

NAMI-1071

LIBRARY, USAARL
FT RUCKER, ALA

USAARL
Serial No. 69-10

ROD AND CONE CONTRIBUTIONS TO S-POTENTIALS FROM CAT RETINA

Roy H. Steinberg



U. S. ARMY AEROMEDICAL RESEARCH LABORATORY

NAVAL AEROSPACE MEDICAL INSTITUTE

June 1969

This document has been approved for public release and sale;
its distribution is unlimited.

This document has been approved for public release and sale;
its distribution is unlimited.

ROD AND CONE CONTRIBUTIONS TO S-POTENTIALS FROM CAT RETINA

Roy H. Steinberg

Bureau of Medicine and Surgery
MR005.04-0088.3

U. S. Army Aeromedical Research Laboratory

Approved by

Ashton Graybiel, M. D.
Head, Research Department

Released by

Captain J. W. Weaver, MC USN
Commanding Officer

2 June 1969

NAVAL AEROSPACE MEDICAL INSTITUTE
NAVAL AEROSPACE MEDICAL CENTER
PENSACOLA, FLORIDA 32512

SUMMARY PAGE *

THE PROBLEM

The problem of whether the rods contribute to S-potentials was studied in the intact eye of the cat.

FINDINGS

S-potentials from luminosity units (L-units) were evoked by small spots of relatively monochromatic light in dark- and light-adapted retinae.

Dark-adapted responses to blue light suggested that rods were excited because both the "on" and "off" latencies were long over a 3.0-log range of intensities.

The spectral sensitivity curve for dark-adapted S-potentials had its maximum at 500 nm and resembled Granit's scotopic dominator.

Scotopically balanced blue and orange lights produced equal-amplitude responses in dark-adapted retinae. After light adaptation the same S-potentials were always more sensitive to the orange light. The Purkinje shift suggested by this result was confirmed by calculating the light- and dark-adapted spectral sensitivities of several individual S-potentials.

The spectral sensitivity curve for light-adapted S-potentials had its maximum at 560 nm and resembled Granit's photopic dominator. In light-adapted retinae, in response to orange light, response latencies even at threshold were always much faster than in dark adaptation.

It is concluded that the rhodopsin rods contribute to S-potentials (L-type) in the cat and that cones contribute to the same responses. If the horizontal cells produce these responses, then either rods and cones synapse with the same cells or rod and cone horizontal cells connect with each other.

ACKNOWLEDGMENTS

I am grateful to Prof. W. A. H. Rushton for his comments and critical reading of the manuscript. I wish to thank Michael L. Walker and Scott Morrill for technical assistance.

*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

Although S-potentials, large intracellular responses whose amplitude is graded with intensity, have been recorded from many classes of vertebrates, most studies have been in fish where they were first discovered by Svaetichin (32). They are categorized on the basis of polarity (15). Luminosity potentials (L-potentials) are always negative (hyperpolarizing) and probably originate in horizontal cells. Chromaticity potentials (C-potentials) respond negatively to some wavelengths but positively to others (depolarizing) and are of uncertain origin. In fish, species differences in responses seemed to correlate with the depth at which the fish were found (15). Deep-water fish gave only L-responses while shallow-water fish gave both L- and C-responses but differed in the subtypes of C-responses. Quite probably these differences are associated with the kind of wavelength discrimination present in each species. In mammals, the same relation to wavelength discrimination might be expected; indeed the cat, the only mammal studied so far, has a weak color sense (14, 16, 25) and exhibits only L-type potentials (1-3, 12, 13, 21, 27).

Initially, S-potentials were thought to depend only upon the activity of cones. Light and dark adaptation were very fast, and the responses could be recorded in retinae where the rod outer segments had been stripped away (15, 20). Recently, some investigators have suggested that the rods also contribute to S-potentials, particularly to the L-type (19, 24). Mitarai et al. (19) in preparations (carp) dark adapted for 12 hours found scotopic responses of L-units at low thresholds and a Purkinje shift after light adaptation (λ max from 470 nm to 590 nm). In addition, the long latencies and slow rise and fall times of the scotopic responses suggested rod activity. Also in carp, Orlov and Maksimova (24) presented color mixture curves with λ max close to the rod and cone absorption curves, but concluded that, although the data indicated two receptor types, both could be cones. On the other hand, Witkovsky (38) also worked with well dark-adapted L-units in carp and did not observe a Purkinje shift, although the waveform was scotopic in the dark, and blue sensitivity was enhanced. In a preparation of carp retina which had an intact blood supply, permitting re-dark adaptation, Watanabe and Hashimoto (34) also did not observe a Purkinje shift. More recently in two types of cyprinid fish, Naka and Rushton (22), although able to identify a scotopic mechanism (low threshold, slow recovery following light adaptation), could not assign it to a particular receptor. It would seem in fish, particularly carp, that in dark adaptation a particular receptor cannot be assigned yet to the scotopic mechanism which activates L-units.

The experiments in fish were usually performed on isolated retinae which cannot be repeatedly dark adapted, and one is considerably handicapped if rod function is under investigation. On the other hand, in mammals, techniques are available for recording from the intact eye which can be repeatedly dark adapted. Since in cat retina, L-units could be recorded and the retina contains a high percentage of rods (33), it seemed reasonable to investigate whether the rods influenced these responses.

PROCEDURE

The preparation and maintenance of the cat and recording technique from the intact eye have been described in previous publications (26, 30). There are a number of additional points pertinent to the study of S-potentials which are to be considered.

RECORDING S-POTENTIALS FROM THE INTACT EYE

It is well known that obtaining and holding S-potentials in the intact mammalian eye is much more difficult than in fish. These responses could be recorded, however, with reasonable success by attending carefully to several factors. Most important is the reduction of retinal pulsations by maintaining the intraocular pressure (2). Special precautions were taken, therefore, to prevent the loss of any intraocular fluid through the #18 hypodermic needle that penetrated the sclera and vitreous. The needle insert was always kept in place until a glass micropipette replaced it. Micropipettes were rapidly inserted, and the junction between the pipette and needle was tightly sealed by means of a silastic (Dow Corning) boot (30). The boot provided free penetration and withdrawal of the microelectrode but prevented leakage of intraocular fluid.

All of the recordings were obtained with glass microelectrodes (3 M-KCl). Although tip diameters were not accurately measured, only those microelectrodes having dc resistances of 15 to 25 M Ω readily recorded S-potentials. These microelectrodes are finer than those needed to record ganglion cell activity, while microelectrodes with higher resistance fail because of difficulty in penetrating the vitreous and retinal surface. The microelectrode was slowly advanced through the retina while recording the local electroretinogram (LERG) in response to a 2.00-mm diam flash of light centered at the microelectrode tip. S-potentials usually were captured by "tapping in" at the retinal level where b-wave amplitude was at its maximum. The extracellular response was always negative, and since S-potentials have the same polarity, inversion from an extracellular to an intracellular polarity was never observed. Just prior to capture, the recording behaved as if the electrode tip were pressing on a membrane since the resistance increased. The capture of an S-potential always was accompanied by a distinct negative shift in the resting potential (3.5 to 36.0 mV) which often occurred in several steps, the responses increasing greatly in amplitude with each shift. In general, it was more difficult to obtain these responses in dark-adapted than light-adapted retinae, and special difficulty was encountered in holding responses that had been obtained in the dark after turning on an adapting light, confirming the observation of Brown and Wiesel (2).

Under these conditions and in the best preparations S-potentials could be obtained on about 30 to 50 per cent of penetrations. The data were drawn from over 100 responses which had remained stable for periods of 10 to 40 min. All recordings, except four, were from penetrations in the area centralis. Responses to light were always negative in polarity (L-type), exhibiting a maximum amplitude in dark-adapted retinae at 35 to 40 mV.

LIGHT SOURCE

The dual-beam ophthalmoscope (tungsten filament lamps) which was used to stimulate the retina with light and the conditions of stimulation also have been described (26). All of the stimuli were in the form of spots of light projected onto the surface of the retina at the most sensitive location for the response. Narrow band interference filters (Optics Technology; halfwidth, 3 to 4 1/2% of peak) interposed in the stimulus beam provided relatively monochromatic stimuli. The relative energies of these lights were measured by an AGD-100 (EG&G) silicon photodiode calibrated by the manufacturer.

The method described by Westheimer (37) was used to estimate retinal illuminance. An aperture in the stimulus beam was focused on a MgO plate and a luminance of 11.0 ft-L read with a Spectra-Pritchard photometer (Photo Research Corp.). After correcting for the angle of incidence, reflectivity, and distance of the source image from the plate, the retinal illuminance without neutral density filters in the beam was found to be 5.8 photopic trolands. To convert to scotopic units the factor Δ was obtained from Wyszecki and Stiles (39), where $\log \text{td. scotopic} = \log \text{td. photopic} + \Delta$, so that at the color temperature of the source (2850°K) there were 6.0 log td. scotopic.

In man a scotopic troland is a unit of retinal illumination formally defined in terms of geometrical optics. A similar unit may be defined for the cat, namely with the same quantum flux per square centimeter on the retina as on the human retina. To obtain cat trolands, therefore, the measurement was corrected for the ratio of squared posterior nodal distances in cat and man (+0.26 log unit), the mean reflectivity of yellow tapeta (35), and the relatively clear preretinal media of the cat as opposed to man (36) (combined correction of 0.24 log unit). A final figure of 6.5 log td. scotopic (cat) was derived for the maximum retinal illuminance provided by the stimulus beam.

RESULTS

RODS

To discover if the rods contributed it was essential to study well dark-adapted retinae. After surgery was completed the preparation was allowed to dark adapt for 1 1/2 to 2 1/2 hours, and while searching for S-potentials, a strong effort was made to maintain the dark-adapted state; i.e., stray light was excluded and the test flash was kept at ≤ 1.0 log above the dark-adapted threshold. Under these conditions all of the recorded S-units responded to flashes that were well within the scotopic range. The smallest responses that could be reliably distinguished were 0.15 to 0.35 mV and were arbitrarily designated as threshold responses produced by flashes of about 0.5 ± 0.2 log td. scotopic.

As mentioned above, dark-adapted S-potentials in fish characteristically exhibit slow rise and fall times at long latencies. Gouras (9) and Gouras and Link (10) have succeeded in associating the long latency of responses in ganglion cells and the ERG of primates with the rods, while cone responses occurred at distinctly shorter latencies. In cat L-units the form of dark-adapted responses at threshold and within 2.5 to 3.0 log above threshold suggests that they are rod responses. Figure 1 presents an intensity sequence in response to a blue flash (433 nm) in a dark-adapted retina. The response at 0.2 log above threshold was a small, maintained voltage which began and decayed at long latencies from the onset and termination of the flash (100 msec and 90 msec, respectively). These latencies remained long, decreasing to only 55 msec for both on and off, despite an increase in intensity of over 2.5 log units. The rise and fall times of the onset and decay phases also changed little as the intensity increased and seemed to be about the same, but the decay had an extra tail. A prominent "notch" on the rising phase of the response was characteristic of most well dark-adapted S-potentials, and with brief flashes (10 msec) several rapid oscillations occurred at this location (28). More complex responses were observed at still higher intensities and are described in the same paper (28).

The long latencies and uniformity of dark-adapted intensity sequences in response to blue flashes suggested that the rods were excited. More conclusive proof, however, was provided by spectral sensitivity functions. In this experiment the dark-adapted L-units were exposed to flashes of increasing intensity at different wavelength maxima, spaced across the spectrum (433 to 666 nm). The spectral sensitivity curves were derived by means of a constant-response criterion applied to the amplitude-intensity functions. In order to assure that the scotopic mechanism was being measured, near-threshold criterion voltages (0.5 to 4.0 mV) were chosen. The relative sensitivity values at the criterion were then converted to a spectrum of equal quantum intensities. The spectral sensitivity functions in dark and light adaptation are presented in Figure 2. In each case the heavy line is the mean curve derived from three or four different S-units. In the dark-adapted retina (Figure 2A) maximum sensitivity occurred at 500 nm, and there was a small secondary hump at 550 nm. The function closely resembled the scotopic dominator obtained by Granit (11) from ganglion cells in the cat (dotted curve, bottom left).

CONES

Since the contribution of cones is well known, it was expected that cat S-units would also show this component. But it was not known if the cones would influence the same responses as the rods. To answer this question responses to blue (433 nm) and orange (600 nm) lights were compared in the dark- and light-adapted states. These flashes were scotopically balanced; i.e., their intensities had been adjusted to produce equal amplitude b-waves in the LERG. It was assumed that they stimulated the rods about equally but that the 600-nm flash was a more effective stimulus for the cones. Responses were first obtained while dark adapted then the adapting light was turned on

433 nm

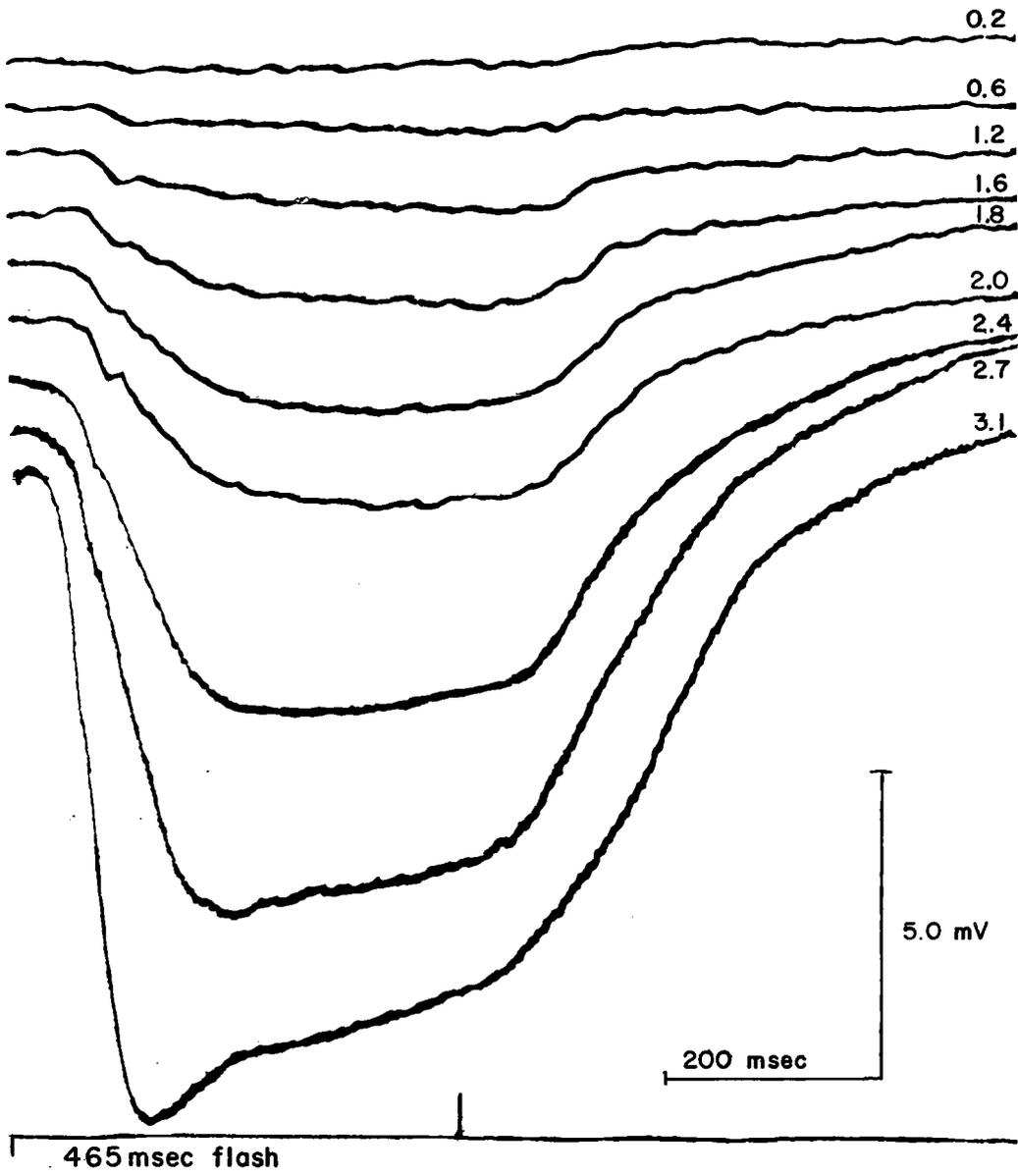


Figure 1

Intensity sequence in response to a blue light (433 nm) in a dark-adapted retina. The intensity of a 465-msec flash was increased in log steps as is indicated in the right margin (in this and all other figures). Flash diam 2.00 mm. Negative responses in this figure and all others are displayed downward.

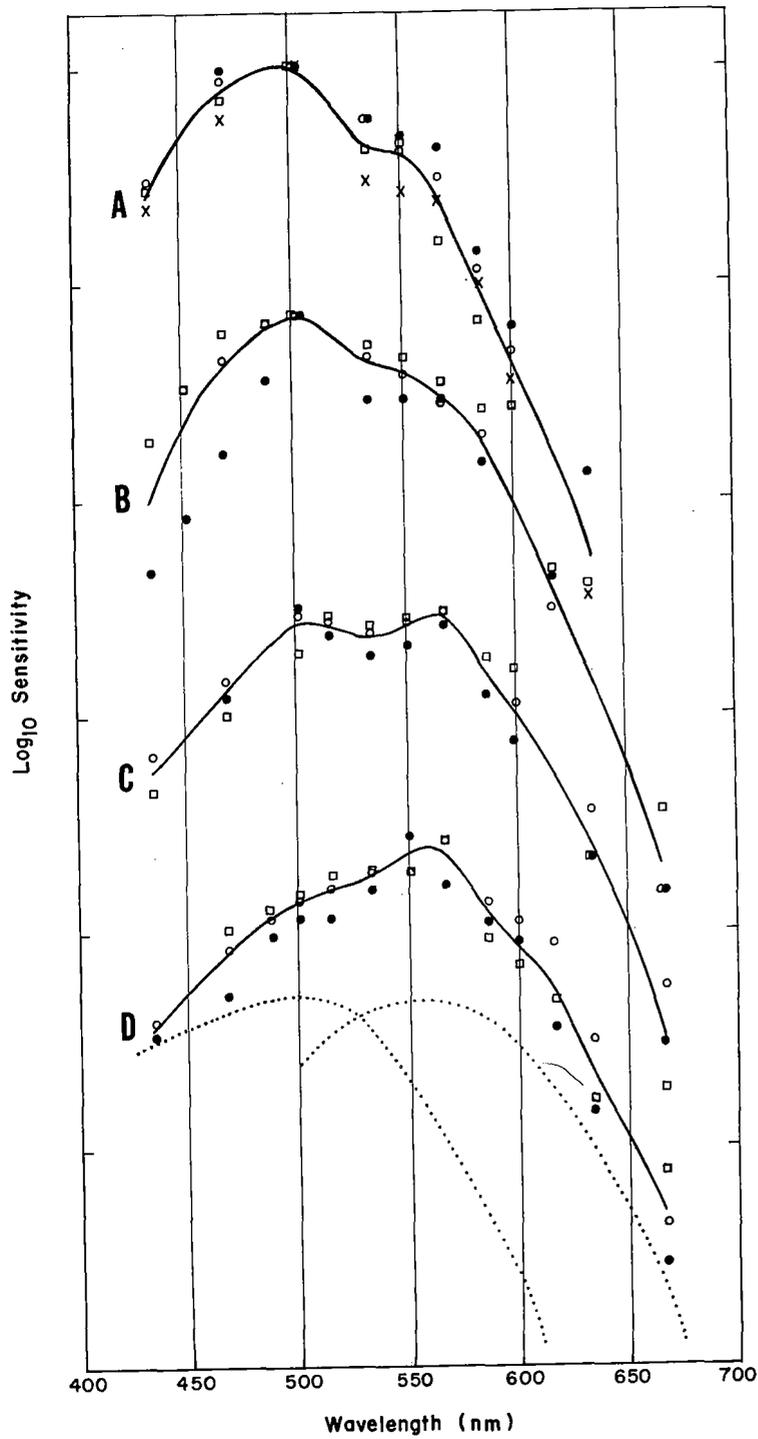


Figure 2

Spectral sensitivities of S-potentials under different conditions of adaptation. The curves are based upon equal-amplitude criteria at a low voltage (0.5 to 4.0 mV), and the sensitivities were adjusted for equal quantum intensity. Each symbol represents a different S-potential and the solid line is the mean of the sample. A. dim red adaptation (Kodak #29). B. moderate light adaptation with white light, 2.5 log td. scotopic. C. stronger light adaptation, 2.5 log td. scotopic. D. Granit's scotopic curves (dotted) were replotted on a log scale and appear at the bottom; left--scotopic dominator, right--photopic dominator. Note that the four spectral sensitivity functions (A-D) have been arbitrarily spaced on the log scale.

and the responses again recorded in the same S-potential. The results were highly consistent (14 S-units); the dark-adapted responses were of equal amplitude, but after light adaptation the 600-nm stimulus produced a much larger response (Figure 3A). In addition, whereas the thresholds were equal in the dark, when light adapted, the threshold for the 433-nm flash rose 1.5 log more than that for the 600-nm flash.

In several cases it was possible to confirm that a Purkinje shift occurred by obtaining spectral sensitivity functions in the dark- and light-adapted state in the same S-unit. An example of one of these is presented in Figure 3B. Observe that the maximum sensitivity in the dark (●) shifted to 585 nm in the light (○) and there was a depression of the 500-nm peak.

The spectral sensitivity functions B-D in Figure 2 present a more comprehensive view of the cone component. They were obtained in the same manner as in A except that the retina was light adapted. With strong light adaptation (D) the 500-nm peak was depressed and the maximum sensitivity then occurred at 560 nm (550 to 585 nm). This function closely followed the photopic dominator obtained by Granit (11), (dotted curve, bottom right, Figure 2). At lower levels of light adaptation (B, C) both scotopic and photopic peaks occurred. Many attempts were made to subdivide further the photopic peak, but selective adaptation with blue (Kodak #47) and red light (Kodak #25, 29) failed to reveal subsidiary peaks, either in the red or the green.

The form of light-adapted responses always differed strikingly from the dark-adapted ones. To best illustrate this point an intensity sequence was obtained (Figure 4) in response to an orange light (615 nm) at a moment when the rod responses were greatly suppressed. Five minutes before the same retinal area had been exposed to intense white light which was calculated to have bleached at least 99 per cent of the rhodopsin (29). Subsequent to a bleach of this intensity the rod branch of the dark-adaptation curve, based on thresholds of S-units, did not begin to recover for 15 to 20 min. Observe in Figure 4 that even a near-threshold response began and decayed with a short latency (35, 40 msec, respectively). The latencies continued to shorten with increasing intensity, until at 2.0 log above threshold they were 18 and 20 msec, and reached a minimum of 12 msec with the brightest flash (3.4). The rise times of onset and decay were again almost symmetrical, but somewhat faster than those attributed to the rods.

Several attempts were made to measure the area from which rods and cones contributed to an individual S-unit. For the rods, the retina dark adapted, a small spot of blue light (433 nm; diam, 0.33) was positioned to produce the lowest threshold L-response. The diameter of the spot was increased in steps until no further increase in response amplitude occurred. Flash intensity was kept at 1.0 log above threshold in order to reduce stray-light effects. In the area centralis, for five different S-units, responses were maximum when spot diameters reached 1.0 to 1.17 mm. In one unusual eye which did not have a tapetum, stray-light effects were minimized and the maximum was at 1.0 mm. The technique for assessing the cone field was the same

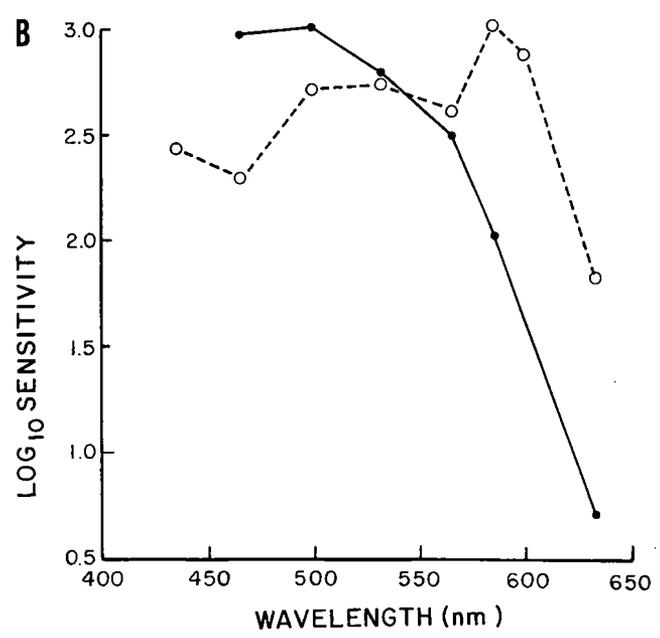
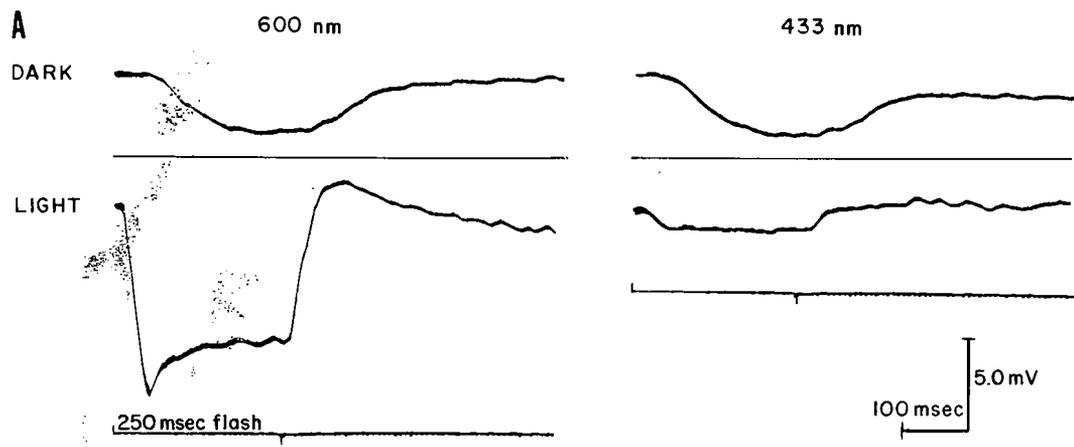


Figure 3

A. Responses of an S-potential to scotopically balanced stimuli (600 nm, left and 433 nm, right) in the dark-adapted (top) and light-adapted (bottom) states. Stimulus duration, 250 msec and diam 2.0 mm; light adaptation at 3.5 log td. scotopic. B. The spectral sensitivity of one S-potential in both the dark- (●) and light-adapted (○) states. The light-adapted function was shifted upwards on the ordinate. Light adaptation at 3.5 log td. scotopic.

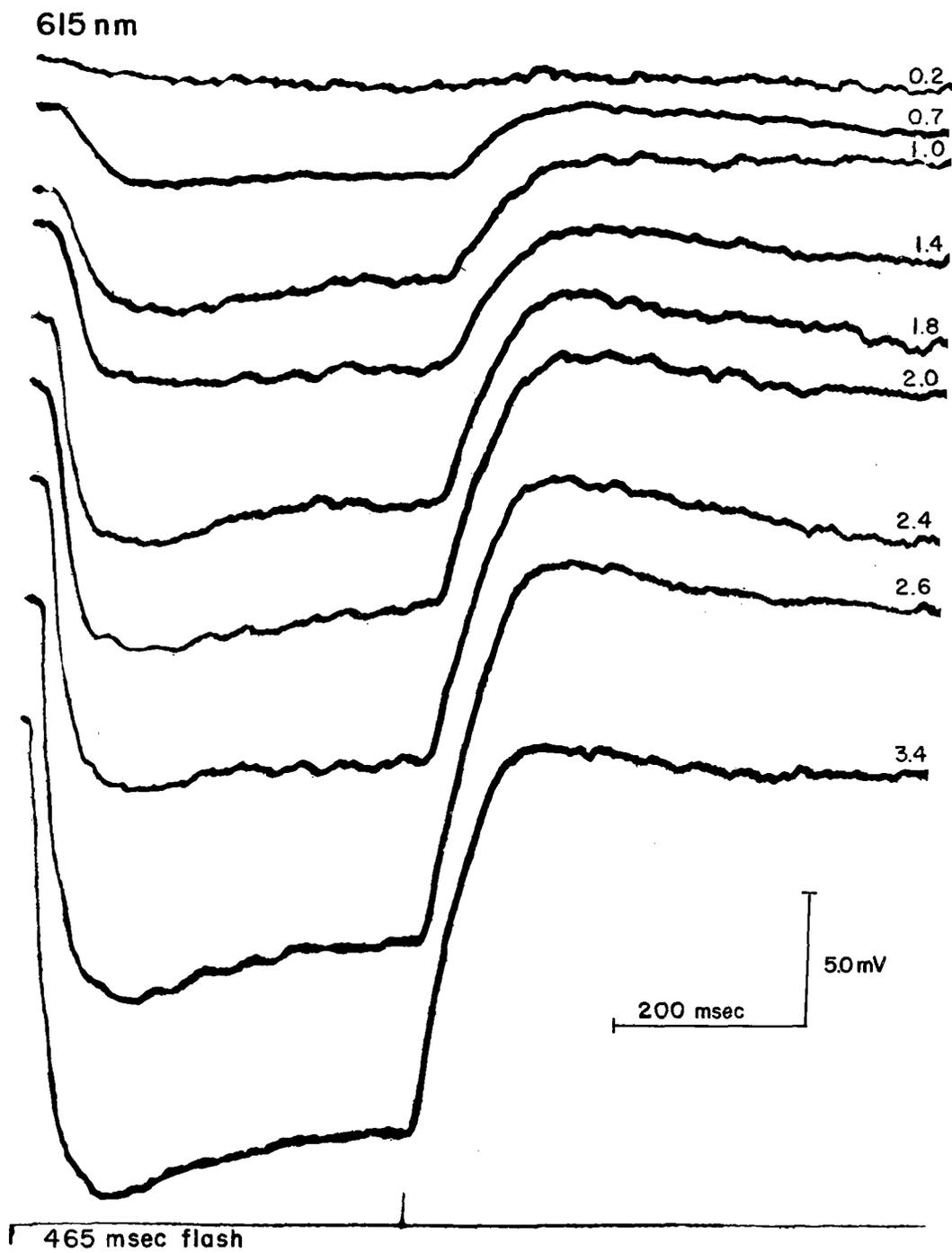


Figure 4

Intensity sequence in response to an orange light (615 nm) in a light-adapted retina. Flash diam 2.00 mm. The sequence was obtained at an interval of 5 min following a flash which was calculated to have bleached at least 99 per cent of the rhodopsin.

except that 615-nm flashes were used in light-adapted retinae. Again the field diameters clustered around 1.00 mm (0.84 to 1.00 mm). There were no large differences, therefore, in the diameter of the area from which rods and cones contributed to these responses.

DISCUSSION

It is generally agreed that the scotopic sensitivity of mixed mammalian retinae derives from the activity of rhodopsin rods while the cones are responsible for photopic sensitivity; for the scotopic dominator agrees well with the rhodopsin absorption curve (4) while the photopic dominator occurs during the cone branch of the dark-adaptation curve. Furthermore, ganglion cell responses (frog) exhibiting the sensitivity of the photopic dominator also show the Stiles-Crawford effect, a cone phenomenon (5). In the present work it seems certain, therefore, that both the rods and cones influence S-units of the L-type, and, in fact, individual units receive contributions from both categories of receptors.

L-potentials in the cat are recorded at the level of the external plexiform and internal nuclear layers (1-3); but, the exact intracellular location of the microelectrode has never been identified. Two lines of evidence implicate the horizontal cell as the source of these responses. First, fish and cat L-potentials behave similarly, and when the recording sites in fish have been stained, the location of the stained spots suggested that the microelectrode tips have been in horizontal cells and their processes (15, 18, 23). Second, an extensive and dense layer of horizontal cells is present in the cat retina (8). In fact, cell density is greatest in the central portion of the retina (270 cells/mm²), the area from which L-potentials were recorded in these experiments.

Unfortunately, the histology of receptor-horizontal cell contacts in the cat is not yet available. Where it has been studied, as in fish (31, 40) and primates (6), horizontal cells were first observed to contact either rods or cones, but recently they have been observed contacting both rods and cones (Kolb, personal communication). Since contacts between horizontal cells have been identified in the cat (7), there would seem to be at least two anatomical explanations for the convergence of rod and cone activity; either both receptor types synapse on processes of the same horizontal cell or rod and cone horizontal cells connect with each other.

REFERENCES

1. Brown, K. T., and Tasaki, K., Localization of electrical activity in the cat retina by an electrode marking method. J. Physiol., 158:281-295, 1961.
2. Brown, K. T., and Wiesel, T. N., Intraretinal recording with micropipette electrodes in the intact cat eye. J. Physiol., 149:537-562, 1959.
3. Brown, K. T., and Wiesel, T. N., Localization of origins of electroretinogram components by intraretinal recording in the intact cat eye. J. Physiol., 158:257-280, 1961.
4. Donner, K. O., The spectral sensitivity of vertebrate retinal elements. In: Visual Problems of Colour, Vol. II. London: Her Majesty's Stationery Office, 1958. Pp 539-566.
5. Donner, K. O., and Rushton, W. A. H., Rod-cone interaction in the frog's retina analysed by the Stiles-Crawford effect and by dark adaptation. J. Physiol., 149:303-317, 1959.
6. Dowling, J. E., and Boycott, B. B., Organization of the primate retina: electron microscopy. Proc. Roy. Soc. B, 166:80-111, 1966.
7. Dowling, J. E., Brown, J. E., and Major, D., Synapses of horizontal cells in rabbit and cat retina. Science, 153:1639-1641, 1966.
8. Gallegos, A., Connexions transversales au niveau des couches plexiformes de la rétine. Actualities Neurophysiologiques, Paris, 1966. Pp 5-27.
9. Gouras, P., The effects of light-adaptation on rod and cone receptive field organization of monkey ganglion cells. J. Physiol., 192:747-760, 1967.
10. Gouras, P., and Link, K., Rod and cone interaction in dark-adapted monkey ganglion cells. J. Physiol., 184:499-510, 1966.
11. Granit, R., Sensory Mechanisms of the Retina. Oxford: Oxford University Press, 1947.
12. Grüsser, O.-J., Receptor potentiale einzelner retinaler Zapfen der Katze. Naturwissenschaften, 44:522, 1957.
13. Grüsser, O.-J., Receptorabhängige R- potentiale der Katzenretina. In: Jung, R., and Kornhuber, H. (Eds.), The Visual System: Neurophysiology and Psychophysics. Berlin: Springer, 1961. Pp 56-61.

14. Gunter, R., The spectral sensitivity of light-adapted cats. J. Physiol., 123: 409-415, 1954.
15. MacNichol, E. F., Jr., and Svaetichin, G., Electric responses from the isolated retinas of fishes. Am. J. Ophthalmol., 46:26-46, 1968.
16. Meyer, D. R., and Anderson, R. A., Colour discrimination in cats. In: DeReuck, A. V. S., and Knight, J. (Eds.), Colour Vision. Boston: Little, Brown and Co., 1965. Pp 325-339.
17. Missotten, L., The Ultrastructure of the Retina. Bruxelles: Editions Arscia S. A., 1965.
18. Mitarai, G., Further identification of the site of origin and some properties of S-potentials in the carp retina. Annual Report. Nagoya University: Research Institute of Environmental Medicine, 1964. Pp 1-8.
19. Mitarai, G., Svaetichin, G., Vallecalle, R., Fatehchand, R., Villegas, J., and Laufer, M., Glia-neuron interactions and adaptational mechanisms of the retina. In: Jung, R., and Kornhuber, H. (Eds.), The Visual System: Neurophysiology and Psychophysics. Berlin: Springer, 1961. P 463.
20. Mitarai, G., and Yagasaki, Y., Resting and Action Potentials of Single Cone. Annual Report. Nagoya University: Research Institute of Environmental Medicine, 1955. Pp 54-64.
21. Motokawa, K., Oikawa, T., and Tasaki, K., Receptor potential of vertebrate retina. J. Neurophysiol., 20:186-199, 1957.
22. Naka, K. I., and Rushton, W. A. H., S-potentials and dark adaptation in fish. J. Physiol., 194:259-269, 1968.
23. Oikawa, T., Ogawa, T., and Motokawa, K., Origin of so-called cone action potential. J. Neurophysiol., 22:102-111, 1959.
24. Orlov, O. Yu., and Maksimova, E. M., S-potential sources as excitation pools. Vision Res., 5:573-582, 1965.
25. Sechzer, J. A., and Brown, J. L., Color discrimination in the cat. Science, 144:427-429, 1964.
26. Steinberg, R. H., Comparison of the intraretinal b-wave and d.c. component in the area centralis of cat retina. Vision Res., 9:317-331, 1969.

27. Steinberg, R. H., High-intensity effects on slow potentials and ganglion cell activity in the area centralis of cat retina. Vision Res., 9:333-350, 1969.
28. Steinberg, R. H., Rod-cone interaction in S-potentials from cat retina. NAMI-1072. Pensacola, Fla.:Naval Aerospace Medical Institute and U. S. Army Aeromedical Research Laboratory, 1969.
29. Steinberg, R. H., The rod after-effect in S-potentials from cat retina. NAMI-1075. Pensacola, Fla.:Naval Aerospace Medical Institute and U. S. Army Aeromedical Research Laboratory, 1969.
30. Steinberg, R. H., Walker, M. L., and Johnson, W. M., A new microelectrode positioner for intraretinal recording from the intact mammalian eye. Vision Res., 8:1521-1523, 1968.
31. Stell, W. K., Correlation of retinal cytoarchitecture and ultrastructure in golgi preparations. Anat. Record , 153:389-398, 1965.
32. Svaetichin, G., The cone action potential. Acta Physiol. Scand. 29; Suppl., 106,565-600, 1953.
33. Wall, G. L., The Vertebrate Eye and its Adaptive Radiation. New York: Hafner, 1963.
34. Watanabe, K., and Hashimoto, Y., S-potential in light and dark adaptation of the live carp. Abstr. XXIII Intern. Congs. Physiol. Sc. Tokyo, 361, 1958.
35. Weale, R. A., The spectral reflectivity of the cat's tapetum measured in situ. J. Physiol., 119:30-42, 1953.
36. Weale, R. A., Light absorption in the crystalline lens of the cat. Nature, Lond., 173:1049-1050, 1954.
37. Westheimer, G., The maxwellian view. Vision Res., 6:669-682, 1966.
38. Witkovsky, P., A comparison of ganglion cell and S-potential responses in carp retina. J. Neurophysiol., 30:546-561, 1967.
39. Wyszecki, G., and Stiles, W. S., Color Science. New York: John Wiley, 1967, P 226.
40. Yamada, E., and Ishikawa, T., The fine structure of the horizontal cells in some vertebrate retinae. Cold Spring Harbor Symp. Quant. Biol., 30:383-392, 1965.

Unclassified

Security Classification

DOCUMENT CONTROL DATA - R & D

(Security classification of title, body of abstract and indexing annotation must be entered when the overall report is classified)

| | | | |
|--|--|---|------------------------------|
| 1. ORIGINATING ACTIVITY (Corporate author) Naval Aerospace Medical Institute Pensacola, Florida 32512 | | 2a. REPORT SECURITY CLASSIFICATION Unclassified | |
| | | 2b. GROUP N/A | |
| 3. REPORT TITLE ROD AND CONE CONTRIBUTIONS TO S-POTENTIALS FROM CAT RETINA | | | |
| 4. DESCRIPTIVE NOTES (Type of report and inclusive dates) | | | |
| 5. AUTHOR(S) (First name, middle initial, last name) Roy H. Steinberg | | | |
| 6. REPORT DATE 2 June 1969 | | 7a. TOTAL NO. OF PAGES 15 | 7b. NO. OF REFS 40 |
| 8a. CONTRACT OR GRANT NO. | | 9a. ORIGINATOR'S REPORT NUMBER(S) NAMI-1071 | |
| b. PROJECT NO. MR005.04-0088.3 | | 9b. OTHER REPORT NO(S) (Any other numbers that may be assigned this report) USAARL Serial No. 69-10 | |
| c. | | | |
| d. | | | |
| 10. DISTRIBUTION STATEMENT This document has been approved for public release and sale; its distribution is unlimited. | | | |
| 11. SUPPLEMENTARY NOTES Joint report with U. S. Army Aeromedical Research Laboratory, Fort Rucker, Alabama | | 12. SPONSORING MILITARY ACTIVITY | |
| 13. ABSTRACT <p>The problem of whether the rods contribute to S-potentials was studied in the intact eye of the cat. S-potentials from luminosity units (L-units) were evoked by small spots of relatively monochromatic light in dark- and light-adapted retinae. The spectral sensitivity curve for dark-adapted S-potentials had its maximum at 500 nm, and the form of dark-adapted responses also suggested that rods were excited. The spectral sensitivity curve for light-adapted S-potentials had its maximum at 560 nm, and response latencies even at threshold were much faster than in dark adaptation. Individual S-potentials exhibited Purkinje shifts. It is concluded that rhodopsin rods contribute to S-potentials (L-type) in the cat and that cones contribute to the same responses.</p> | | | |

Unclassified

Security Classification

| 14. KEY WORDS | LINK A | | LINK B | | LINK C | |
|---|--------|----|--------|----|--------|----|
| | ROLE | WT | ROLE | WT | ROLE | WT |
| S-Potentials Luminosity potentials Chromaticity potentials Retina, dark-adapted Retina, light-adapted | | | | | | |

Unclassified

Security Classification