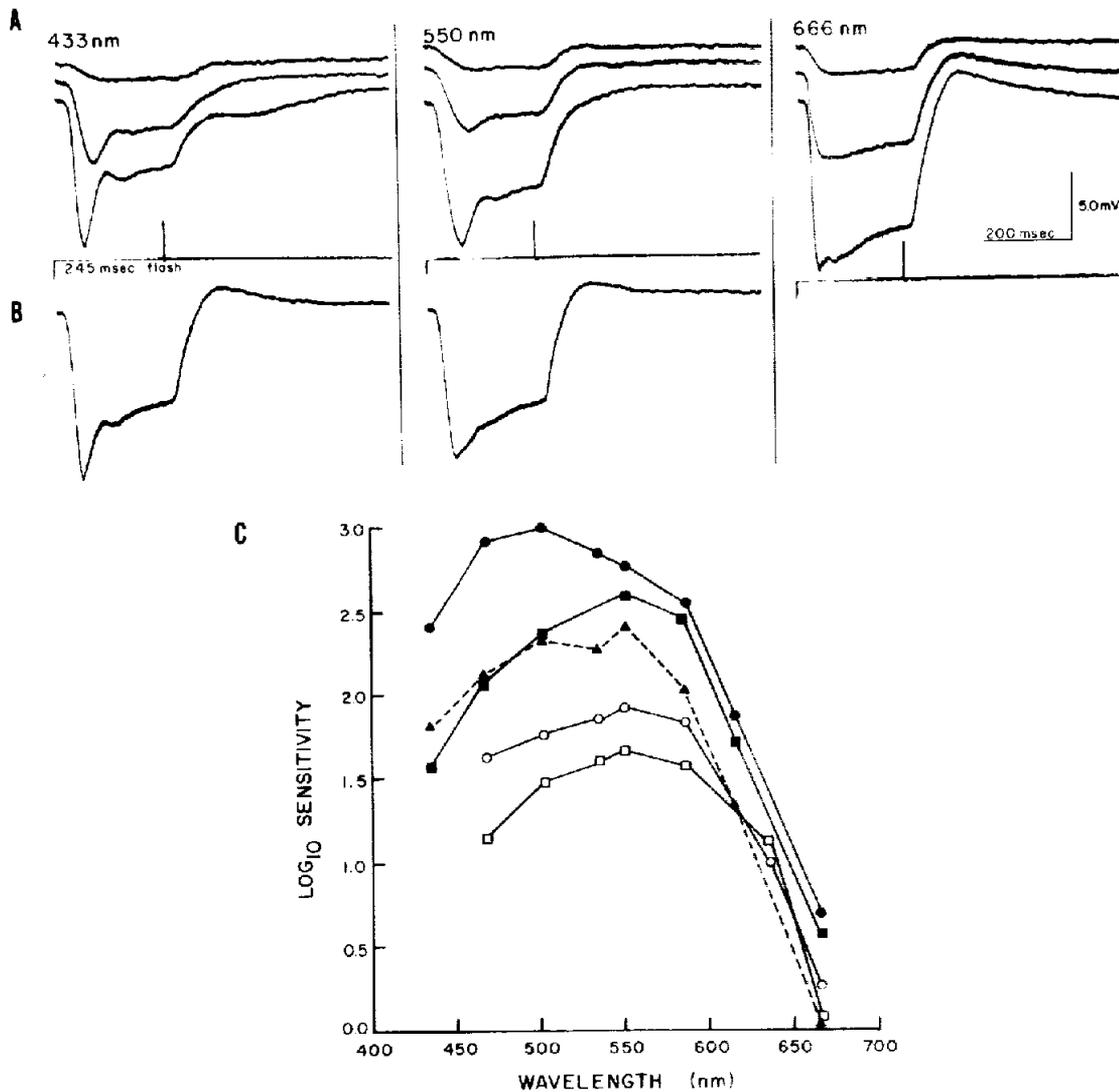


Figure 2

Response form and spectral sensitivity. A. Brief intensity sequences to three different monochromatic flashes (433, 550, 666 nm) in a retina dimly illuminated with red light (Kodak #29). The responses were matched for approximately equal amplitudes. B. At a higher level of light adaptation (white light, 2.5 log td. scotopic). The responses were chosen to match the largest responses presented in A at 433 and 550 nm. C. Spectral sensitivity functions from the amplitude-intensity curves obtained from the data in A (closed symbols) and B (open symbols). From A, initial peak voltage (●) and maintained voltage (■) at the same criterion (5.0 mV). The amplitude of the maintained response was measured as the voltage level at the "off." (▲) initial peak voltage at a higher criterion (10.0 mV). From B, initial peak voltage (○) and maintained voltage (□) at the same criterion as in A (5.0 mV).

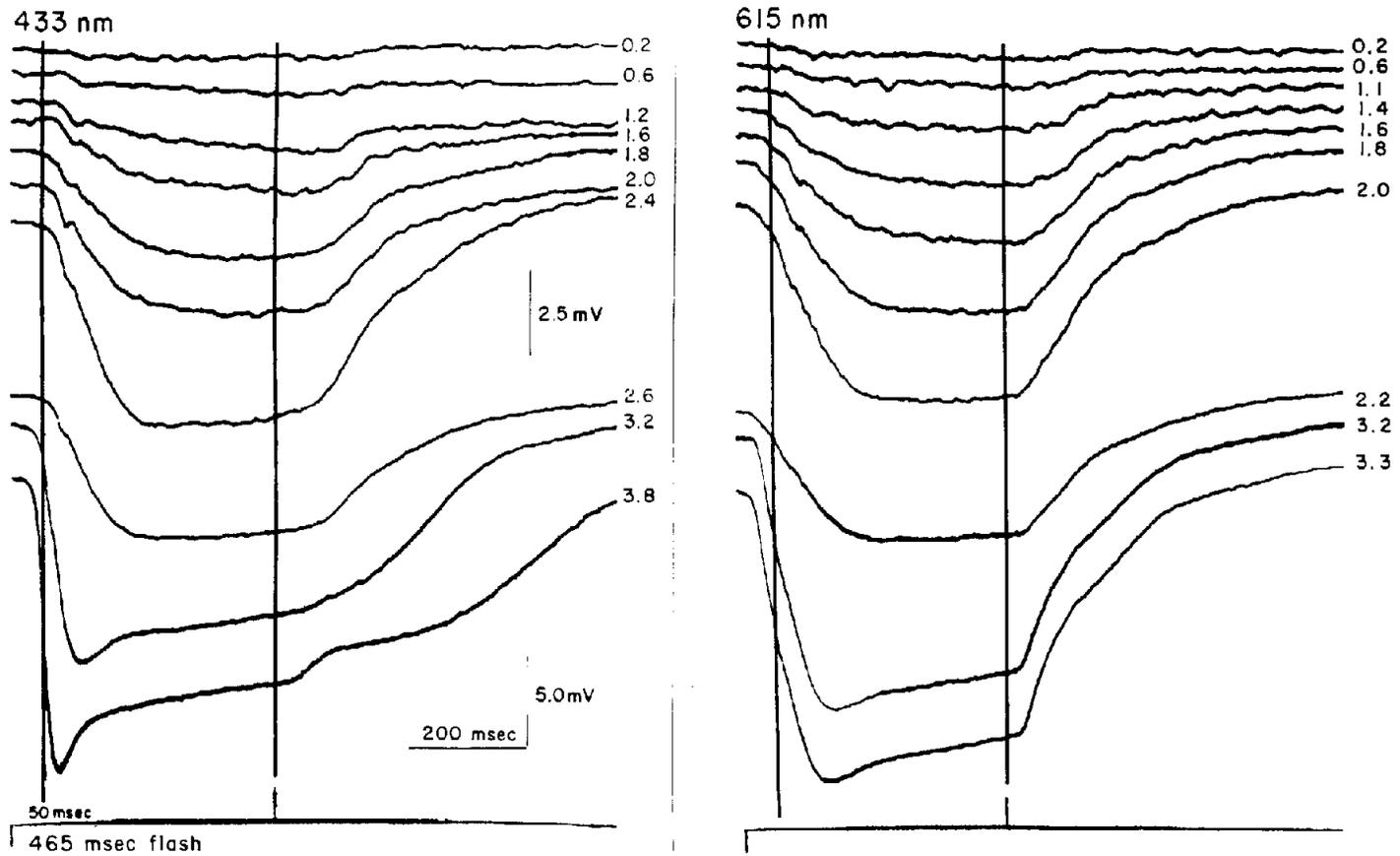


Figure 3

Intensity sequences in response to blue (433 nm) and orange (615 nm) lights in a dark-adapted retina. Flash duration, 465 msec; diam 2.00 mm. Note that the last three responses were photographed at a lower amplification.

615-nm flash at high intensities was a powerful stimulus to rods as well as cones, as indicated by the increase in duration of part of the response at high intensities (2.1 to 2.8). A similar effect had occurred in response to white light (Figure 1). At 2.5 and 3.0 log above threshold the increase in duration could be considered to originate from the rods. But at the maximum available intensity (6.7) the abrupt decay (cone) also increased in latency and decreased in slope (Figure 1). The origin of this second aftereffect is taken up in the discussion.

### V-Log I Curves

Figure 5 presents V-Log I curves for these responses. The curves in A and B were drawn through points taken from four S-units, and have been laterally displaced on the Log I axis. Both the initial peak (A, 1, 2; B, 1) and maintained voltages (A, 3, 4; B, 2) are plotted. If only the rods contributed to these responses, then at a critical intensity we would expect the V-Log I functions to evidence rod saturation. But, even in response to blue light in dark-adapted retinae the cones intruded at high intensities, and so the V-Log I function for the initial peak continued to rise (A, 1). There is a bend in the curve at  $\sim 3.5$  log above threshold, however, which suggests that the rod function began to reach a ceiling at that level; an estimate of this ceiling has been plotted (A, 2).

This trend is much more clearly defined in the maintained response by a definite ceiling at  $\sim 3.0$  log above threshold (A, 4). The decrease in the slope of the maintained voltage relative to the initial voltage at 2.0 to 2.5 log above threshold graphically describes the peaking of the rod response already observed in the oscilloscope tracings. Thus, the maintained response of the rods saturated before cone excitation masked the rod response, as evidenced by both the slope change and the ceiling.

Naka and Rushton (9-11) have shown that the V-Log I relation for cones in fish fits a tanh template so that,  $V=U \cdot I/(I+I_{1/2})$ , where V is the recorded potential amplitude, U the height of the ceiling, I the energy of the light stimulus, and  $I_{1/2}$ , the value of I when  $V=1/2U$ . Both the peak and maintained V-Log I curves in Figure 5A fit tanh templates and the estimated ceilings closely approximate U. Since the tanh curve describes the S-potential as a function of light energy for one receptor mechanism (11), in this case the rods, further hyperpolarization (Figure 5A, 1 and 3) must arise from the addition of a less sensitive mechanism, most likely cones.

The V-Log I curves obtained with orange lights in dark-adapted retinae were quite different, suggesting that a different receptor dominates the response. The initial voltage (B, 1) and the maintained voltage (B, 2) both rose much more steeply than the blue-light functions (Figure 5). In addition, neither voltage tended to level off at high intensities. Since ceilings were not found, neither curve can fit a tanh template. The cone mechanism did saturate in light adapted retinae, however, and then fit a tanh template.

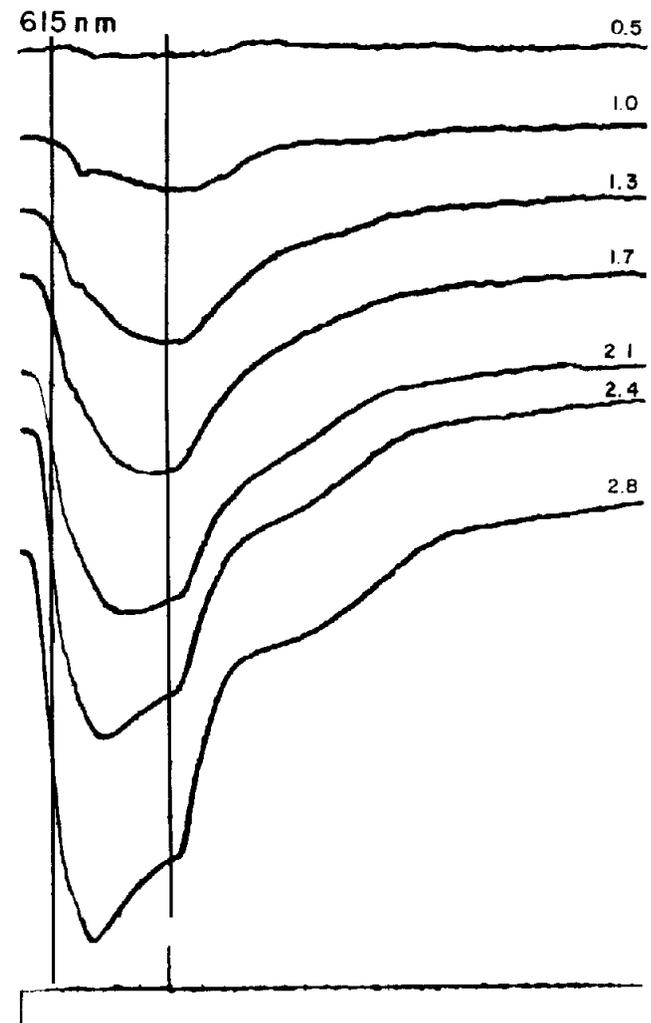
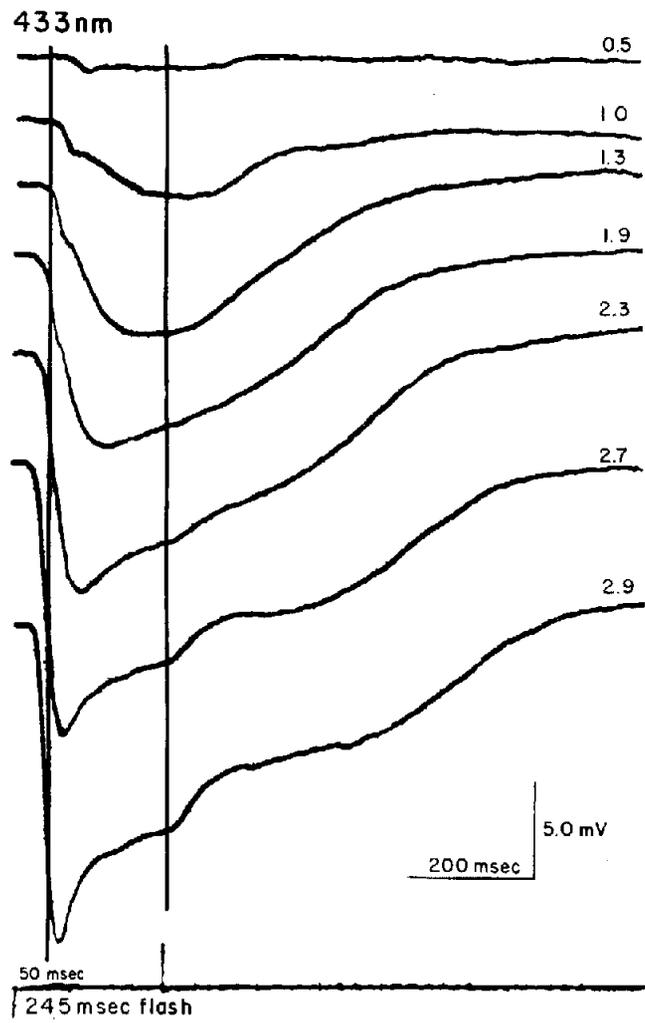


Figure 4

Intensity sequences in response to blue (433 nm) and orange (615 nm) lights in a dark-adapted retina. Flash duration 245 msec; diam 2.00 mm.

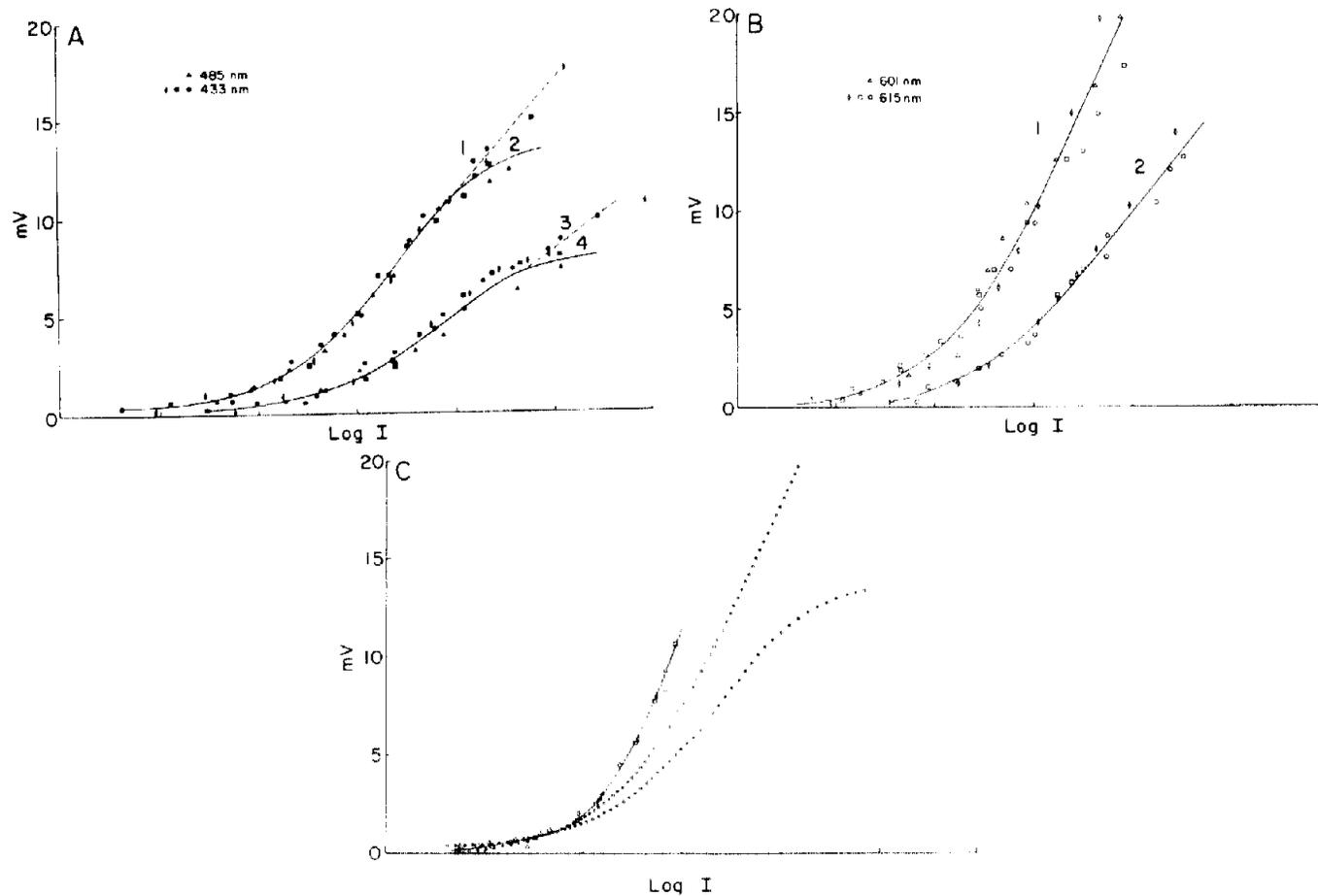


Figure 5

V-Log I curves. A. 433-nm and 485-nm flashes in dark-adapted retinae. Each symbol is a different S-potential. The curve on the left (1, 2) is a plot of the initial peak voltage. The dashed line (1) traces the actual increase in amplitude when the intensity is  $> 3.0$  log above threshold while the unbroken line (2) traces the suggested course of the rod function. The maintained voltage is plotted (3, 4) in the same way, but the function has been arbitrarily shifted to the right. B. 615-nm and 601-nm flashes in dark-adapted retinae. 1, initial peak voltage; 2, maintained voltage. C. The solid line is the V-Log I curve for flashes of white light after strong bleaches (3-10 min following lights which bleached at least 99% of the rhodopsin). Curves A, 2 (●●●) and B, 1 (○○○) have been superposed.

Additional evidence that the cone function rises more steeply than the rod is presented in C. After strong bleaches the V-Log I curve in response to orange flashes (solid line) was not unlike the dark-adapted curve (ooo) but quite unlike the blue-light function (●●●) which was dominated by the rods.

### Exceptional Responses

The population of S-potentials (N-59) in the area centralis was remarkably uniform with respect to the weight of the contributions from rods and cones as assessed by intensity sequences to blue and orange flashes. In five cases, however, responses to the blue and orange lights were practically identical except at the highest intensities. In Figure 6, for example, the cone component just appeared at 3.3 and 3.8 (601 nm) in the form of a short-latency decay-phase. At lower intensities, responses to the orange flash (601 nm) closely resembled responses to the blue flash (433 nm). It seems, therefore, that these S-potentials had a strong rod component and a very weak or negligible cone component when compared to the rest of the sample. It was expected that responses in the periphery would also be of this unusual type. Only four responses were sampled (3 1/2 disc diam nasal to the optic disc), but each one resembled the dominant type found in the area centralis.

### Brief Flashes

Brief flashes (10 msec) allowed more certain identification of the rod and cone responses because differences in latency and duration were relatively exaggerated. In Figure 7A, for example, a 433-nm dark-adapted response (1.4) began at 60 msec and continued for  $\sim 200$  msec. Observe the oscillations on the rising phase which helped to identify the rod response. In the 615-nm sequence a shorter latency component (18 msec) appeared (arrow, 0.7) at 0.7 log above the threshold for the slower response which followed it; as intensity increased (1.4 to 2.2) both components increased in amplitude. In Figure 7B the cone component was isolated by dimly light adapting the retina and depressing the rod response (light on). Observe that the cone component increased uniformly in amplitude (1.7 to 2.4), had a shorter duration than the rod component ( $\sim 125$  msec), and did not exhibit oscillations or a notch on the rising phase (14). Turning off the background light returned the rod component to the response.

Finally, in the experiment illustrated in Figure 8 algebraic addition received a direct test using brief flashes. The background conditions were adjusted so that a red (633 nm) flash produced a predominantly cone-type response while a blue flash (433 nm) produced rod-type responses of about the same amplitude. The two flashes illuminated the same retinal region, however, so that one flash excited the rods while the other flash excited the cones which contributed to the same S-unit. The interval between the two flashes was altered to cover a range of conditioning testing intervals (180 msec) in which interaction between the two inputs could be observed. The open circles in Figure 8 are the responses which would have occurred if the voltages from the two contributions algebraically added. It is clear that in each case, the actual response closely

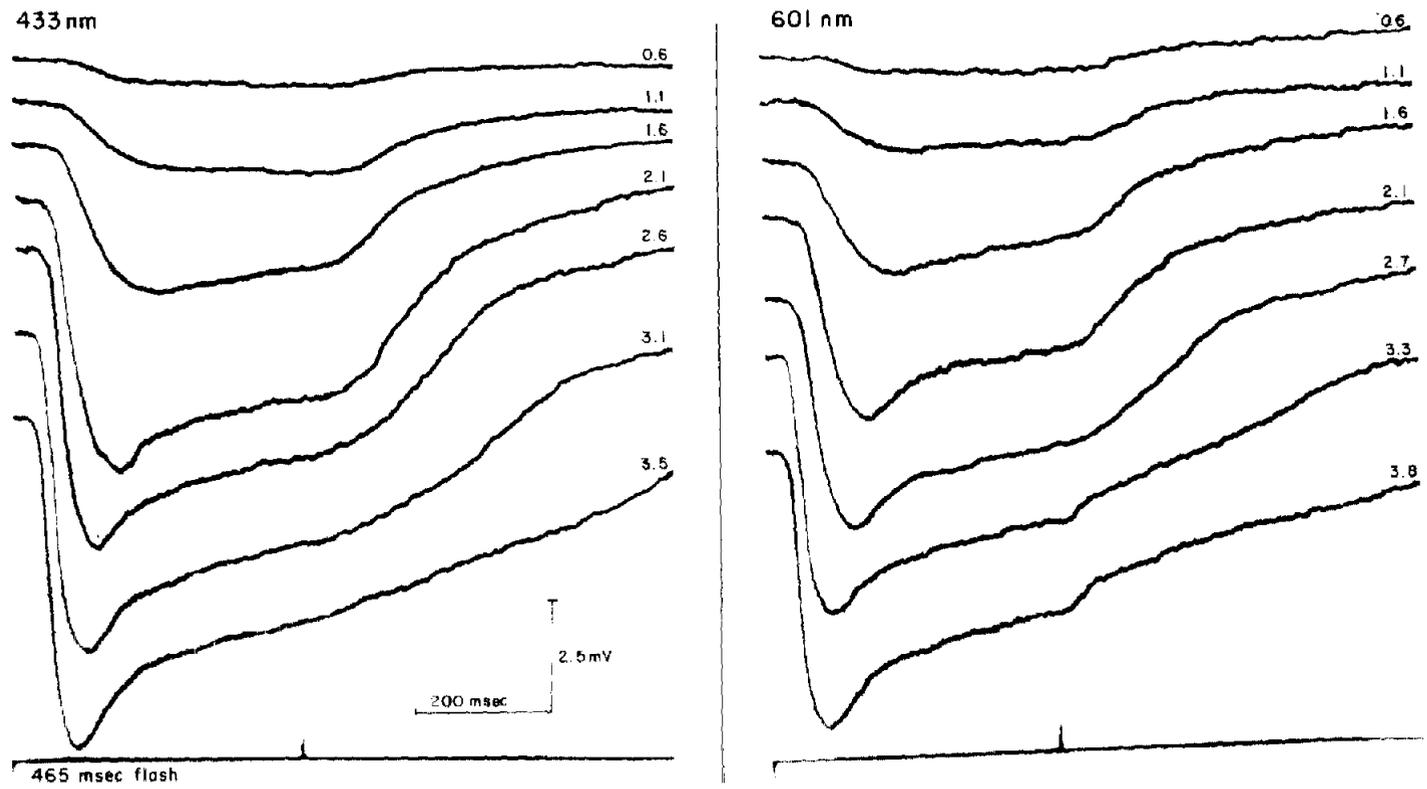


Figure 6

Intensity sequences in response to blue (433 nm) and orange (601 nm) lights in a dark-adapted retina. Flash duration 465 msec; diam 2.00 mm.

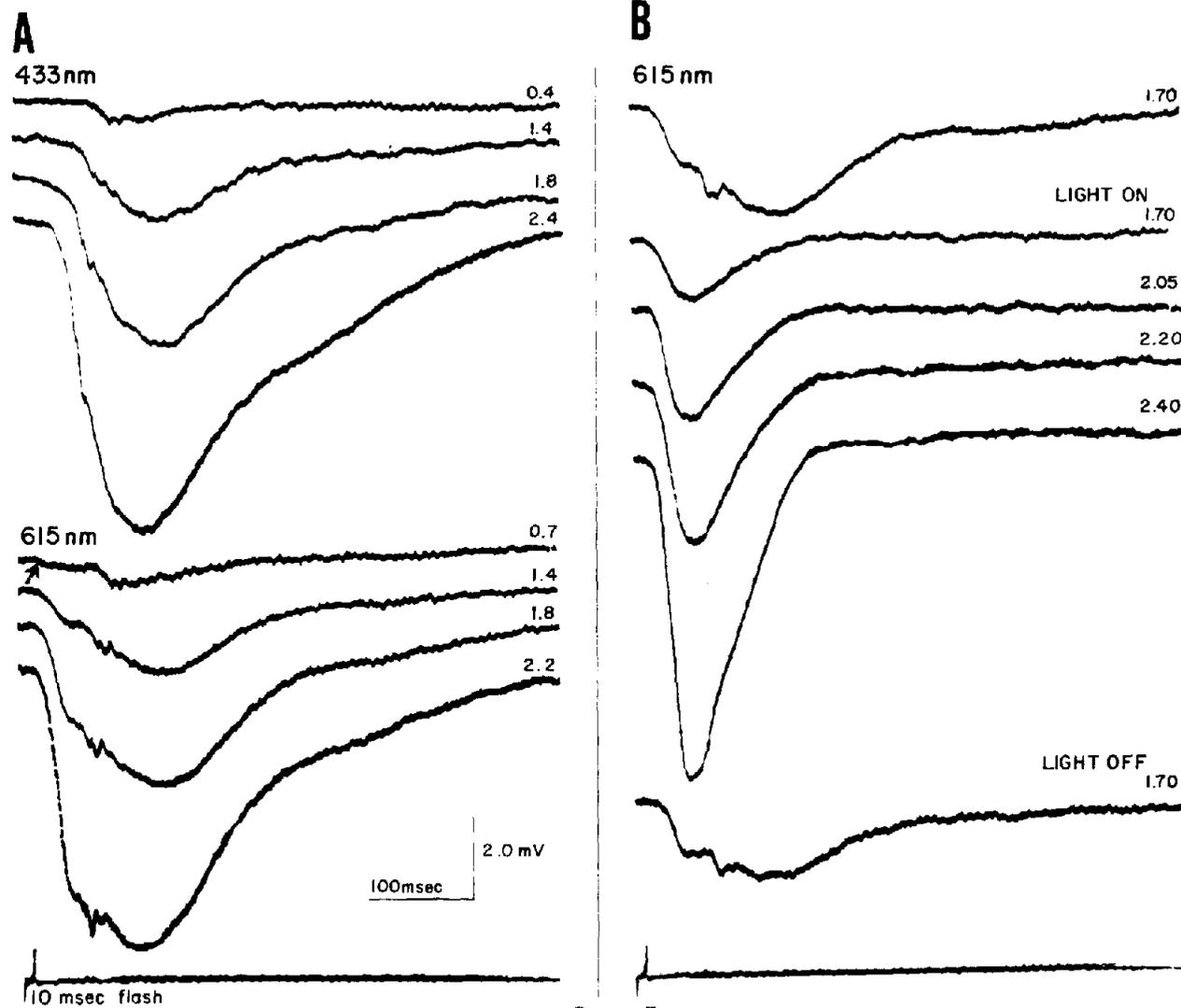


Figure 7

Responses to 10-msec flashes. A. Intensity sequences in response to blue (433 nm) and orange (615 nm) lights in a dark-adapted retina. B. The stimulus was a 10-msec flash of orange light (615 nm). Top, control response, dark adapted. Light on, intensity sequence while the same retinal area was dimly illuminated with white light. Light off, control response after extinguishing the background light.

approximated the calculated response and at no interval did the responses from the two flashes interfere or subtract in any way. This finding was consistent for a sample of S-potentials (N=7) from two different retinae.

## DISCUSSION

### FORM OF THE ROD AND CONE RESPONSES

The interaction between the rod and cone components could be examined because of the distinctly different form of responses from the two receptors. This observation has additional significance for our understanding of receptor function because the horizontal cells, by connecting directly to them, may accurately reflect their output. In support of Gouras's (4, 5) and Gouras and Link's observations (6) in ganglion cells and ERG's from the monkey periphery, rod responses occur at much longer latencies than cone responses. Threshold rod responses of S-units were observed at  $\sim 100$  msec compared to 40 msec for threshold cone responses. An additional finding is that the latencies of decay exhibit differences between rod and cone responses of about the same order, and serve equally well to distinguish the two receptors.

The rod response also changed in a special way as a function of flash intensity. At about 2.5 log above an arbitrary threshold the maintained voltage failed to increase as rapidly as the initial voltage and the response acquired an initial peak. Peaking was most prominent in partially light-adapted retinae in response to flashes that mainly excited rods. Although it was not possible to determine the total range of the rod response, a projection of the V-Log I curves suggested that the maintained response began to level off at  $\sim 3.0$  log above threshold compared with 3.5 log for the initial peak. Cone responses in dark-adapted retinae tended to remain rectangular, i.e., equal initial and maintained voltages. With strong light adaptation or following intense flashes cone responses also tended to peak (un-published observation). This characteristic of the receptors closely resembles the behavior of slow potentials recorded from compound eyes (1, 8).

At about 0.4 to 0.6 log beyond the intensity at which an initial peak appears the response begins to increase in duration. This effect can be followed over a large intensity range and is the subject of a subsequent report (15). It is worth noting, however, that it is a property of the rods which the S-unit reflects. A second duration effect was also observed at the highest intensities and here the interpretation is more difficult. At these intensities the S-potential usually has reached its maximum voltage and it cannot be decided, therefore, whether the receptor (cone) or the S-unit initiates the increase in duration.

The present work and the previous paper (14) support the conclusions of Brown and Murakami (2) that both the rods and cones influence cat S-potentials. In their paper, Brown and Murakami (2) emphasized slowness of decay as the unique characteristic of

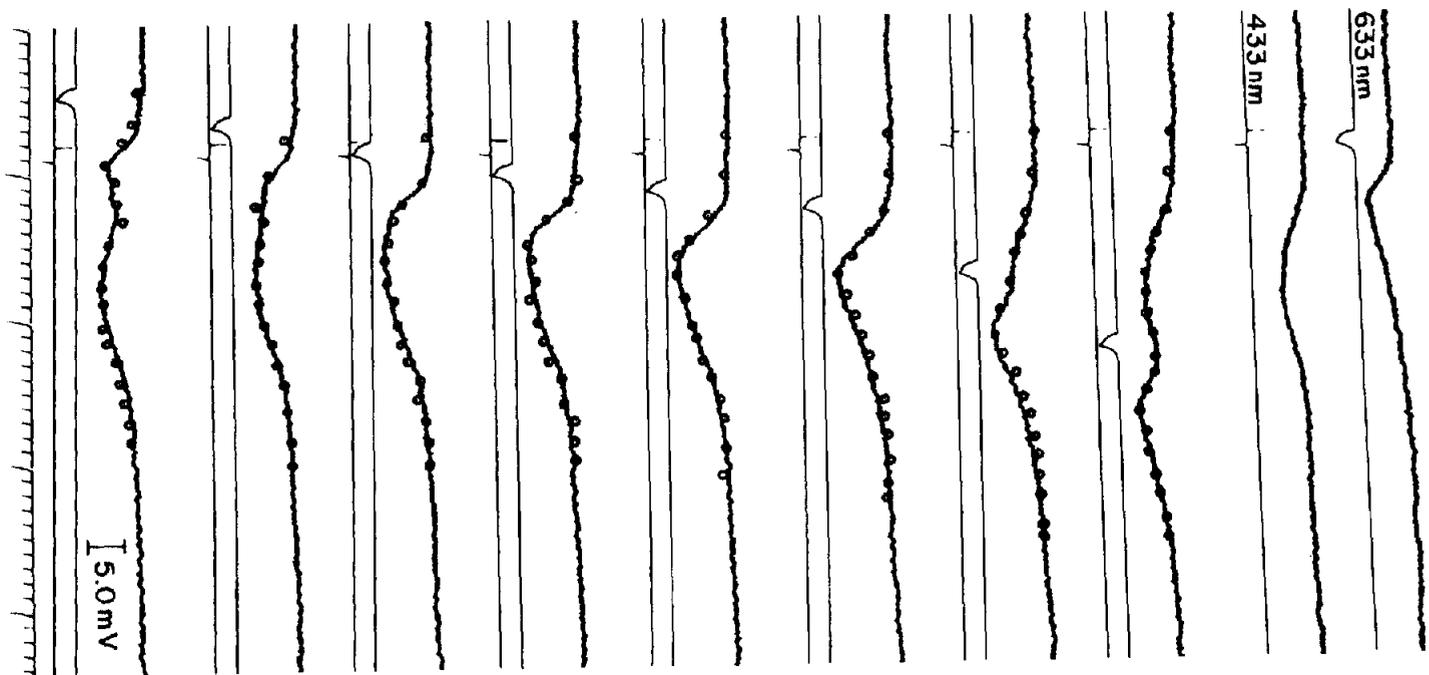


Figure 8

Responses to 10-msec blue (433 nm) and red (633 nm) lights at varying intervals, -40 to +140 msec. Weak background light adaptation. Control responses to each flash appear at the top. Flash diam 2.00 mm. The flashes were superposed on the retina. The circles show the response that would occur if the voltages from the 633-nm and 433-nm flashes algebraically added. Time, 10 msec and 100 msec.

rod-dominated responses. The study of threshold responses in dark-adapted retinæ has shown, however, that although the fall (and rise) time of the rods is slower than that of the cones, the marked slowing referred to by Brown and Murakami (2) is an intensity effect. Their data actually support this interpretation since the slow decays were produced by flashes that were well above the threshold of this effect. In fact, the intensities were sufficiently high to increase the latency of the abrupt decay (2, Figure 4), an effect which could originate either in the cones or in the S-unit as mentioned above. These authors also concluded that the receptive field of S-units includes a small central area where the responses do not change with light and dark adaptation. They showed that "dark-adapted" responses to large spots (diam 2.18 mm) exhibit the markedly slow decay while responses to 0.18-mm spots show only a rapid decay under the same conditions. It is significant, however, that only 2 min were allowed for dark adaptation, whereas responses to small spots also assumed the rod form and exhibited the scotopic action spectra in well dark-adapted retinæ (unpublished observation). An alternative interpretation for their data would be that with the larger flash, many rods are stimulated more intensely because of stray light and more of these intensely stimulated rods would contribute to the response. Thus the high-intensity effect would be more apt to appear in response to the larger stimuli. But small intense flashes in the dark-adapted retina also produce the same change in decay (unpublished observation). Finally, in the present work the rod and cone receptive fields appeared to have about the same diameters and responded uniformly throughout (14).

#### ROD-CONE INTERACTION

The course taken by the rod and cone signals from receptor to ganglion cell axon is incompletely understood. Bipolar cells, in primate and man, synapse either with the rods (rod bipolar) or the cones (flat, midget bipolars), but laterally connecting amacrine cells and the dendritic surfaces of diffuse ganglion cells provide countless opportunities for interaction between the signals (3, 7). Gouras and Link (6) were able to demonstrate mutual interference between the rod and cone signals at monkey ganglion cells. Rod and cone responses in the ERG, however, did not interfere (5). It seemed certain then, at least for the primate, that interaction occurred but only after the signals reached the inner plexiform layer (5). The present work offers evidence for the summation of rod and cone signals at the horizontal cell layer in the cat. White flashes to dark-adapted retinæ produced response increments throughout a large range (6 log), and the responses were compounded from both the rod and cone inputs. Similarly, the form of the response to colored flashes is a function of the degree to which the rods and cones are excited by the specific wavelength distribution of the flash. Finally, the double-flash experiment confirms that in one set of conditions, i.e., brief flashes of moderate intensity and weak adaptation, the rod and cone voltages are algebraically summed by the S-unit.

The function of horizontal cells still remains a mystery. Recently, Brown and Murakami (2) suggested that cat horizontal cells mediate reciprocal lateral inhibition

between the rods and cones. Supportive evidence was not obtained in the present work. For example, in dark-adapted retinae it was not apparent that rods controlled the S-unit as suggested by Brown and Murakami (2). Rather, the cone input was observed whenever the cones were adequately stimulated. In light-adapted retinae the rods did undergo a decrease in sensitivity, but evidence has been presented (12, 15) that this occurs before the S-unit. The evidence presented here only shows that the rod input to the horizontal cell does not seem to prevent cones from also contributing to the response in dark-adapted retinae. It is still possible, however, that horizontal cells alter the transmission of signals between receptors and bipolar cells in such manner that rods and cones oppose each other, but this is a problem for future investigation.

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