AN INVESTIGATION OF ROD-CONE INTERACTION AS A POSSIBLE MECHANISM FOR EXPLAINING THE DESATURATION FOUND IN INTERMITTENT 510 NM MONOCHROMATIC LIGHT

Thesis for the Degree of Ph. D.
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JAMES WILLIAM WALTERS
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This is to certify that the

thesis entitled

AN INVESTIGATION OF ROD-CONE INTERACTION AS A POSSIBLE MECHANISM FOR EXPLAINING THE DESATURATION FOUND IN INTERMITTENT 510 NM MONOCHROMATIC LIGHT

presented by

JAMES WILLIAM WALTERS

has been accepted towards fulfillment of the requirements for

Ph D degree in Experimental Psychology.

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Major professor

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AN INVESTIGATION OF ROD-CONE INTERACTION AS A POSSIBLE MECHANISM FOR EXPLAINING THE DESATURATION FOUND IN INTERMITTENT 510 NM MONOCHROMATIC LIGHT

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The perceived phenomena of hue, saturation and brightness generated by various monochromatic stimuli have been shown by R. J. Ball (1964) to be greatly altered when the stimulus is interrupted at approximately 10 Hz with a pulse to cycle fraction of 1/4. Perhaps the most striking change found by Ball was a total desaturation of 510 nm light of sufficient intensity at this rate. Because the scotopic mechanism is maximally sensitive to wavelengths around 510 nm, and because this mechanism is generally found to give only colorless responses regardless of wavelength, it was postulated that scotopic involvement may be responsible for the desaturation noted by Ball.

In order to investigate this hypothesis, two 21 year old subjects, one male and one female, were presented with a variety of intermittent monochromatic stimuli, some of which produced the desaturation response noted above. Stimulus parameters manipulated included

wavelength, rate of intermittency, stimulus intensity, surround intensity and pulse duration. The relative size of the electroretinogram scotopic b-wave response was used as an indicy of scotopic activity. An achromatic surround was used to reduce the ERG stray light response. The amount of scotopic activity under conditions which produced desaturation was compared with those that did not. In general, those conditions which produced the most desaturation also produced the most scotopic activity. A notable exception occurred with the 460 nm stimulus, which is bluer than 510 nm. At 460 nm an increase in scotopic b-wave activity was noted in conjunction with a reduction in desaturation relative to the 510 nm condition. The data were discussed in terms of a model based on Gouras' findings (Gouras, 1965, 1966, 1967; Gouras and Link, 1966) which show an interaction between scotopic and photopic activity at the ganglion cell level in Macaca mulatta. The results of this study were not conclusive with regard to such a model, but were sufficient to suggest further research aimed at disclosing the mechanisms responsible for the desaturation phenomenon.

Thesis Committee:
Dr. S. Howard Bartley, Chairman
Dr. T. M. Allen
Dr. Glenn I. Hatton
Dr. John I. Johnson

Approved:_____

Date:_____

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The task of acknowledging all of those who have helped make this work possible is not easy, if only because there have been so many.

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My long association with Dr. R. J. Ball, whose research provided the basis for this study, has been most rewarding. His friendly counsel and constant encouragement has always been appreciated.

Finally, my largest debt is owed to my family, to my parents for their constant support over the years, to my in-laws for their enthusiastic interest, and most importantly to my wife, without whose help this work and the degree with which it is associated would not have been possible.

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INTRODUCTION

Statement of the Problem

In 1964 Richard J. Ball published an article describing the effects produced by making monochromatic light intermittent. A number of wavelengths were looked at under intermittent conditions and compared with a steady light of the same wavelength. Changes in hue, saturation and brightness were evaluated, as rate and intensity were varied.

By far the most striking result obtained by this procedure occurred at 510 nm where under certain conditions a total desaturation of the normally blue-green light could be produced. This phenomenon was found to be effected by a number of parameters, among which are wavelength, rate of intermittency, intensity, and pulse train duration. Chief among Ball's findings are the following facts:

1. If wavelength is altered from 510 nm toward the red end of the spectrum, the desaturation is attenuated very rapidly so that at 530 nm the phenomenon is no longer present. When wavelength is shifted toward the blue portion of the spectrum

a reduction in the amount of desaturation is also noted, however the attenuation is not as fast. At 480 nm a slight desaturation can still be seen. The only other wavelengths at which desaturation was found by Ball were in the 600-610 nm range. At these wavelengths Ball found slight and sometimes moderate desaturation accompanied by a hue shift toward the yellow when the intermittent target was compared with a steady target of identical wavelength.

2. Variations in rate (while holding the pulse-to-cycle fraction constant[1]) showed that the desaturation is optimal at 10 Hz. As rate is increased the amount of desaturation falls off very rapidly so that at 14 Hz it is not present. As rate is lowered the desaturation disappears more slowly so that at 6 Hz the desaturation is still noticeable.

Unpublished work done by Ball has shown that single pulses appear desaturated if their duration is appropriate. My own partial replication of this work shows that for pulses of 510 nm light a moderate desaturation is noted with pulse

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[1]The pulse-to-cycle fraction (abbreviated PCF) denotes the ratio between the duration of a square wave pulse of light and the duration or period of the cycle. Ball found the optimum PCF for producing washout to be 1/4 PCF.

durations of 10-45 msec. For longer and shorter pulse lengths the desaturation is less. Above 65 msec the desaturation is not very apparent. Similarly, below 10 msec it falls off very rapidly. These new facts suggest a difficulty with evaluating the effects of rate while changing pulse length, which is essentually what is done when PCF is held constant. The advantage of holding PCF constant is, of course, that of being able to hold the total amount of luminous flux constant as rate is varied. More will be said about this and related concepts in the discussion section. Until then, two points should be kept in mind: (A) The desaturation produced by single pulses of 510 nm light is markedly less than that produced by a 10 Hz train of pulses of the same wavelength. (B) The desaturation under both the single pulse condition and for the 10 Hz train is maximized when the pulse duration is about 25 msec (pulse length for a 1/4 PCF, 10 Hz train is 25 msec).

3. If intensity is lowered below a certain value desaturation disappears. (The intermittent target must be well into the photopic range before the desaturation phenomenon occurs.)

Two facts of this phenomenon would seem to suggest a scotopic involvement. These are that the critical wavelength is 510 nm, or that wavelength at which the rods are maximally sensitive, and that the response to the chromatic stimulus is one of apparent achromaticity. A fact which would seem to run counter to this kind of interpretation is that the stimuli are all well above the level at which scotopic involvement is normally expected, indeed, the phenomenon requires a certain minimum photopic level in order for it to appear.

It will be the purpose of this thesis to investigate the mechanism or mechanisms underlying the above described phenomenon with particular emphasis placed on the question of whether or not a scotopic involvement is indicated.

Historical Prespective

As it is normally conceived, the duplicity theory of vision postulates a number of characteristics of the visual mechanism. Among these are that the rods, or scotopic receptor elements of the eye, provide us with our "night" vision, while the cones, or photopic elements, are responsible for "day" vision. While it is considered that there is a twilight or mesopic range of intensity in which both mechanisms operate, it is generally believed that high levels of illumination are dealt with by the

photopic mechanism, while the scotopic mechanism is relegated to handling the very low levels of illumination. It is this conception of these two systems which must be dealt with if a scotopic mechanism is to be shown to explain the achromatic desaturated appearance of the intermittent 510 nm light.

There is a good deal of evidence which suggests that the rods and the scotopic mechanism as a whole remains functional at high levels of illumination. Bartley and Bishop (1942) have shown a double response to the onset of achromatic illumination in gross records taken from the rabbit's optic nerve. This duplicity of response was not present for dim pulses of short duration, however, as pulse length was increased and intensity raised, a second response of shorter latency appeared in front of the original response. Later, Bartley (1942) varied intensity and pulse duration presented to human subjects and found a "two flash" response to single pulses of light. Within a given range of intensities the response could be made to go away by making the pulse too short or too long.

It should be noted that the intensity levels used with the rabbits ranged from 300 to 18,000 candles per square foot, while those used with the human subjects ranged from 1.9 to .0343 candles per square foot. This latter range at which Bartley found the two flash response to single pulses in humans is relatively low. While it is

above photopic threshold it still can be considered in the mesopic range. My own pilot work has shown a two flash response for pulses of limited duration well into the photopic range.

The interpretation generally given the two flash phenomenon is that two receptor populations (or mechanisms) with different latencies are both responding to the same light pulse. The scotopic, rod, mechanism has been shown electrophysiologically in monkeys to have a latency of approximately 150 msec at threshold while the photopic, cone, threshold latency is approximately 50 msec (Gouras, 1966).

Another line of evidence bearing on the existence of a scotopic mechanism at photopic levels is provided by an evaluation of the electroretinogram (ERG). The b-wave of the ERG is its most prominent feature. It is generated in the inner plexiform layer of the retina and is thought to represent the activity of bipolar cells (Brown, 1968). These cells serve to connect the receptors with the retinal ganglion cells (Polyak, 1941; Dowling and Boycott, 1965). The human ERG b-wave, evoked with achromatic light, is invariably scotopic in nature even when high photopic levels are used. Restricting the retinal image to just the fovea is not sufficient to eliminate the scotopic activity as the stray light induced by such a target will still generate enough scotopic activity to completely

cover photopic activity. This effect is so pervasive that while the ERG was first recorded by Holmgren in 1865, the photopic activity was not noted until 1942. Motokawa and Meta (1942) were first to reveal the presence of photopic activity by using pulses of red light, to which the cones are more sensitive than the rods.

The above evidence all points to the existence of scotopic activity at photopic levels, both perceptually and electrophysiologically. Nothing in the above gives an indication of how these two mechanisms interact, however. Scotopic and photopic activity have been reported in the same retinal ganglion cells (Granit, 1944; Barlow, Fitzhugh and Kuffler, 1957; Donner and Rushton, 1959; Chapman, 1961). Similarly, LGN cells have also been found responding to both types of activity (DeValois, Smith, Kitai and Karoly, 1958; Wiesel and Hubel, 1966). That this is the case is somewhat surprising inasmuch as the perceptual end result is quite different for the two mechanisms. A partial answer as to how these mechanisms are kept separate at the ganglion cell level is provided by Gouras (1965, 1966, 1967; Gouras and Link, 1966). Gouras not only has documented the existence of both scotopic and photopic activity in the same retinal ganglion cells in the Rhesus monkey, but has also made significant progress toward the understanding of how these two systems interact. A brief summary of some of the basic findings of Gouras follows:

1. Rods and cones are frequently found contributing to the same ganglion cell in the parafoveal retina of monkeys (Macaca mulatta).
2. The b-wave of the ERG has a photopic and a scotopic component. At threshold the latency of the photopic b-wave is approximately 50 milliseconds and that of the scotopic system is 150 milliseconds.
3. The onset and duration of the b-wave correspond to a large degree with the transient changes in the ganglion cell activity. (Spikes appear to begin just prior to the ERG b-wave deflection when relatively low levels of illumination are used.)
4. Whenever the photopic and scotopic components of the ERG b-wave are present and sufficiently close together, only that component which appears first successfully elicits a ganglion cell response.
5. This inhibition of one system by the other works equally well no matter which system precedes the other. However, under all but very special conditions the scotopic system is inhibited by the photopic system, owing to the shorter latency of the latter.
6. The interaction between the two systems is not evidenced by an alteration in the amplitude of the ERG b-wave and hence must occur after the

generation of the b-wave but before the alteration of the ongoing ganglion cell activity.

The above facts relate to single pulses of light or trains of pulses of low frequency, one pulse every 2 or 3 seconds (Gouras, 1966). At these rates and (subphotopic) intensities, only a scotopic response is elicited in the ERG and the subsequent ganglion cell activity. As the light intensity is increased above photopic threshold the faster photopic response appears in both the ERG and the ganglion cell. At this point the ERG continues to show a scotopic b-wave but the ganglion cell no longer shows a corresponding scotopic response. It has been previously stated that the threshold latencies for the scotopic and photopic systems were 150 msec and 50 msec respectively. These latencies both become shorter as intensity is increased. At high intensities Gouras (1967) says only that the photopic latencies are shorter than 50 msec and the scotopic latencies are longer than 50 msec. At moderate and high intensities, then, the situation is one of having the photopic response followed closely in time by a scotopic response, the latter of which is blocked after the formation of the b-wave but before the activation of the ganglion cell.

Gouras has shown inhibition of the photopic response by a scotopic one as well. He has done this by introducing in the same retinal area two spots of

monochromatic light, one light being 419 nm and capable of eliciting only a scotopic response, the other being 610 nm and capable of eliciting only a photopic response. When these two lights are presented out of phase (the blue light followed by the red), it is possible to precede the expected elicitation of a photopic ganglion cell response by a scotopic one. When this happens the photopic ganglion cell response does not appear.

There would seem to be a basic question posed by this finding in relation to the phenomenon generated by intermittent trains of pulses of higher rates. That question is, does the scotopic activity initiated by pulse P, in a sufficiently long train of pulses, ever inhibit the activation of the ganglion cell by the photopic activity initiated by pulse P+1? This question is similar to the question children sometimes ask themselves regarding the tick tock of a clock, that being, does the clock ever stop going tick tock and start going tock tick? When applied to photopic-scotopic activity generated by a train of pulses, the problem can be visualized by the following two diagrams, one for a pulse train of low rate and the other for a higher rate:

Low Rate P S P S P S P S P S P S

High Rate P S P S P S P S P S P S P S P

In the second train, the grouping of scotopic-photopic activity is such that the scotopic activity

appears to precede the photopic activity, in which case one might consider the possibility of the scotopic, rather than the photopic activity, dominating.

Experimental Design

The problem of ascertaining whether or not the mechanism described by Gouras is responsible for the phenomenon described by Ball is a difficult one. In humans only the EEG and ERG are readily available as indicies of the underlying neurophysiological processes in vision. Of these the ERG is by far the more analytical, especially with regard to determining the presence of either photopic or scotopic processes. It will be recalled from the summary of Gouras' work that the interaction between scotopic and photopic activity was not evidenced in any reduction in amplitude of the ERG b-wave. Gouras has shown, however, that the ganglion cell activity is closely related in time to the ERG b-wave, and that inhibition of photopic activity by scotopic activity does occur when the appropriate temporal manipulations are made. Consequently, it will be the purpose of this thesis to investigate the presence or absence of a photopic and scotopic b-wave, and the temporal relationship between the two. It is the hypothesis of this investigator that for intermittent trains of pulses, those conditions of rate, wavelength and intensity which produce total desaturation

as shown by Ball, will also be the conditions under which (1) a strong scotopic activity will be present, and (2) the temporal relationship will be such that the photopic activity will be preceded closely in time by the scotopic activity. It is further hypothesized that, where moderate desaturation for single pulses is found, a strong scotopic component will be present, while for pulse durations and wavelengths which do not produce desaturation, it will be absent.

Because a great deal of research relevant to this topic has been done with white light, it would also seem appropriate to investigate the effects of variations in intensity, rate and pulse duration on the ERG when white light is used. The fact that Bartley has found a two flash response to single pulses of white light (Bartley and Bishop, 1942; Bartley, 1942) and "Brightness enhancement"[1] for intermittent trains of white light (for an excellent review see Bartley, 1968), adds impetus to this approach. In all fairness it should be noted that Bartley's work is the antecedent of Ball's work and not the reverse. The emphasis of this thesis has been placed on Ball's work because of the additional analytical leverage afforded by the added wavelength parameter. Bartley's brightness

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[1]Brightness enhancement is defined by Bartley (1968) as . . . "the brightness produced by intermittent photic stimulation which is greater than the brightness produced by a steady stimulus of the same luminance."

enhancement and Ball's desaturation phenomenon have many similarities, but there are differences as well. It remains for the data to show just what relationships can be drawn between the two phenomena.

METHOD

Subjects

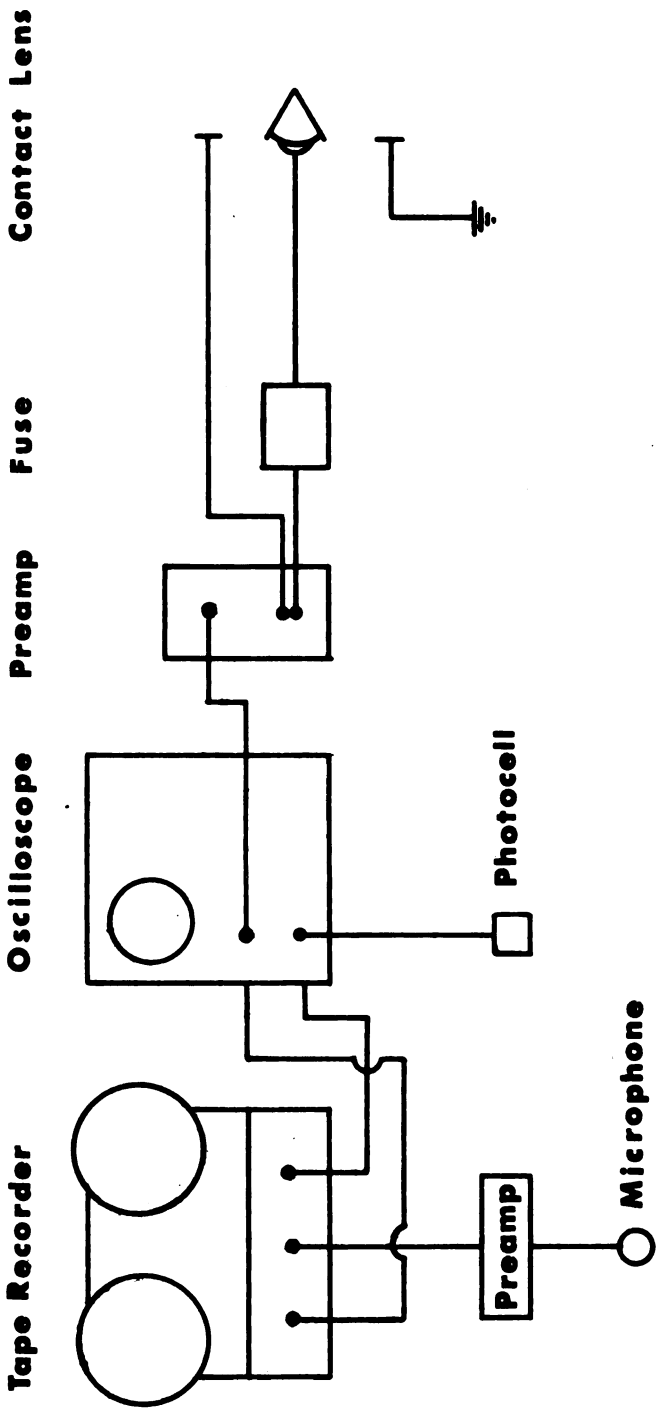
Two subjects were used, one 20 year old male (J.H.) and one 20 year old female (K.K.). Both were color normal as determined by the use of American Optical Pseudoisochromatic color plates. Both were myopic and accustomed to wearing contact lenses.

Stimulus

The stimulus was an intermittent 14° target in Maxwellian View surrounded by a freely viewed achromatic field of 37 or 246 trolands. The intermittent target was presented under one each of the following conditions: intensity--475 and 47.5 trolands; rate of intermittency--2, 6, 10 and 14 Hz with a 1/4 pulse to cycle fraction; chromatic composition--achromatic, or monochromatic at 460, 510, 540, 580, 610 and 640 nm.

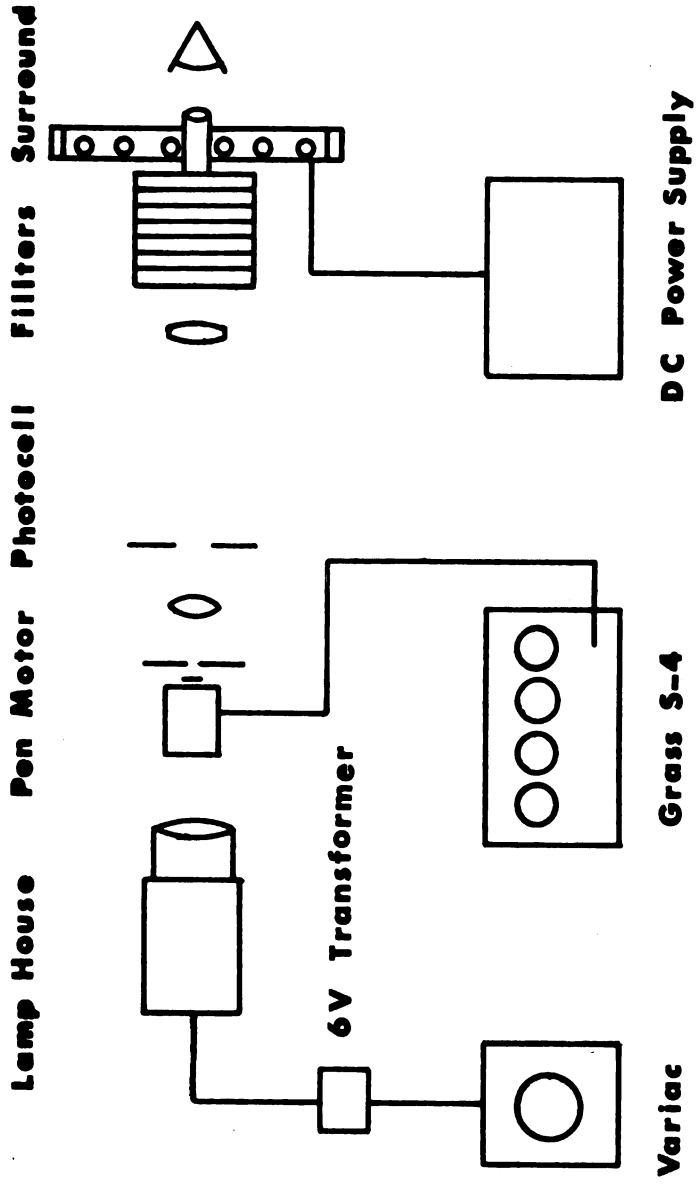
Apparatus

The apparatus can be divided into three systems: the stimulus system; the recording system; and the analysis system (see Figures 1-4).



RECORDING SYSTEM

Figure 1



STIMULUS SYSTEM

Figure 2

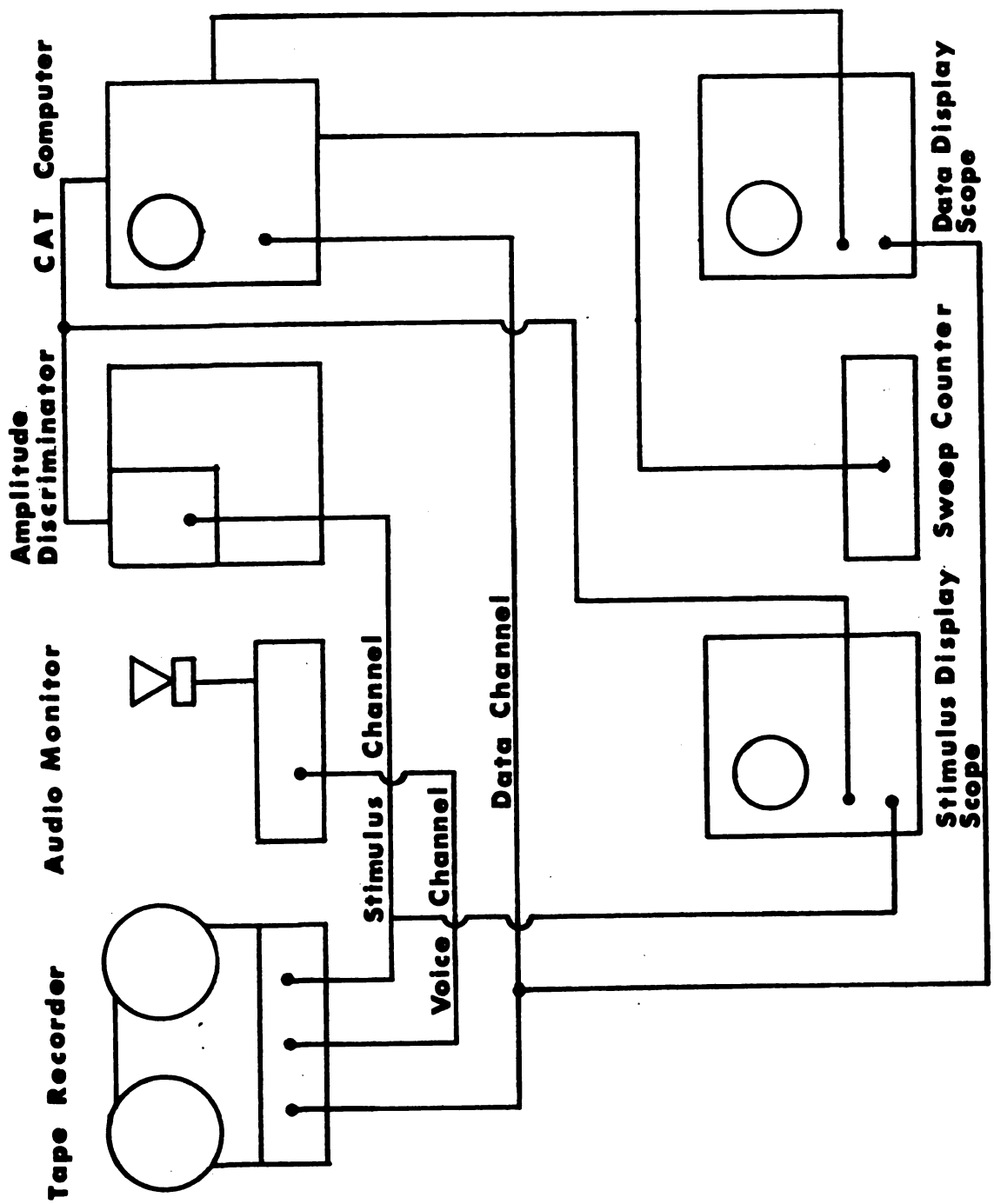

Tape Recorder
Audio Monitor
Amplitude Discriminator
CAT Computer
Stimulus Channel
Voice Channel
Data Channel
Stimulus Display Scope
Sweep Counter
Data Display Scope
ANALYSIS SYSTEM

Figure 3

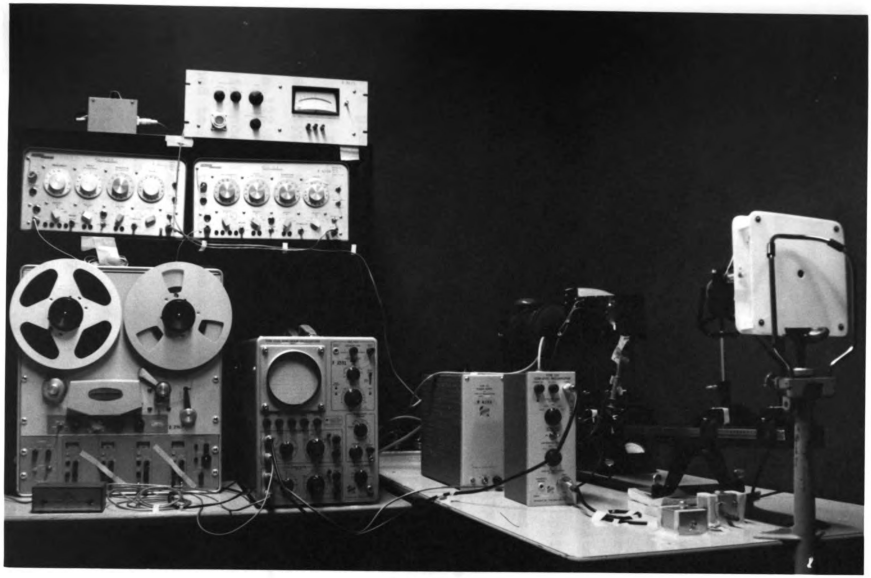


Figure 4

The stimulus system was mounted on a 1 meter Cenco Optical Bench. The light source was a 6 volt, 18 amp ribbon filiment lamp housed in a Cenco Optical Bench Illuminator #86605. The light from the illuminator was focused to a point, where it was interrupted in a square wave fashion (rise and decay time less than 2 msec.) by an aluminum flag actuated by a Brush pen motor. The pen motor was driven by a Grass model S-4 square wave generator. After this point the diverging beam was collimated by a series of two lenses. A small portion of the collimated beam was diverted to a photo cell; the rest was passed through the appropriate Kodak neutral density filters. If monochromatic light was desired, the appropriate Oriel Standard 50 Å filter was also used. The collimated beam was then focused inside the subject's pupil with a Cenco eye piece.

The recording apparatus consisted of an Obrig "Jacobson type" scleral contact lens connected to a Tektronixs 122 preamplifier through a .002 amp "little Fuse." The reference electrode was a silver-silver chloride type attached to the temple. The subject was grounded at the earlobe via a Grass ear clip electrode. The preamplifier was connected in a double ended "push-pull" fashion. The low pass filter was set at .8Hz; the high pass filter at 1000 Hz. The gain setting was approximately 1000. The output of the preamplifier was connected to the top trace

of a Tektronixs 502A Oscilloscope. The output of the stimulus monitor photocell was connected to the bottom trace. Both vertical amplifiers of the oscilloscope were set for single ended D.C. operation. The upper trace was maintained at 50 mv/cm. The outputs of both oscilloscope traces were fed into separate recording channels of an Ampex SP-300 FM tape recorder. Both channels were set to operate in the FM mode. A third channel was used to record verbal information which was relevant to the data input. This channel was maintained in the AM mode.

The analysis system was used to average the electroretinogram over 100 trials in order to retrieve the stimulus related activity from noise. This was accomplished by the use of a Technical Instruments Incorporated Computer of Averaged Transients Model 400B, operating in the "C" mode with the modulator cards in place for the purpose of digitizing the analog ERG signal. The total analysis time was .5 sec per sweep with all 400 bins in use. Consequently the data was stored, summed and displayed in 400 2.5 msec bins. Triggering of the CAT was accomplished by playing the square wave signal into a Technical Instruments Incorporated Model 605 peak detector, the output of which was connected to the external trigger input of the CAT. The voice channel was played into a Grass audiomonitor. At the end of each set of 100 averaging sweeps the stored data was displayed on a 502A oscilloscope and photographed with a Polaroid scope camera.

Procedure

Before the collection of data could begin it was first necessary to establish the exact values of the stimuli to be used. A consideration of Ball's work was sufficient for determining the values to be used for rate and wavelength. The correct intensities to be used had to be empirically determined, however. This was done by setting up the apparatus to produce a 10 Hz, 1/4 PCF, 510 nm bipartite (half the field was steady) stimulus. The intensity was then lowered in .1 log unit steps until the desaturation had all disappeared. A 1.0 ND filter was then subtracted from the total number of neutral density filters being used, thus raising the intensity by one log unit. This restored the desaturation to its maximum level. The total energy in this 14° Maxwellian View stimulus was then measured with a matched pair of Charles M. Reeder thermopiles Model #RBL-500 which had been previously calibrated with an Eppley standard lamp. The output of the thermopile was fed to a Keithley Model 149 milli-microvoltmeter. The read-out in microvolts was converted to microwatts. This value was then converted to lumens. Assuming 680 lumens/watt at 555 nm the total luminous flux was calculated using the formula $F = 680 \sum_{0}^{\infty} P_\lambda V_\lambda \Delta_\lambda$ lumens, where P_λ is radiant flux in watts at each wavelength, V_λ is the CIE standard observer

luminosity coefficient and Δ_λ is the band width. Because the band width associated with the interference filters being used was small (50 Å at 1/2 peak intensity) the above formula was simplified to $F = 680\ P_\lambda V_\lambda$. Knowing that the stimulus subtended an angle of 14° and assuming a retinal-nodal distance of 17.2 mm, the area covered by the imaged target on the retina was calculated. From this point it was an easy task to convert the luminous flux to trolands by using the conversion 3.6×10^{-9} lumens/mm^2 = 1 troland.[1] The resulting troland value for the 510 nm stimulus was determined to be 451 trolands. With the 1.0 ND filter in place this value is, of course, reduced by one log unit to a value of 45.1 trolands. The other wavelengths were all calibrated with the thermopiles and then reduced as near to the 451 trolands as possible using ND filters no smaller than .1 ND. The values arrived at ranged from 442 to 504 with a mean of 475 trolands. The 460 nm stimulus is not included in these figures because it was found to be much brighter than would be expected on the basis of the CIE data. Consequently a 128 troland value was used at this wavelength. This value was sufficient to make the 460 nm target appear

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[1]For further information regarding this method the reader is referred to R. M. Boynton's chapter in Sidowski (Ed.) Experimental Methods and Instrumentation in Psychology, McGraw-Hill, 1966.

as bright as the other stimuli at their 475 troland level.[1]

The intensity of the white light stimuli was determined by matching it to the 570 nm stimuli (which had an exact value of 492 trolands). In this way white light was roughly equated to the other stimuli. It was then determined that this level of white light was sufficient to produce brightness enhancement, and that the introduction of a 1.0 ND filter caused it to disappear. The surround intensity sufficient to nullify the ERG stray light response was determined by turning up the intensity until no further decrement was noted in the scotopic b-wave component of a 10 CPS, 1/4 PCF white light stimulus. This value was empirically determined to be 37 trolands by comparing it with a 570 nm stimulus of known intensity. Later a brighter surround at 246 trolands was used because it was noted that the blue stimuli were somewhat more effective in eliciting a stray light response than was the white light.

The data presented in the next section were collected from 2 subjects. The subjects were asked to refrain from blinking during the data collection and generally could do so for periods up to 90 seconds at one time.

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[1]The data later showed that the 128 troland 460 nm stimulus produced approximately the same photopic b-wave amplitude as did the rest of the stimuli at 475 trolands.

Their ability to do this was enhanced by the fact that the humidity in the room was kept very high during the recording session by the use of a humidifier. The data collection was timed by counting 60 one second sweeps of the oscilloscope. In this manner enough data was always collected to assure 100, 1/2 second averaging sweeps during data analysis.

Both subjects were presented with all 6 wavelengths and 4 pulse frequencies at the 475 and 47.5 troland intensity with the 37 troland surround during the initial phase of this study. Within each session for subject K.K., wavelength was held constant while pulse frequency was varied, while for subject J. H. pulse frequency was fixed and wavelength was varied. In addition, subject K. K. was presented with single pulses of varying durations at 510 nm, 610 nm and white light as well as a series of 4 sessions using a 246 troland surround.

Calibration of the averaged ERG's was accomplished by averaging a 25 microvolt square wave over 100 trials. The display of the computer was then adjusted to correspond to approximately 12.5 μv per centimeter on the scope. Because the ERG records have been reduced to 55% of their original size for inclusion here, 1 centimeter of amplitude in the data figures represents 22.7 microvolts. The 5.5 cm length of each train represents .5 seconds elapsed time.

RESULTS

The results are depicted in Figures 5 through 29. Figure 5 shows a 25 microvolt square wave calibration signal (full scale) which has been averaged 100 times. This signal can be compared with the two representative ERG's taken from the 475 troland portion of Figure 8. It should be noted that the square wave calibration signal has been distorted somewhat by the capacitance coupled preamplifier used in the recording system. This distortion is commonly called integration. The square wave was negative going (negative up) with respect to ground, and had a duration of 50 msec. It can be seen that the signal, upon its return to zero or ground level, overshoots and goes positive. The letter "i" in the figure denotes the place of maximum overshoot. Given ERG signals of the same order of magnitude and duration, one can expect the same amount of overshoot. Consequently, the 570 nm ERG record in Figure 5 probably shows some overshoot at the base of the photopic b-wave. This portion is labelled "i", but it is by no means entirely due to integration. It is probably more correct to think of it as being accentuated by the integrative effects. The ERG records in Figure 5 have their a- and b-wave components labelled as

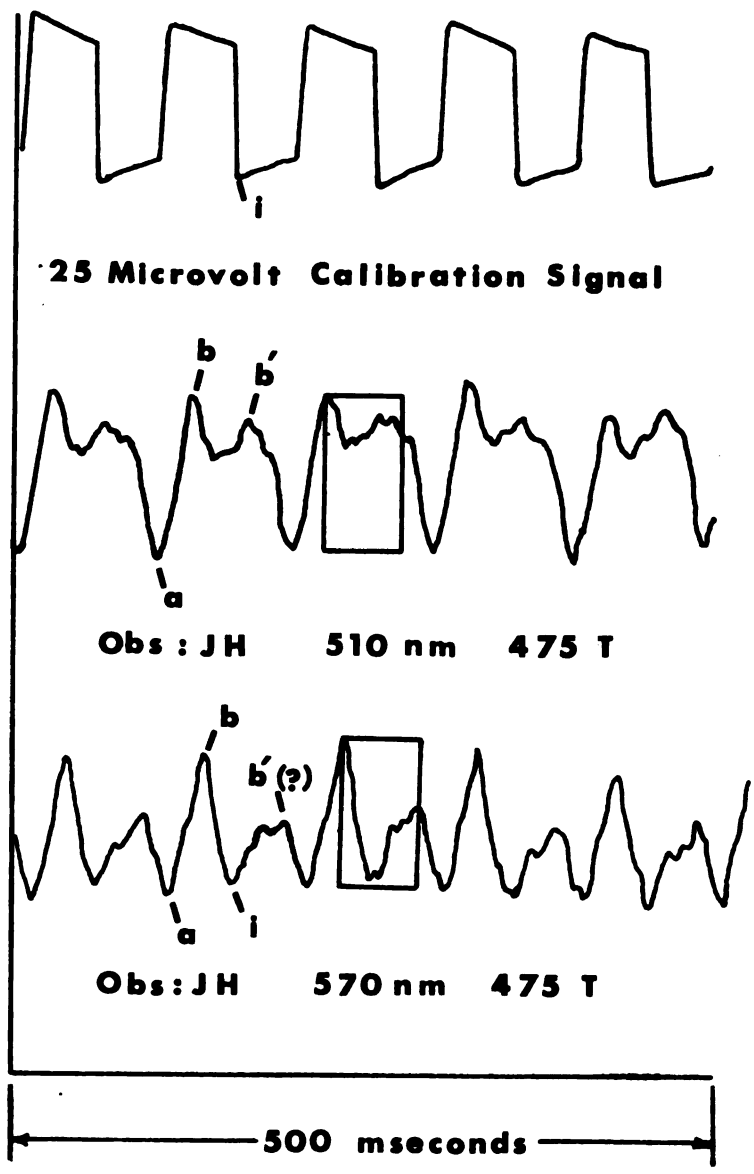
i
25 Microvolt Calibration Signal
b
b'
a
Obs : JH 510 nm 475 T
b
b'(?)
a
i
Obs: JH 570 nm 475 T
500 mseconds

fig 5

well. The letter "b" is used to indicate the photopic b-wave process, while the letter "b'" is used to indicate the scotopic b-wave process.

The 510 nm ERG record shows a very clear and strong photopic b-wave followed by a strong scotopic b-wave. The 570 nm ERG record shows a much less predominnant peak following the photopic b-wave. Because of the integration effects it is difficult to determine how much of this peak represents a scotopic b-wave.

The rectangles overlaying a portion of the ERG's in Figure 5 are illustrative of the analysis technique used to generate Figures 23-29. In order to quantify the amount of scotopic activity present, a rectangle, 1 cm. in width, (representing 50 msec.) with a height equal to the distance from the bottom of the a-wave to the peak of the photopic b-wave, was superimposed (as shown) on a representative ERG configuration for each of the monochromatic high intensity conditions depicted in Figures 6-22. The area of the rectangle under the curve was taken to be representative of the amount of scotopic b-wave activity. Because the height of the ERG's varied somewhat from one record to the next, this area is represented in the graphs as a percentage of the total area of the rectangle. In those cases where the scotopic b-wave amplitude exceeded the photopic b-wave amplitude the additional area under the curve and directly above the rectangle was added to

the total area. When this happened a percentage figure in excess of 100% resulted.

Each data figure in this thesis represents a single recording session, hence comparison between ERG records contained within a given figure are not subject to inter-session variance due to changes in electrode placement, interelectrode resistance, etc.

In all ERG records, the duration of the stimulus pulse is a function of the pulse frequency (except where noted.) A pulse to cycle fraction of 1/4 was maintained throughout. It follows, then, that at 2 Hz the pulse length was 125 msec., at 6 Hz--41.6 msec., at 10 Hz--25 msec., and at 14 Hz--17.8 msec. The onset of each of these pulses precedes the onset of the downward deflection of the a-wave process by roughly 2-3 msec.

Figures 6 through 10 depict the records obtained from subject J. H. Figure 6 shows the ERG's obtained for all wavelengths and both stimulus intensities at the 2 Hz rate. None of these conditions are capable of eliciting the desaturation response. It should be noted, however, that the b-wave at the 460 nm and 510 nm wavelengths and 475 troland intensity is markedly larger than it is at the other wavelengths. This is most probably due to scotopic involvement even though two separate processes cannot be distinguished. It should also be noted that the low intensity condition produces a consistently similar

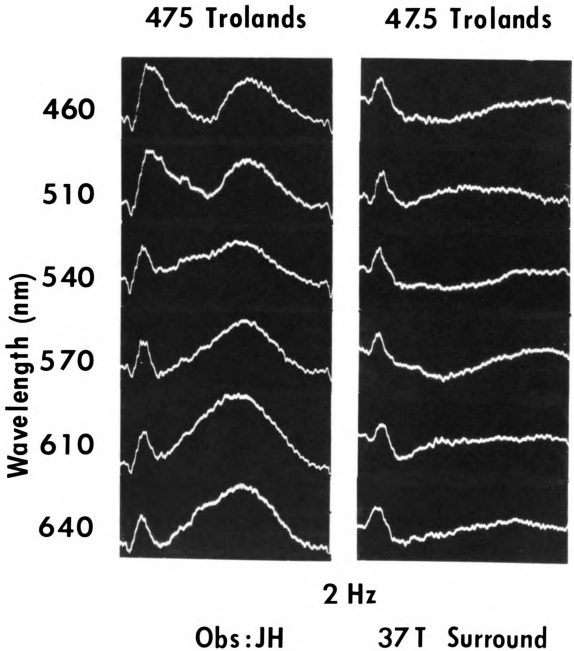
475 Trolands
47.5 Trolands
460
510
540
570
610
640
Wavelength (nm)
2 Hz
Obs: JH
37 T Surround

Figure 6

photopic b-wave activity over the entire spectrum. The large wave following the b-wave in the high intensity condition is probably a c-wave originating in the pigment epithelium (Brown, 1968). These were the only records which showed this type of activity to such a marked degree.

Figure 7 shows the records obtained at the 6 Hz rate for all wavelengths and both stimulus intensities. The 510 nm, 475 troland condition at this rate is capable of producing some desaturation which can be described as slight to moderate when compared to the same wavelength and intensity at 10 Hz. It will be noted that both the 460 nm and 510 nm high intensity condition show a strong scotopic b-wave with the 460 nm condition producing the strongest. At this rate the 460 nm wavelength shows little, if any, desaturation. It should also be noted that the low intensity stimulus produces no noticeable scotopic activity regardless of wavelength.

Figure 8 contains the 10 Hz ERG's from subject J. H. at all wavelengths and both stimulus intensities. The 510 nm, 475 troland 10 Hz condition is that which produces the most desaturation. Both subjects reported total desaturation under these conditions. At the same intensity the 460 condition produced what was termed slight desaturation by subject J. H. and moderate desaturation by subject K. K. Both subjects reported no

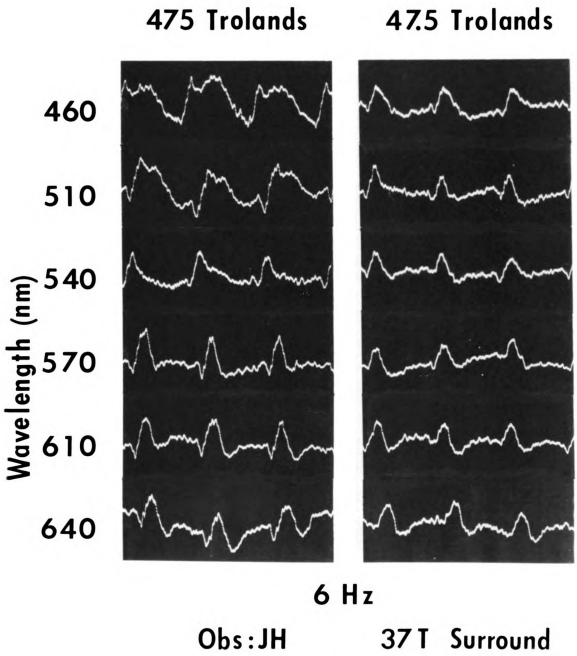
475 Trolands
47.5 Trolands
460
510
540
570
610
640
Wavelength (nm)
6 Hz
Obs: JH
37 T Surround

Figure 7

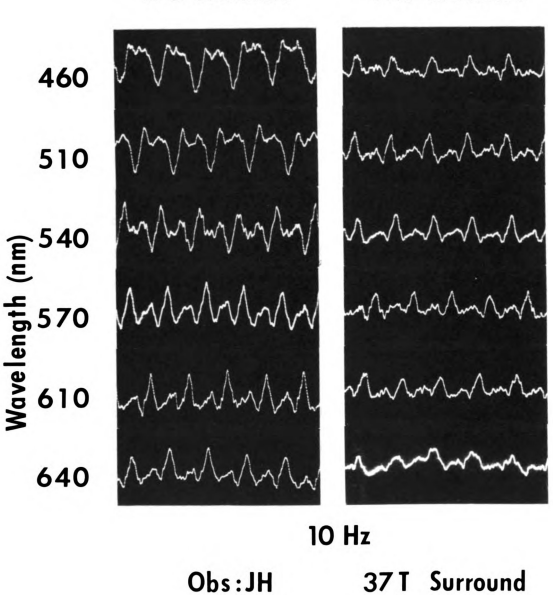
475 Trolands
47.5 Trolands
460
510
540
570
610
640
Wavelength (nm)
10 Hz
Obs: JH
37 T Surround

Figure 8

desaturation of note at 540 nm or longer wavelengths. As with the other frequencies, the 460 nm and 510 nm conditions produce the most scotopic activity. This is clearly indicated by the second b-wave following each a-wave. The 540 nm condition also shows some scotopic activity, but it is greatly reduced over the previously mentioned wavelengths. No scotopic activity is noted with the low intensity light, nor is any desaturation ever noted at the low intensity level.

Figure 9 shows the 14 Hz condition for all wavelengths and both intensities. At this rate of intermittency no desaturation is noted and the ERG records show no scotopic activity of note regardless of wavelength or intensity used.

Figures 10 through 14 are records obtained from subject K. K. under identical stimulus conditions as those used for the above discussed data obtained from subject J. H. Rather than holding frequency constant and varying wavelength, however, the reverse was done. In this way, changes in the ERG's induced by changes in frequency for any given wavelength could be evaluated within a single session. The results were consistent with those already discussed with only minor differences.

Figure 10 shows the data obtained for all frequencies at the 460 nm wavelength. These records showed very strong scotopic activity for even the 14 Hz condition.

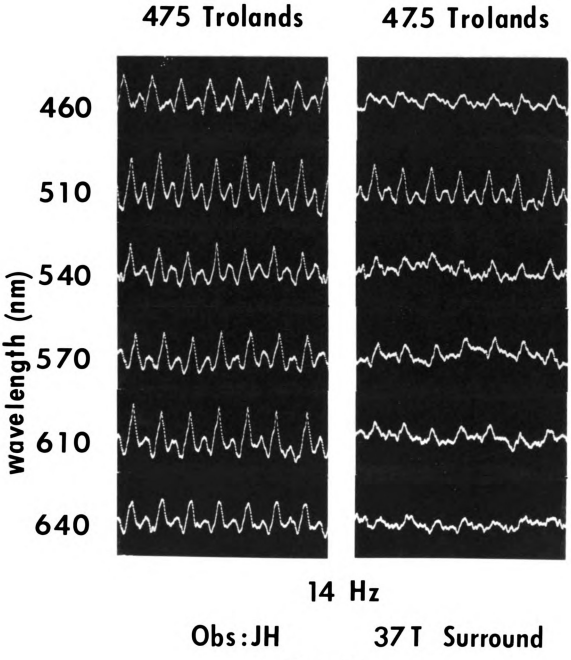
475 Trolands
47.5 Trolands
460
510
540
570
610
640
wavelength (nm)
14 Hz
Obs:JH
37 T Surround

Figure 9

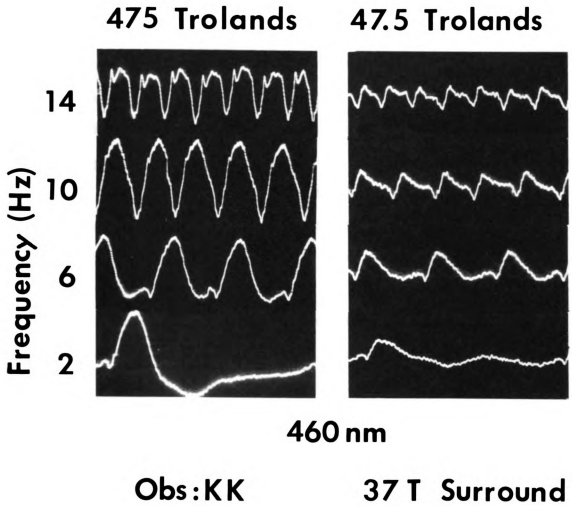
475 Trolands
47.5 Trolands
Frequency (Hz)
14
10
6
2
460 nm
Obs: KK
37 T Surround

Figure 10

At 2 Hz the amplitude was so great that for this wavelength the record shown was reduced by 1/2 for inclusion in this figure. The extreme scotopic activity found here led to the additional work with the higher intensity surround, to be reported later.

Figure 11 shows the 510 nm condition for all frequencies. Little or no scotopic activity is seen at 14 Hz. When the intensity is lowered to 47.5 trolands, the scotopic activity is eliminated at all frequencies. Hence, at 510 nm the scotopic activity is present at those frequencies and intensities which produce the desaturation, but basically absent for those frequencies and intensities which do not.

Figures 12 through 15 show the data for the 540, 570, 610 and 640 nm wavelengths, respectively. At the 540 nm wavelength some scotopic activity is evidenced by the lack of a downward notch following the photopic b-wave. The 570, 610 and 640 nm wavelengths show very little if any scotopic activity. It will be recalled that such a notch was explained to be due, in part, to amplifier integration. That no such notch is present at the 10 Hz and 6 Hz conditions is an indication that an active negative going process is still in evidence. A comparison of the 540 nm records with the 610 nm records should make these differences quite plain.

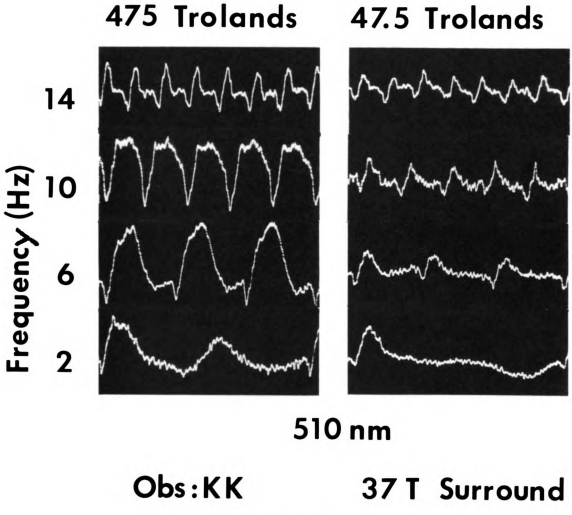
475 Trolands
47.5 Trolands
14
10
6
2
Frequency (Hz)
510 nm
Obs:KK
37 T Surround

Figure 11

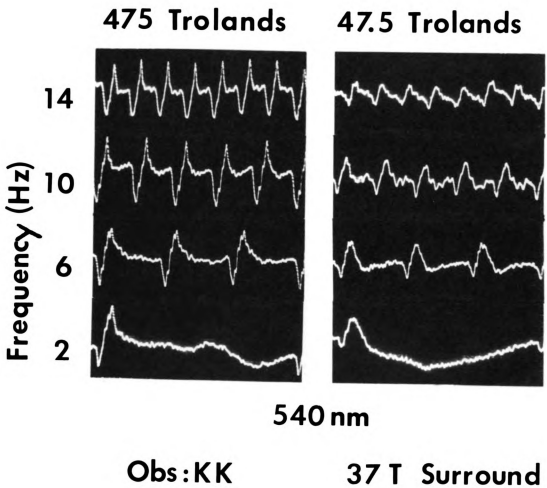
475 Trolands
47.5 Trolands
14
10
6
2
Frequency (Hz)
540 nm
Obs: KK
37 T Surround

Figure 12

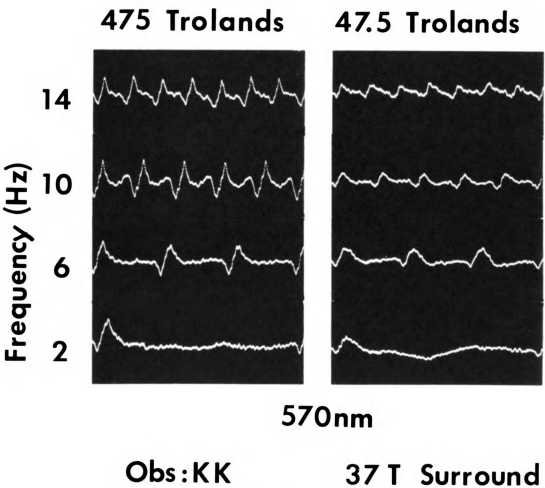
475 Trolands
47.5 Trolands
Frequency (Hz)
14
10
6
2
570nm
Obs:KK
37 T Surround

Figure 13

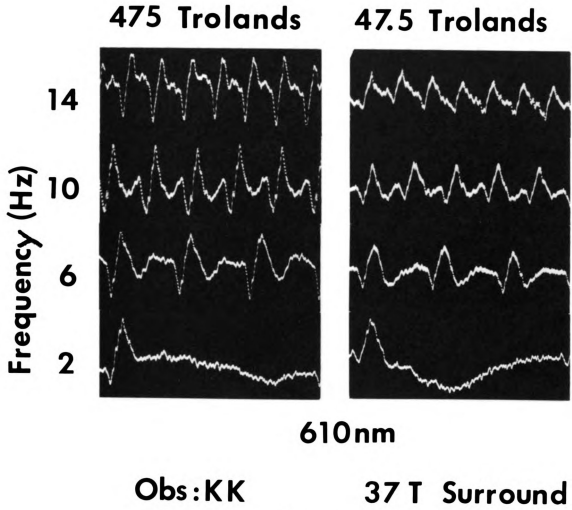
475 Trolands
47.5 Trolands
14
10
6
2
Frequency (Hz)
610nm
Obs:KK
37 T Surround

Figure 14

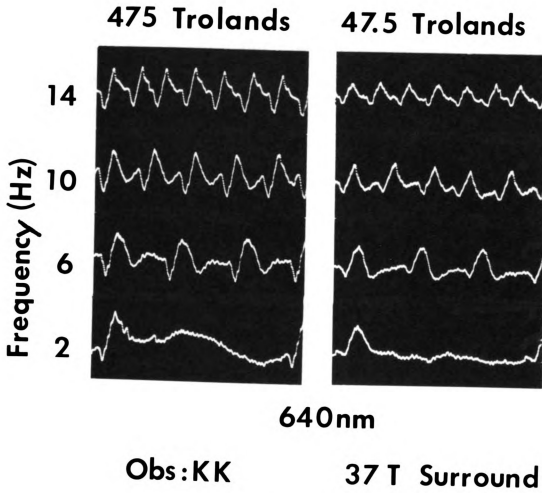
475 Trolands
47.5 Trolands
14
10
6
2
Frequency (Hz)
640nm
Obs:KK
37 T Surround

Figure 15

Figures 16 and 17 deal with the desaturation of single pulses in the unpublished work of Ball. It will be recalled that a moderate desaturation was found for single pulses of 510 nm light, if the pulse length was appropriate. If scotopic activity is to explain the apparent desaturation in these stimuli, then one might expect to see it maximized under those conditions producing the most desaturation. Pulse lengths of 5, 25, 45, 65 and 85 msec were used. According to Ball the maximum desaturation would be expected at the 25 msec condition. This was corroborated by observer K. K. in this study for the 510 nm stimulus. For comparison purposes a 610 nm stimulus was also used. No desaturation was noted for this stimulus. A third white light condition was also run under the same temporal manipulations. It was identical in brightness to the other monochromatic stimuli.

Figure 16 shows the 510 nm single pulse condition. The 5 msec duration shows no scotopic component, but the 25, 45, and 65 msec pulses show an ever increasing amount with each 20 msec increase in duration. The 85 msec condition shows a diminuation of scotopic activity. Again the low intensity condition gives no indication of a recruitment of scotopic activity regardless of the pulse duration. Indeed, the similarity of the responses for the different pulse durations is quite striking as only the 5 msec condition shows any noticeable differences in amplitude.

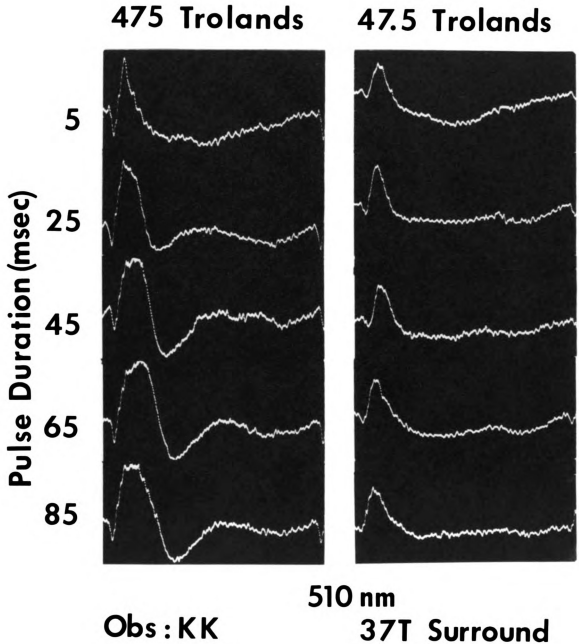
475 Trolands
47.5 Trolands
Pulse Duration (msec)
5
25
45
65
85
510 nm
Obs : KK
37T Surround

Figure 16

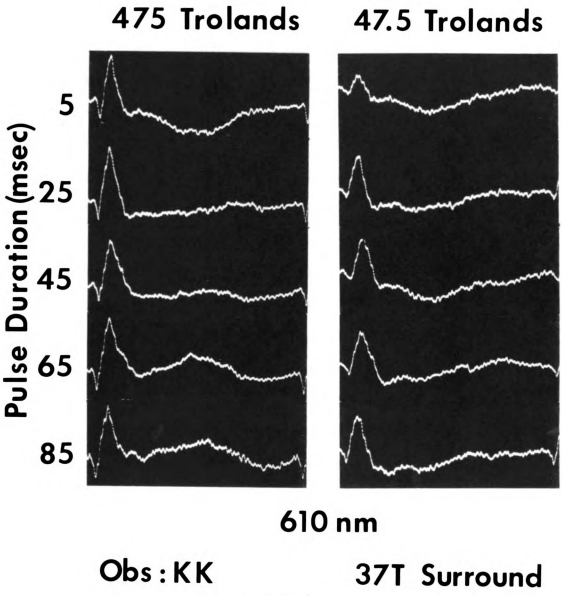
475 Trolands
47.5 Trolands
Pulse Duration (msec)
5
25
45
65
85
610 nm
Obs : KK
37T Surround

Figure 17

Figure 17, which depicts the 610 nm condition shows no significant amount of scotopic activity at either the high or the low intensity condition, and consequently provides an interesting comparison with the 510 nm condition. Only the 65 msec condition shows a slight widening of the b-wave suggesting a hint of scotopic activity.

Figure 18 is a white light condition which was subjectively determined to be of equal brightness to the other monochromatic stimuli. This intensity level had also shown the marked whitening at 10 Hz which accompanies brightness enhancement. It will be noted that the single pulse condition shows no detectable scotopic activity over the range of pulse durations used here.

Figures 19 through 22 are stimulus conditions which were run under the brighter 246 troland surround condition. The brighter surround was deemed necessary in order to determine if there was still contamination due to stray light. The increased surround intensity had a diminishing effect on the perceived desaturation. At the 510 nm, 10 Hz condition which formerly produced total desaturation, the desaturation was now only extreme on a rating scale which runs none, slight, moderate, extreme and total.

Figure 19 shows the 460 nm condition for all rates and both stimulus intensities. No desaturation is noted under any of these conditions, however some scotopic

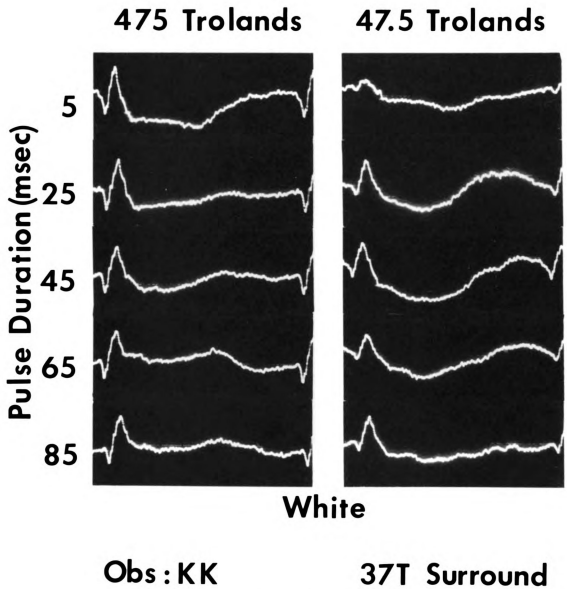
475 Trolands
47.5 Trolands
Pulse Duration (msec)
5
25
45
65
85
White
Obs : KK
37T Surround

Figure 18

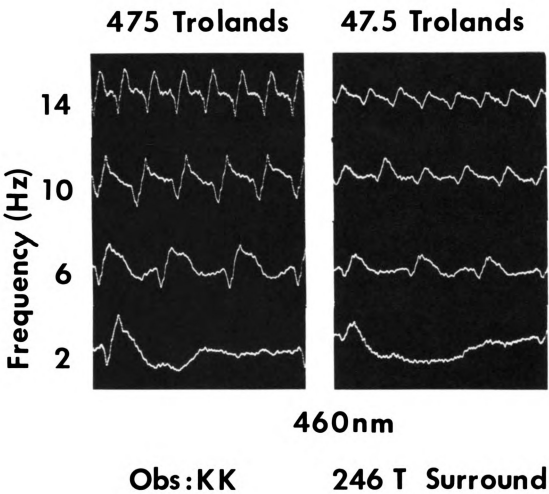
475 Trolands
47.5 Trolands
Frequency (Hz)
14
10
6
2
460nm
Obs:KK
246 T Surround

Figure 19

activity is still detectable. At 6 Hz a secondary peak in the b-wave is still noticeable. At the other frequencies the lack of an integrative downward deflection also serves as an indication of an active scotopic process.

Figure 20 shows the records obtained for the 510 nm condition at all frequencies and both intensities. Here no scotopic peaks are seen, but again the lack of an integrative type dip indicates some scotopic activity still present.

Figure 21 shows the 6 Hz condition for all wavelengths. Here an orderly progression of decreasing scotopic involvement can be seen as the wavelengths change from the blue toward the red. The 460 nm and 510 nm conditions both show wider b-waves than the rest of the conditions, indicating a longer latency scotopic process. Beginning at 570 nm a slight dip following the b-wave can be seen, which continues to develop through 610 to 640 nm. As with the other figures, the low intensity condition shows little change over the range of wavelengths.

Figure 22 shows the 10 Hz condition with the 246 troland surround. Here again the scotopic activity is noticeably present for the blue and green wavelengths, but not to a very large degree. As mentioned earlier the 510 nm, 10 Hz, 475 troland condition with the high intensity surround did show a slight decrement in perceived desaturation as it was rated as extreme rather than total.

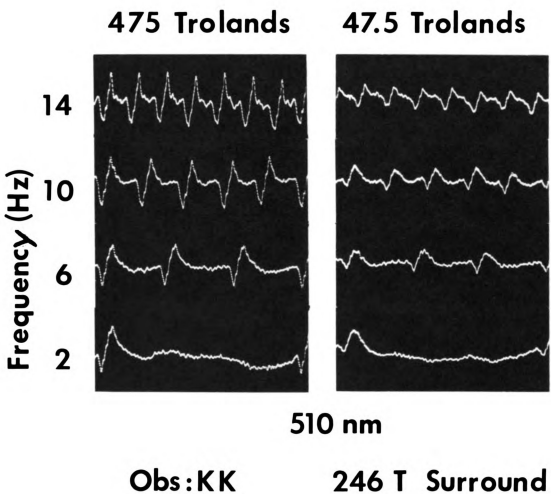
475 Trolands
47.5 Trolands
Frequency (Hz)
14
10
6
2
510 nm
Obs:KK
246 T Surround

Figure 20

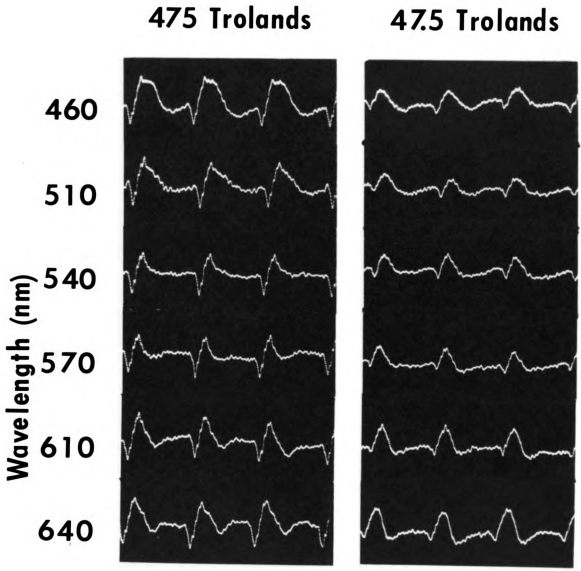
475 Trolands
47.5 Trolands
460
510
540
570
610
640
Wavelength (nm)
6 Hz
Obs: KK
246 T Surround

Figure 21

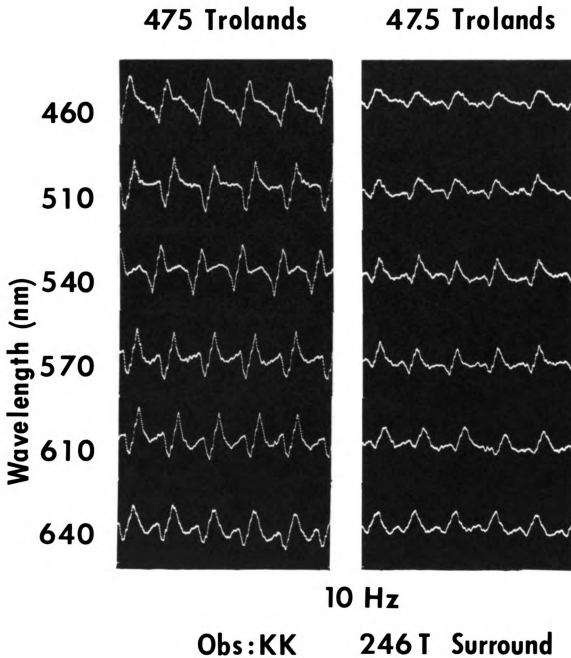
475 Trolands
47.5 Trolands
460
510
540
570
610
640
Wavelength (nm)
10 Hz
Obs: KK
246 T Surround

Figure 22

Figures 23 through 29 represent a graphical summary of the changes in magnitude of scotopic involvement for the 475 troland stimulus as pulse frequency, wavelength and pulse duration were varied. The method for quantifying the scotopic activity has been discussed in association with Figure 5. While this method is not totally free of extraneous influences, the results, nevertheless, correspond closely to the author's subjective evaluation of the data.

Figure 23 summarizes the data obtained from subject J. H. (Figures 6, 7, 8 and 9). Each symbol represents data compiled during a single recording session, since within each session pulse frequency was held çonstant while wavelength was varied. The 2 Hz condition (solid circle) is probably spuriously high as shown here due to the c-wave activity generated under that condition. An inspection of Figure 6 shows the c-wave developing a shorter latency as the middle wavelengths are reached. Consequently, the area under the curve in the 50 msec time period (which specifies these data points) is increased. It is apparent, however, that this increase is not due to scotopic activity. The 10 Hz condition (open circle) and the 6 Hz condition (open triangle) both show a relatively sharp drop as wavelength is increased toward the red end of the spectrum. This drop in scotopic activity is consistent with the corresponding drop in observed desaturation,

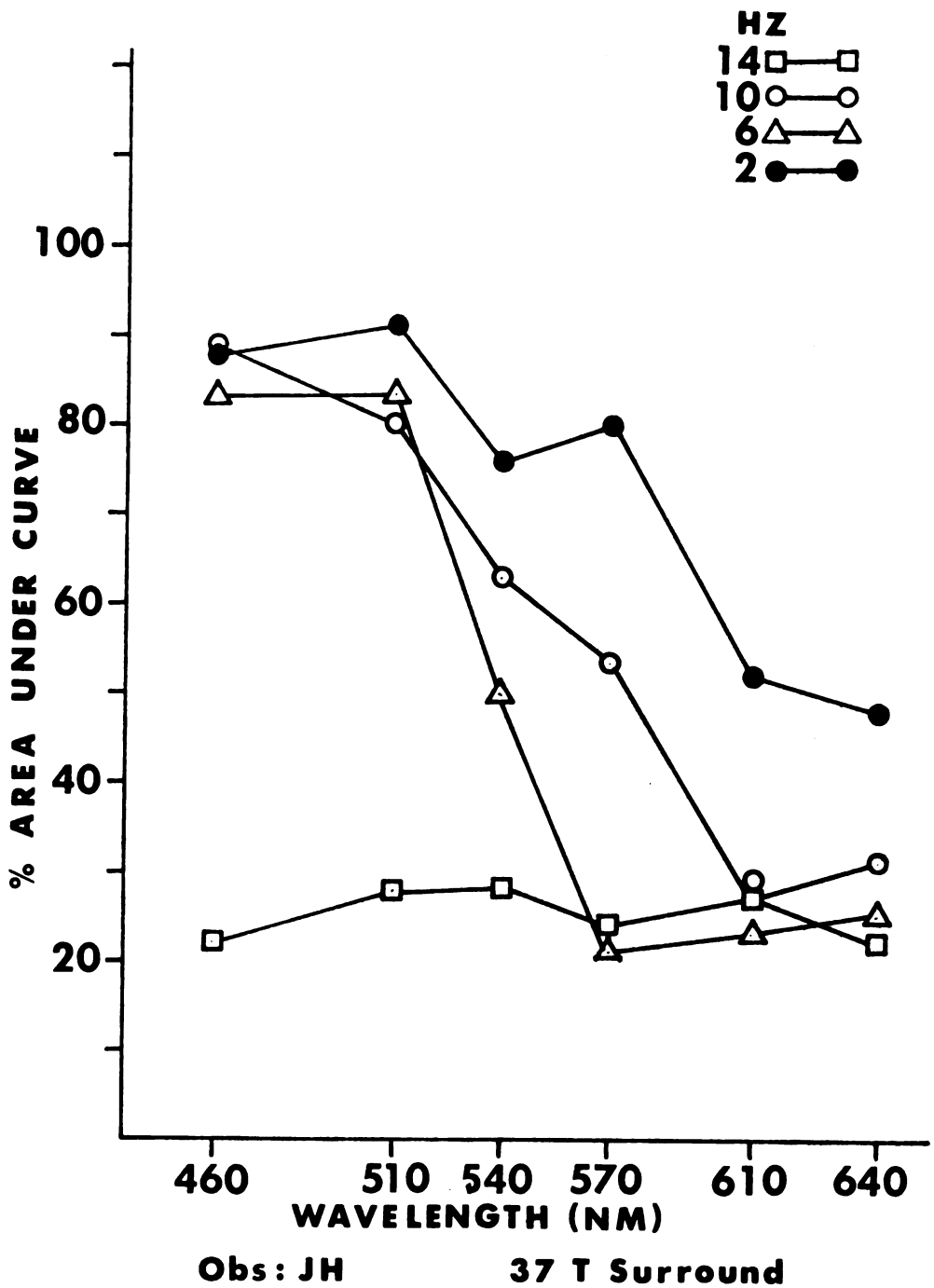
HZ
14
10
6
2
100
80
60
40
20
% AREA UNDER CURVE
460
510
540
570
610
640
WAVELENGTH (NM)
Obs: JH
37 T Surround

fig 23

but it appears to be slower inasmuch as desaturation is not observed at 540 nm, while the scotopic activity is not fully diminished until 570 nm (for the 6 Hz condition) and 610 nm (for the 10 Hz condition). The 14 Hz condition shows no change as wavelength is varied, suggesting that no scotopic activity is present.

Figure 24 represents the data in Figures 6, 7, 8 and 9 as a function of pulse frequency. Consequently, each vertical line of data points (above each frequency number) represents a single recording session. No clear trend appears here except at the 14 Hz condition where no scotopic activity appears to be present. This trend has already been noted in Figure 23, hence the main value of this figure is perhaps derived from the ease with which the data in this form can be compared to the data obtained from subject K. K.

Figure 25 shows the data obtained from subject K. K. (Figures 10, 11, 12, 13, 14 and 15). The stimulus conditions were the same as those presented to subject J. H., however wavelength was held constant during each session and pulse frequency was varied. This means that each symbol represents data obtained from a single recording session. As represented the data show that only the 460 nm and 510 nm conditions give large amounts of scotopic activity. It should be noted that no data point exists for the 460 nm, 2 Hz condition. This is due to the

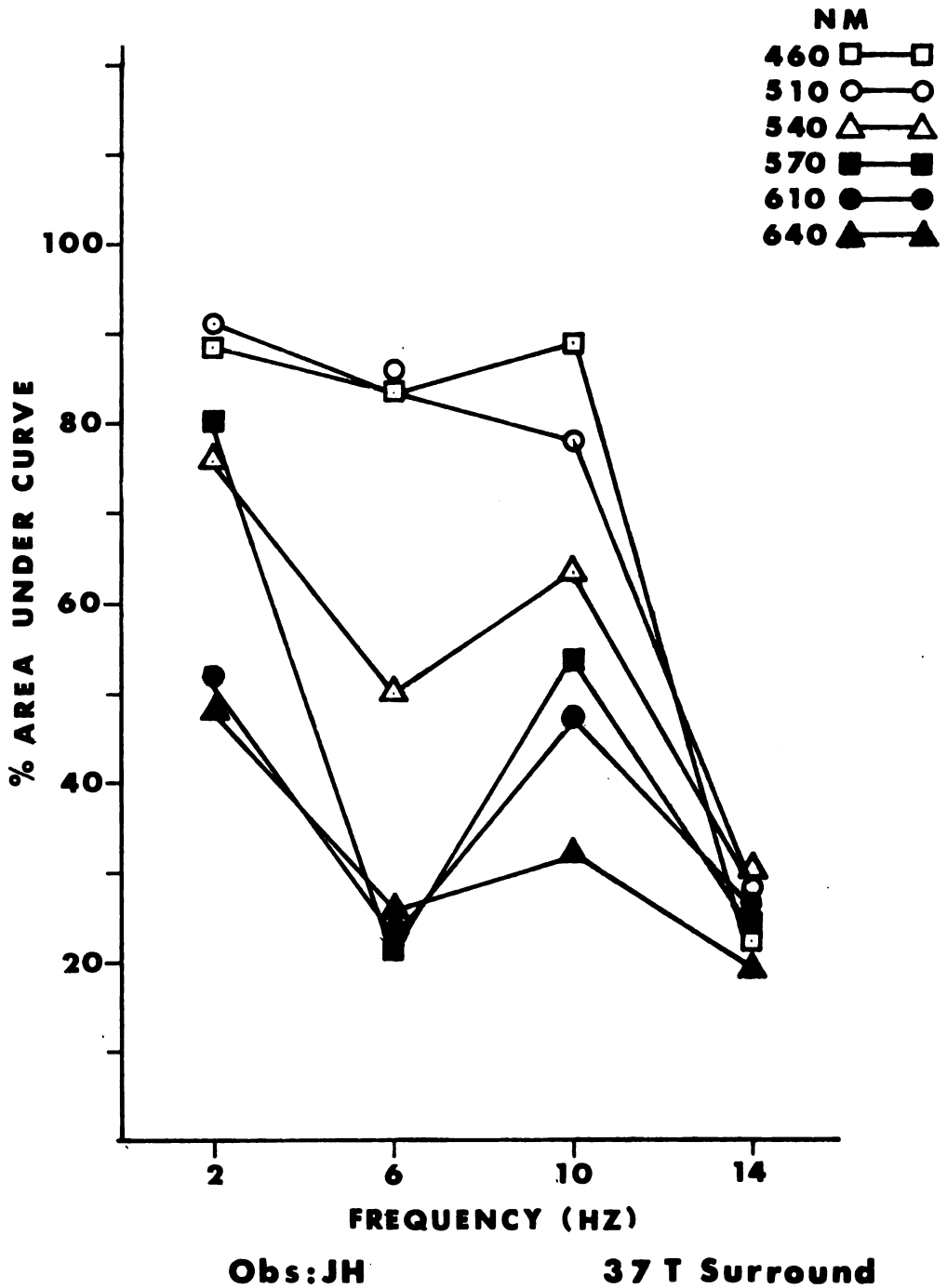
NM
460
510
540
570
610
640
100
80
60
40
20
% AREA UNDER CURVE
2
6
10
14
FREQUENCY (HZ)
Obs:JH
37 T Surround

fig 24

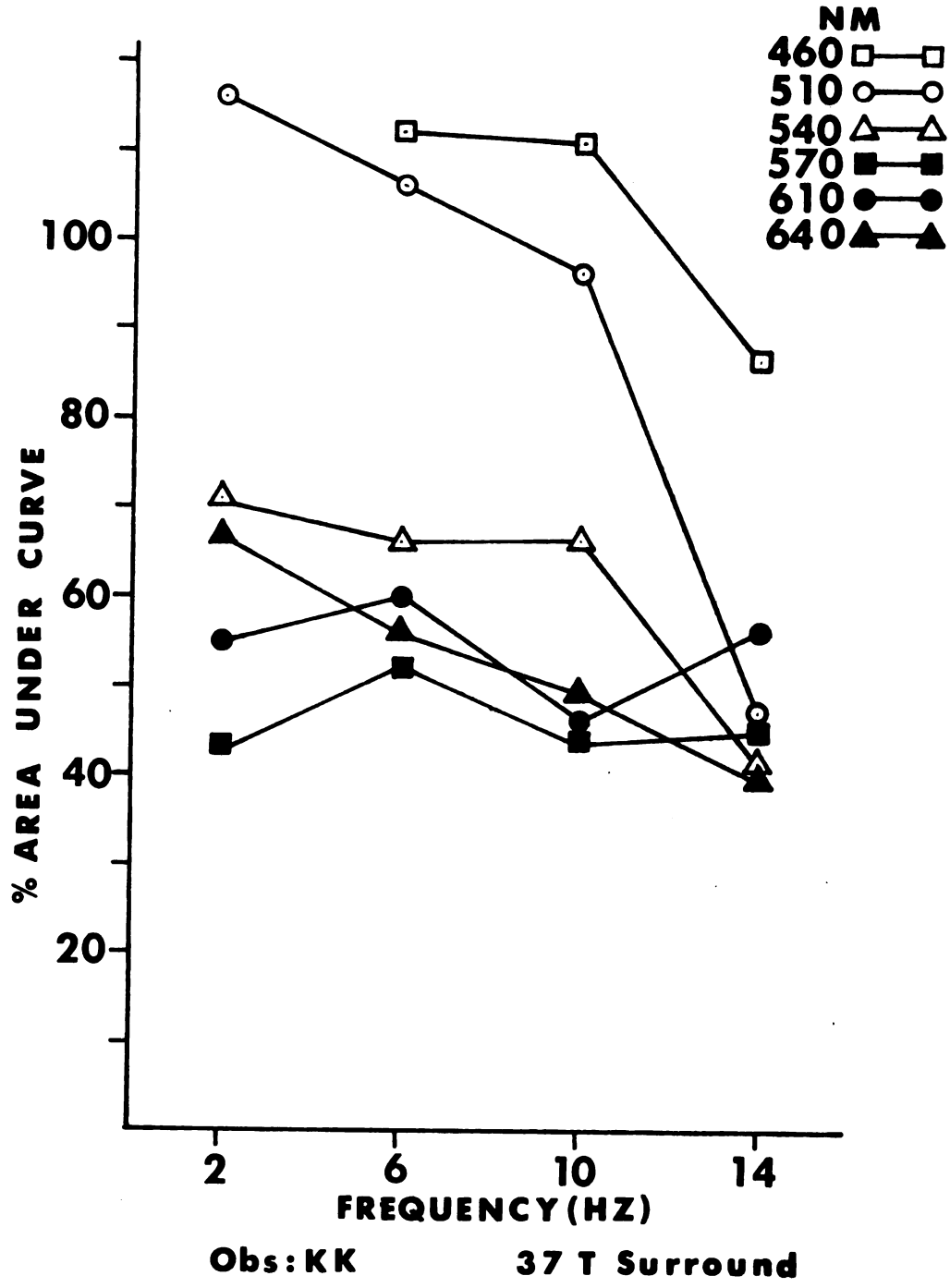
NM
460
510
540
570
610
640
100
80
60
40
20
% AREA UNDER CURVE
2
6
10
14
FREQUENCY (HZ)
Obs: KK
37 T Surround

fig 25

inapplicability of the criterion employed here to that condition (see Figure 10). As with the data obtained from J. H., the 14 Hz condition produces the least scotopic activity. However, at the 460 nm condition there is still a significant amount of scotopic activity, which is a departure from what was found with subject J. H. This fact appears to reflect the general increase in overall scotopic activity found with subject K. K. as compared with subject J. H.

Figure 26 represents the same data found in Figures 10-14 but now plotted as a function of wavelength. This means that each vertical line of data symbols represents a single recording session. Here the predominance of scotopic activity at the 460 nm and 510 nm conditions can again be plainly seen. When compared to Figure 23 the differences between the data obtained from the two subjects are quite apparent. Figure 26 shows a sharper drop in scotopic activity as wavelength is increased for subject K. K. than Figure 23 shows for subject J. H., while at the same time the generally higher values for subject K. K. represent an increased scotopic involvement over that which was found for subject J. H.

Figure 27 graphically represents the data presented in Figures 16 and 17, which depict scotopic activity as a function of pulse length for 510 nm and 610 nm. The conclusion that the 610 nm condition elicits

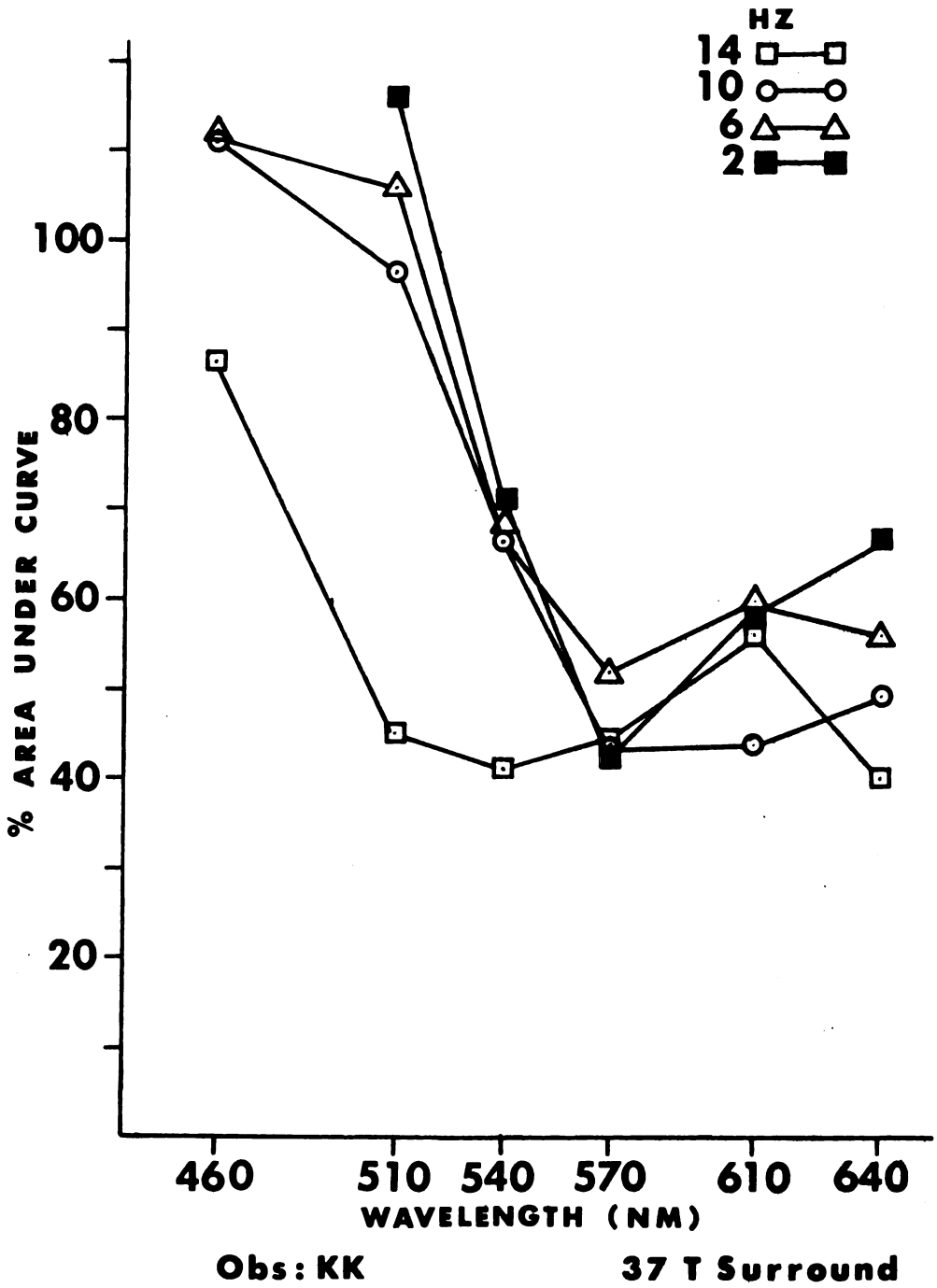
HZ
14
10
6
2
100
80
60
40
20
% AREA UNDER CURVE
460
510
540
570
610
640
WAVELENGTH (NM)
Obs: KK
37 T Surround

fig 26

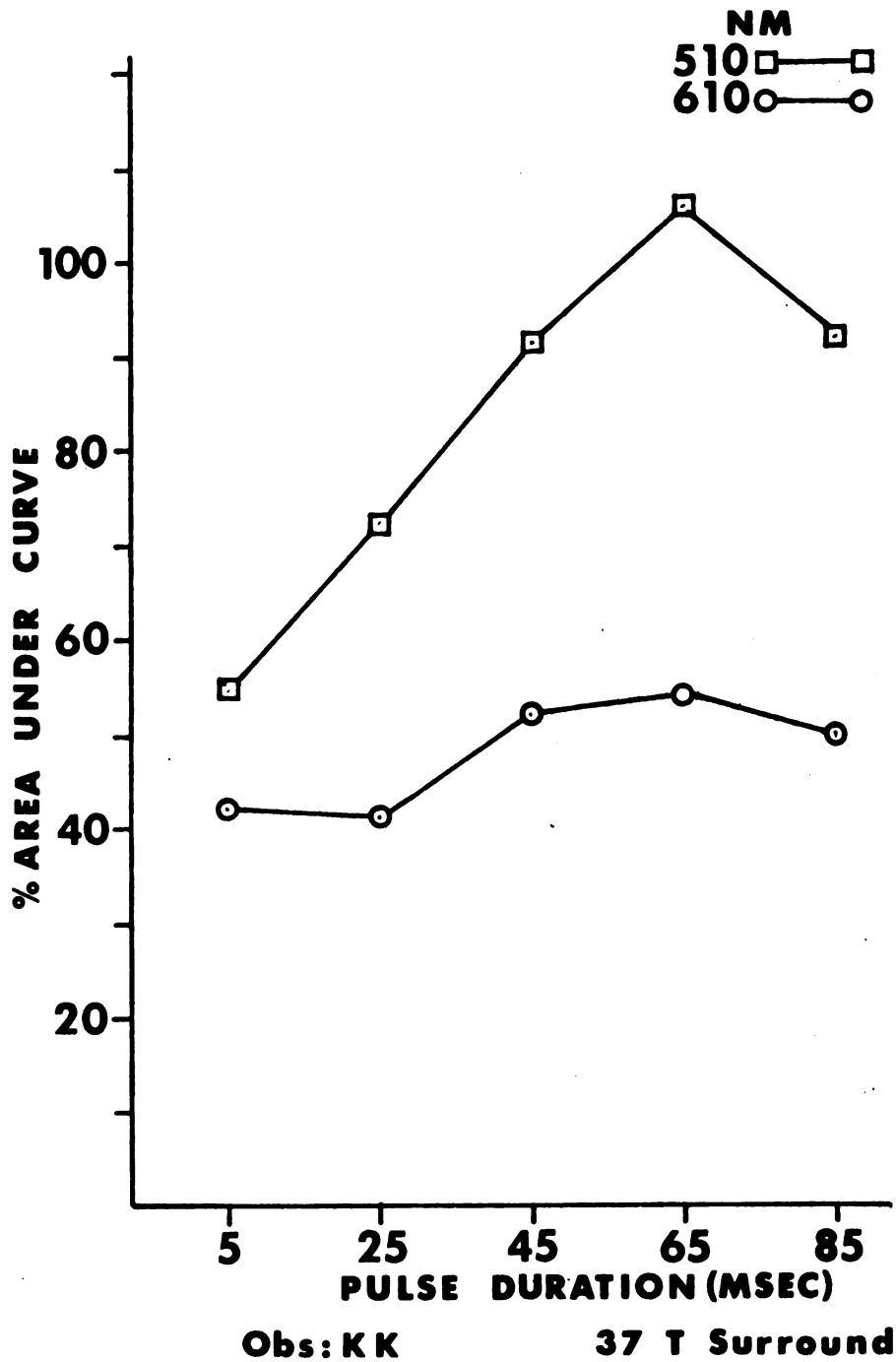
NM
510
610
100
80
60
40
20
% AREA UNDER CURVE
5
25
45
65
85
PULSE DURATION (MSEC)
Obs: K K
37 T Surround

fig 27

little or no scotopic activity while the 510 nm condition does are borne out by this graph. It is also apparent that the scotopic b-wave activity appears to be maximized at 65 msec., a duration somewhat longer than that which produces maximum desaturation (10-45 msec.).

Figure 28 graphically depicts the data found in Figures 19 and 20. The 246 troland surround was employed in these sessions. The 460 nm and 510 nm conditions were chosen as they represent the two wavelengths at which the largest scotopic activity had been found when the 37 troland surround was used. A comparison of Figure 28 and Figure 25 shows that the scotopic activity at the 2, 6 and 10 Hz conditions has been noticeably reduced. The activity at the 14 Hz condition, however, is reduced only for the 460 nm wavelength. In spite of these reductions, there still exists a maximum of scotopic activity at the 6 and 10 Hz conditions, though for the 510 nm wavelength it is quite small.

Figure 29 graphically shows the data presented in Figures 21 and 22. Here the 246 troland surround was used in conjunction with the 10 Hz and 6 Hz pulse frequencies. When compared with the same stimulus conditions enclosed with the 37 troland surround (Figure 26), it can be seen that the scotopic activity is again greatly reduced by the high intensity surround. A maximum scotopic activity can still be seen, however, at the 460 nm

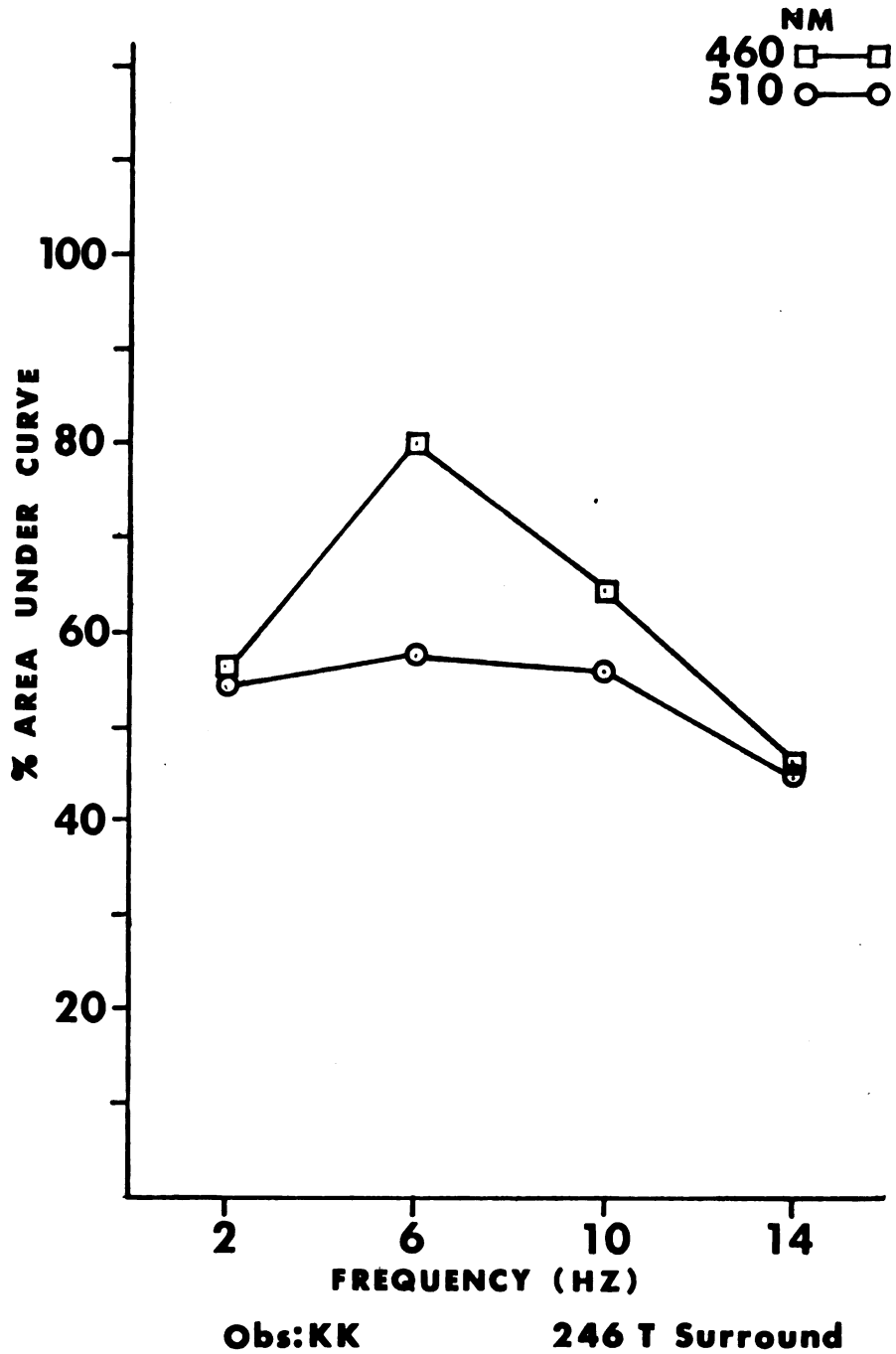
NM
460
510
100
80
60
40
20
% AREA UNDER CURVE
2
6
10
14
FREQUENCY (HZ)
Obs:KK
246 T Surround

fig 28

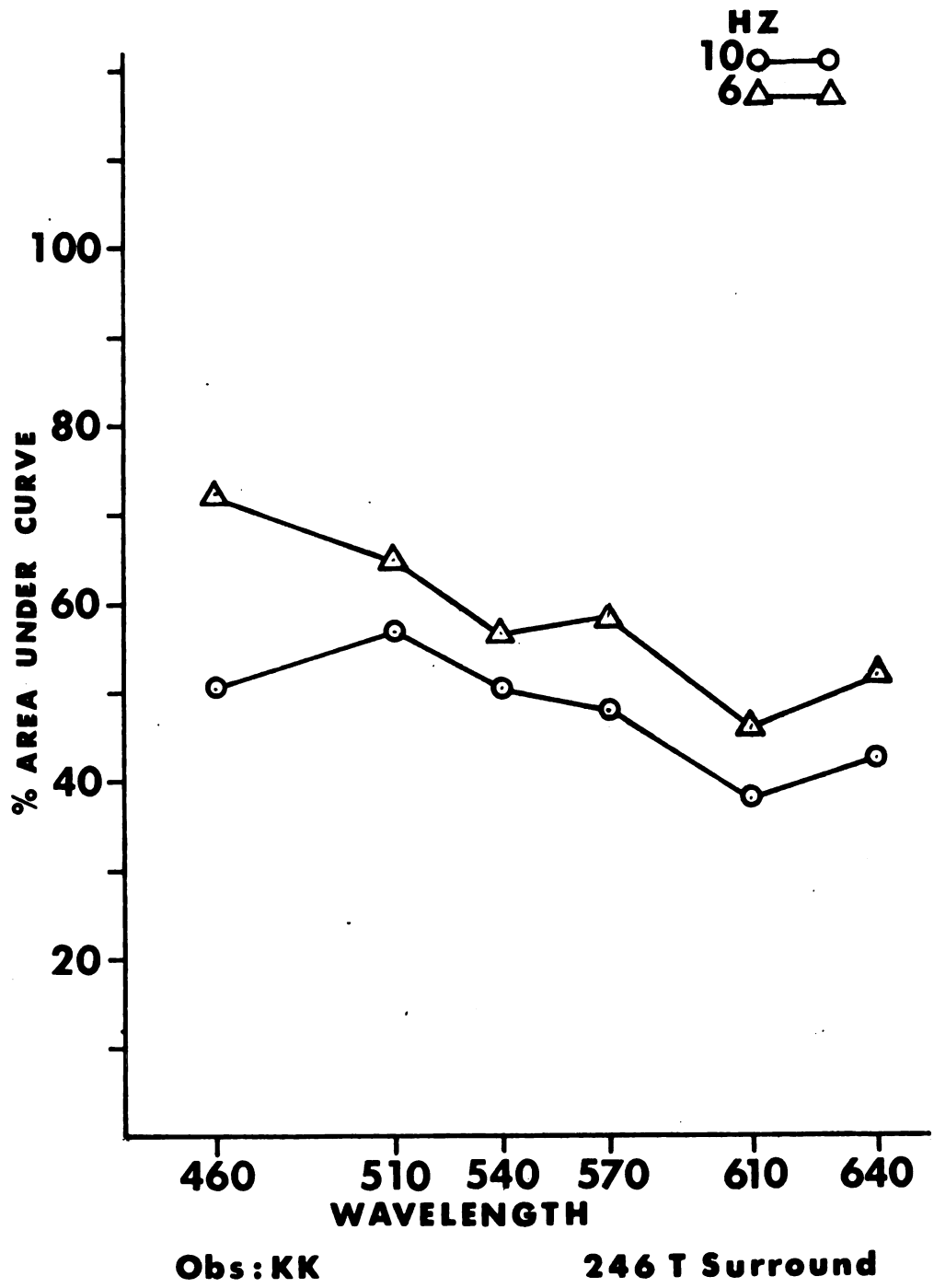
HZ
10
6
100
80
60
40
20
% AREA UNDER CURVE
460
510
540
570
610
640
WAVELENGTH
Obs: KK
246 T Surround

fig 29

wavelength for the 6 Hz frequency and the 510 nm wavelength for the 10 Hz frequency.

The temporal characteristics of the photopic and scotopic b-waves induced by the various pulse trains have not been graphically represented. Throughout the records obtained from the two subjects used in this study, the scotopic process appears to peak consistently between 30 and 50 msec. after the peak of the photopic b-wave. At the 510 nm wavelength no scotopic activity is seen at the 14 Hz frequency for either subject. Both subjects show strong scotopic activity at the 10 Hz condition, however. At 10 Hz the distance between photopic b-waves is 100 msec peak to peak. It can be seen, then, that the scotopic b-wave produced by pulse n precedes the photopic b-wave produced by pulse n+1 by approximately 50-70 msec. This estimate may be a little high because of the intervening a-wave associated with pulse n+1. The a-wave's polarity is opposite from that of the b-wave with the result that the observed scotopic b-wave can possibly be diminished prematurely when pulses are presented closely together in time.

DISCUSSION

Conclusions

The introduction section of this thesis set forth a case for relating scotopic activity to the desaturation of intermittent 510 nm light. The hypothesis set forth was that "for intermittent trains of pulses, those conditions of rate, wavelength and intensity which produce total desaturation as shown by Ball will also be the conditions under which, (1) a strong scotopic activity will be present, and (2) the temporal relationship will be such that the photopic activity will be preceded closely in time by the scotopic activity. It is further hypothesized that, where moderate desaturation for single pulses is found, a strong scotopic component will be present, while for pulse durations and wavelengths which do not produce desaturation it will be absent."

The three stimulus parameters important to the desaturation phenomenon, namely wavelength, pulse rate and intensity, all had an effect on the scotopic b-wave activity. The desaturation phenomenon decreases very rapidly as wavelength is changed toward the red end of the spectrum so that at 530 nm it has essentially disappeared. Changes toward the blue end effect the

desaturation much more slowly, however, as the subjects of this experiment still reported desaturation to a moderate degree for the 460 nm stimulus.

Scotopic activity as evidenced by the presence of a scotopic b-wave was very strong at 510 nm, but diminished rapidly so that at 570 nm there was little, if any, evidence of scotopic activity relative to the photopic activity present. In the blue region below 510 nm (460 nm) the scotopic b-wave activity was found to be even stronger than it was at 510 nm. This is not surprising in light of the fact that the stimuli were photopically balanced. This was done at the 460 nm wavelength by inspection, as the CIE determined value appeared high. Nonetheless, between 510 nm and 460 nm the efficiency of the photopic system falls off much more rapidly than does the efficiency of the scotopic system. Consequently, one would expect a greater scotopic involvement at 460 nm over the 510 nm wavelength, given that the two wavelengths were photopically balanced. It can be seen that both the desaturation phenomenon and the scotopic b-wave activity diminish as wavelengths get longer than 510 nm. As wavelengths become shorter than 510 nm, the desaturation phenomenon diminishes, while the scotopic b-wave gets larger. These facts are not totally consistent with the hypothesis as stated, then, inasmuch as scotopic b-wave increase with desaturation decrease is the opposite of the trend which was expected.

Changes in pulse rate had an effect on perceived desaturation and on the scotopic b-wave. As rate increases above 10 Hz, the ability of the scotopic mechanism to function appears drastically impaired, as evidenced by a marked decrease in scotopic b-wave activity even at optimum wavelength conditions. Increased rate also has a drastic effect on the perceived desaturation, with no desaturation present at 14 Hz and a 1/4 PCF, regardless of wavelength. The changes in desaturation as pulse rate is lowered are much slower, so that at 6 Hz a fair amount of desaturation is still noticeable though reduced in magnitude. The scotopic b-wave activity increases in magnitude as the rate is lowered to 6 Hz. At 2 Hz and 1/4 PCF the scotopic b-wave activity has fallen off somewhat and no desaturation is present. These results are probably complicated by changes in pulse length. It will be recalled that pulse length changes because the pulse to cycle fraction is maintained at a constant 1/4. In this way the overall adaptation level was maintained. Nevertheless, Ball's unpublished data for single pulse conditions where pulse length was varied show that pulses with a duration of 10-45 msec. produce moderate desaturation. Longer and shorter pulse durations produce little or none. In this study it was found that scotopic b-wave activity increased as pulse length was increased up to 65 msec., at 85 msec. however, a drop in scotopic activity was noted.

With regard to the hypothesis, then, the scotopic activity peaks at a longer pulse duration than does the perceived desaturation, a fact which, again, is not totally consistent with the hypothesis. These data also suggest that decreased pulse length may be largely responsible for the diminished scotopic activity at the 14 Hz condition. Conversely, as rates are lowered and pulse length becomes longer, the scotopic b-wave activity also increases up to a point beyond which a reduction is again noted.

The intensity variable which effects the desaturation phenomenon so markedly has dramatic affects on the scotopic b-wave. In every case where a reduction in intensity produced an elimination of the desaturation phenomenon it also eliminated the scotopic b-wave process. The fact that a reduction in intensity produces a reduction in scotopic activity at first appears contradictory inasmuch as one normally thinks of the scotopic process as being reserved for low levels of illumination. This result can be explained, however, if one considers the scotopic mechanism's relative inability to follow intermittent light. K. T. Brown (1968) has shown that the scotopic receptor response turns itself on and off very slowly when compared with the photopic receptor response. This inability appears to be reflected in the magnitude of the scotopic b-wave process for which the receptor response is the antecedent. This correlation between the

disappearance of the scotopic b-wave and the disappearance of the desaturation with reduced intensity is consistent with the hypothesis.

Enclosing the intermittent stimulus in a surround has dramatic effects on the amount of scotopic b-wave activity noted in the ERG records. The well-known Stiles-Crawford effect, which relates to the marked drop in effectiveness of light incident on the retina at an angle other than perpendicular, holds only for photopic vision. The effect does not occur under conditions where scotopic mechanisms are involved. Consequently, the scotopic (rod) receptors are sensitive to stray light, which by definition is incident on the retina from many angles. Determining exactly how much surround is necessary to just get rid of the stray light effects without interfering with the intermittent target is not possible.

Two surround levels were used in this study. The 37 troland level had no noticeable effect on the desaturation effect. The 246 troland level caused a slight reduction in the perceived desaturation. This slight reduction was accompanied by a major reduction in the scotopic activity.

The apparatus used in this experiment was not capable of producing a surround of greater intensity than the 246 troland level which was reported. Earlier pilot work using Ball's apparatus showed that bright

surrounds (as bright or brighter than the intermittent target) were effective in totally eliminating the desaturation phenomenon. In Ball's apparatus the targets subtended less than a degree of visual angle and the surround subtended 6°. Bright surrounds are, of course, capable of invading the intermittent target area with stray light. In this study it was not possible to determine if this was the case with the high intensity (246 troland) surround. Such an invasion is a plausible explanation for the slight decrease in desaturation noted, however.

The information which can be drawn from these data with regard to the hypothesis is far from conclusive. There exists a fair correlation between the presence of scotopic activity and the presence of the desaturation phenomenon. This correlation is not perfect, as indicated by the several conditions which produce large scotopic activity with little desaturation. The general trends of the data are encouraging, however, and provide enough support for this line of investigation to suggest further work.

Related Studies and Further Research

In order that the trends revealed in these data might be discussed more fully with regard to further research, a brief look at some related research is necessary.

The work of Gouras and colleagues (Gouras, 1966; Gouras and Link, 1966) has already been discussed. It will be recalled that Gouras described the interaction of photopic and scotopic inputs at the ganglion cell level. Later work by Gouras (1968) goes further in this area and describes wavelength specific activity in the ganglion cells of Macaca mulatta. A summary of Gouras' 1968 findings are as follows:

1. Two types of on-center ganglion cells can be identified on the basis of their response pattern. The type Gouras calls "phasic" responds at the onset of the stimulus with a burst of activity which quickly subsides to the ongoing resting level regardless of how long the stimulus is maintained. The second type responds in a maintained fashion to a stimulus for its duration. For this reason Gouras has labelled it "tonic."
2. Tonic cells show a center surround organization with inputs from all three photopic receptor types. The excitatory center receives inputs from only one cone type, either red, green or blue, and inhibitory inputs from another cone type in its surround.
3. Phasic cells receive inputs from only green and red cones, both of which are excitatory in the

center and inhibitory in the surround. These cells also receive inputs from the rods. No blue cone inputs have been found for these cells.

4. Tonic cells outnumber phasic cells, but both are found adjacent to one another throughout the retina. Phasic cells are more common in the periphery, while tonic cells are more common near the fovea.

It is interesting to note that the two types of responses noted in ganglion cells of Macaca mulatta are similar in shape to the two types of ERG components found in the inner plexiform layer. The fact that the response of the phasic type ganglion cell corresponds to the transient b-wave has already been discussed. This latest work of Gouras (1968) shows that there is another type of ganglion cell responding in a maintained or tonic fashion much the same as does the D. C. component of the ERG.

At higher levels the nature of the neural activity becomes more complex. Wiesel and Hubel (1966), recording in the LGN (213 cells) of Macaca rhesus, have found 3 types of cells in the 4 dorsal layers. Type I cells were much more common (77%) than the other types. They showed a center surround organization to white light as well as opponent-color responses to diffuse light. This opponent-color response has a spatial distribution as well, of which 5 varieties have been described by the authors.

They are, in order of their frequency of occurrence, (1) red on-center, green off-surround; (2) red off-center, green on-surround; (3) green on-center, red off-surround; (4) green off-center, red on-surround; and (5) blue on-center, green off-surround. Of the 17 cells of this type which were tested for rod inputs, only 4 showed any scotopic activity.

Type II cells made up a small percent (7%) of the cells tested. These cells did not show a center surround organization, but did show an opponent color process. Two types were found: (1) blue-on, green-off; and (2) green-off, blue-on. Two cells of this type were tested for rod inputs and neither showed any.

Type III cells comprised 16% of the cells investigated by these authors. These cells showed a center surround organization but no opponent color processes because the center and surround had the same spectral sensitivities. In general, these cells typically showed a wide range of sensitivity corresponding roughly to the photopic sensitivity curve. When 4 of this type of cell were tested for rod inputs, 2 showed no significant change while 2 showed a large change in sensitivity.

The interpretation of Wiesel and Hubel's data obtained from the LGN is complicated somewhat by not knowing which of the three types of neural processes in the LGN (afferent, efferent or internuncial) the data

are coming from. If all three levels are being recorded from, then one might be looking at the neural transmission of visual input in these different stages of processing rather than at one stage in the pathway. Given this difficulty, it is hard to evaluate the differences between the kinds of activity Gouras finds and the types Weisel and Hubel find. One such difference is that while Gouras finds scotopic activity only in the phasic cells in which he could find no blue receptor inputs, Wiesel and Hubel find scotopic activity associated with both type I and type III cells, and because of their small sample of 2, it is not sure that type II cells do not have scotopic inputs as well.

That none of this complexity is found by Gouras at the ganglion cell level suggests the possibility of a transformation of the neural signals at the level of the LGN. If such a transformation is being performed in the LGN, the way to uncover it is not recording in the LGN itself, but rather by recording both in the ganglion cells (or optic tract) and again in the optic radiations. This might be termed a "black box" approach to the LGN, but it appears to be the most logical way to determine what kind of information processing the LGN is doing.

The implications that the work of Gouras and Wiesel and Hubel has for the topic under investigation are the following. A model for scotopic-photopic

interaction in the "phasic" cells was set forth in the introduction of this thesis. The purpose of this thesis was to determine if scotopic and photopic activity co-exists, in what could be considered to be a plausible temporal relationship, under stimulus conditions which also produced the desaturation phenomenon described by Ball. It was found that there is a general correspondence between scotopic activity and the existence of the desaturation phenomenon, but that the blue wavelengths showed an unpredicted increase in scotopic b-wave activity with corresponding decrease in the perceived desaturation. Wiesel and Hubel's data indicate that there exists a great many possibilities for interaction between scotopic and photopic activity at higher levels. It is possible that such an interaction is responsible for the reduction in perceived desaturation at 460 nm, even though the scotopic activity is not reduced.

It is clear that no amount of recording at the retinal level will reveal neural processes which are central in their origin. With this in mind, the following research is suggested:

1. The behavioral determination of the desaturation phenomenon in Macaca mulatta.
2. Microelectrode recording in the optic tract and optic radiation for stimuli which produce the desaturation phenomenon. Perhaps the most

valuable stimuli in this respect would be single pulses of variable duration from 5-85 msec.

3. A correlation of ERG and single unit recording to a larger degree than has been done by Gouras and others.

The above suggested research is extensive, to say the least. However, it is the kind of research which appears to be necessary in order to get at the interesting problem of scotopic-photopic interaction and its neurological and perceptual implications.

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