

Nonlinear Transient Responses from Light-Adapted Wolf Spider Eyes to Changes in Background Illumination

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ABSTRACT Retinal action potentials were recorded at the corneas of light-adapted wolf spider eyes in response to large positive and negative step changes in background illumination. These incremental responses were superimposed upon the steady-state DC responses to the background illumination. Both positive and negative step responses had peaks which overshoot the DC levels to which they decayed. The overshoot was greater for positive than for negative steps. Short term DC responses measured after one-half sec were larger for negative than for positive steps; these short-term DC responses were thus asymmetrical. However, responses to short positive and negative flashes were not asymmetrical; rather, they varied linearly with flash amplitude. Asymmetries were thus delayed in onset. The short-term DC responses were found to be different from the steady-state DC responses to maintained changes in background illumination. There was an approximately exponential decay or creep from the short-term to the steady-state DC responses. It is proposed that the dynamics of delayed asymmetries can explain the waveforms of the short-term transient responses.

A basic unsolved problem in visual physiology is how photic isomerization of visual pigment in a primary visual receptor cell leads to electrical activity of that or other cells. It seems reasonable to suppose that something of this visual transduction process can be learned from the dynamics of the electrical responses. From a general viewpoint, these dynamics may be easier to study in invertebrate eyes, such as those of arthropods, for the initial electrical activity in these eyes in response to light is a sustained depolarization of the distal ends of the receptor cells (Hartline, Wagner, and MacNichol, 1952). These distal depolarizations can be recorded intracellularly in some species; they can also be recorded extracellularly at the corneas of illuminated eyes as retinal action potentials. Retinal action potentials are especially suitable for studies of light-adapted eyes, as they can be recorded from intact animals in which fatigue of a preparation with long periods of illumination is absent.

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The present paper contains a description of the waveforms of retinal action potentials from the purely ocellar eyes of light-adapted wolf spiders. These eyes appear to contain no second order neurons (Melamed and Trujillo-Cenóz, 1966). Thus the electrical responses recorded at the corneas of these eyes are most likely those of primary visual receptor cells.

The waveforms of retinal action potentials from light-adapted arthropod eyes to incremental flashes are in many ways like those from dark-adapted arthropod eyes, as for example described originally by Hartline (1928). Following a flash, there is an initial, or peak, response which overshoots the final, DC value to which it subsides. For the most part, these responses are not linear functions of the flash size. In the dark-adapted eye, the response upon termination of a flash only slowly returns to the original base line (Bernhard, 1942), whereas in the light-adapted eye, there may be an undershoot of the base line following termination of an incremental flash (Hartline, Wagner, and MacNichol, 1952; DeVoe, 1962; Stieve, 1965; Pinter, 1966). When the incremental flash is small enough, the linear response to a negative flash or step is simply the mirror image of the overshooting response to a positive flash or step (DeVoe, 1962; Ratliff, Hartline, and Miller, 1963; Pinter, 1966). All this may be contrasted with the flat-topped waveforms of linear response of the dark-adapted *Limulus* ommatidium; overshoot is observed only in nonlinear responses (Fuortes and Hodgkin, 1964). It is as though light adaptation results in the responses of the eye becoming oscillatory without necessarily becoming nonlinear. In the retinal action potentials from light-adapted beetle eyes, however, overshoot continues to be observed only in nonlinear responses to positive incremental flashes; there is never any overshoot in linear responses to small incremental flashes or in responses to any size of negative (i.e., decremental) flashes (Kirschfeld, 1961).

Second, since there is a sustained background illumination upon the light-adapted eye, there is a sustained background potential elicited by this illumination. While this background potential can be seen to be the continuation of the DC response to a long flash (Hartline, Wagner, and MacNichol, 1952), it is in short order obliterated by drifts in most DC recording situations or by AC amplification. Despite the fact that all incremental responses are superimposed upon this background potential, it is usually ignored in favor of incremental, rather than total, response. It will be argued in this paper that it is not always justifiable to ignore the background potential.

Third, because the background illumination upon a light-adapted eye may be reduced (negative stimulus) as well as increased (positive stimulus), it is possible to record the response of the eye to negative increments in illumination up to and including complete termination of the background illumination. Incremental retinal action potentials from light-adapted beetle eyes to such negative stimuli behave quite differently from those elicited by positive

stimuli. As already mentioned, there is no overshoot, but more important, the incremental DC responses to negative steps are much greater than those to positive steps of equal size (Kirschfeld, 1961). The positive and negative step responses of light-adapted beetle eyes are thus asymmetrical.

Similar asymmetries are seen in the retinal action potentials recorded from light-adapted wolf spider eyes in response to step changes in background illumination. These asymmetries are the subject of this paper. In what follows, it will be argued that the asymmetries take time to develop so that there is overshoot in both positive and negative step responses. At the end of this paper, a schema will be presented to show how these overshoots would thus arise. In the following paper, a model will be developed to test the schema quantitatively and to explore what physiological mechanisms might underlie the observed dynamics of nonlinear response.

METHODS

Preparation of the Animal Intact, adult wolf spiders were used for these studies. The eyes of such animals could be kept illuminated for hours without detectable fatigue or deterioration of the preparation. The two species of wolf spiders used were *Lycosa baltimoriana* (Keyserling), which was collected in the Pine Barrens of New Jersey, and *Lycosa miami* Wallace, which was collected in the Everglades National Park, Florida. No differences were noted in the visual responses from these two species. The animals were kept in individual plastic cages, as all spiders are cannibalistic, and were fed on meal worms (larvae of *Tenebrio molitor*). Caged individuals of *L. baltimoriana* have lived for up to $\frac{3}{4}$ yr, and individuals of *L. miami* up to $1\frac{1}{2}$ yr.

The spiders were restrained in a clamp (DeVoe, 1962), to which their carapaces were waxed. An exceptionally good wax that was found to resist all attempts of the spiders to break loose consisted of one third rosin, two thirds beeswax (Wilson and Weis-Fogh, 1962). This was gently applied with an electrically heated nichrome wire loop. Animals so treated were later released and survived as long as those that were never used; subsequently, some even molted normally.

The spiders were grounded through their mouthparts by placing them upon a cotton pad soaked in saline; in this pad was a grounded, chlorided silver wire. An animal usually "attacked" and grasped this pad with its fangs, thereby pressing the pad to its mouth. Two other, differential connections were made to the animal by means of glass pipettes of tip diameter 0.3–0.5 mm. These pipettes were filled with 0.23 M NaCl which approximates the osmolarity of spider blood (Rouschal, 1940; Rathmeyer, 1965). One pipette went to the top of the illuminated eye, which was always one of the posterior median eyes (secondary eyes). Before placing the pipette upon it, this eye was gently scraped with glass from a broken bubble in order to remove the waxy epicuticle (Hartline, 1928). The other pipette was placed on the posterior portion of the carapace over a small hole made with a needle; bleeding from this wound was negligible. At this posterior location, no pickup from the illuminated eye was recorded, even upon the strongest stimulation of an eye (Magni, Papi, Savely, and Tongiorgi, 1965).

The experiments to be reported were performed at 21° to 25°C. During any one experiment, however, the temperature of the animal, as monitored by a thermistor thermometer placed next to the animal, varied by no more than 2.5°C and usually by less.

Optical Stimulation The light for most of the experiments described here was obtained by focusing upon the eye the output of a Sylvania R1131C glow modulator tube. The glow tube was driven on and off by a 1 kc square wave whose duty cycle could be controlled by the stimulus waveform (MacDonald, 1960). As the spider eye cannot respond to frequencies above about 120 cps (DeVoe, 1964), the apparent brightness is proportional to the duty cycle of the tube; that is, to the proportion of the time that the tube is on. To establish the ambient background illumination for all experiments, the glow tube was set to be on 50% of the time. Then, electrical inputs (see below) applied to the glow tube circuitry could change the duty cycle of the tube between 5 and 95%; this corresponded to $\pm 90\%$ changes in the background illumination. A gating circuit also allowed the light to be turned off completely (-100% step). A feedback circuit employing a photocell was used to maintain the peak light output of the glow tube constant despite thermal effects which occurred during maintained changes in the duty cycle. This stabilization of peak light output was necessary if the duty cycle alone was to determine the apparent brightness. Neutral density filters were used to vary the ambient backgrounds themselves.

The driving voltage waveforms applied to the input of the glow modulator tube circuitry were derived from Tektronix 162 waveform generators. Inverting amplifiers were used to generate negative gate voltages, and both positive and negative voltages could be attenuated to produce between 0 and 90% increases and decreases, respectively, in the ambient background illumination.

Two other optical stimulators were used in a few experiments. One was a two channel stimulator previously described (DeVoe, 1966). It was used to provide much larger positive step changes in background illumination than the glow tube could alone. The other made use of a fiber optic bundle (American Optical Co., LGM-1) to bring the light from a Bausch and Lomb high intensity monochromator to the eye; this light was controlled by a photographic shutter.

To determine the orders of magnitude of light intensities used, the outputs of the glow modulator tube and of the two channel optical stimulator were calibrated using a Salford Electrical Instruments photometer. The intensities are given as illumination in lux incident upon the eye. Due to the high curvature of the lenses of these eyes (which are somewhat less than 1 mm in diameter), a considerable fraction of the incident light probably never entered the eye, so that the figures for incident illumination can only be considered to be relative. In addition, the relative brightnesses of the two light sources in the two channel optical stimulator as seen by the spider were different from the relative brightnesses determined with the photometer. The photometer calibration of the brighter source is therefore given in human photopic lux, while the illumination from the other channel is given in "spider lux" relative to the first. Finally, the output of the fiber optic was calibrated with a Kettering radiometer (Yellow Springs Instrument Co., Yellow Springs, Ohio) and was converted to human

photopic lux using the luminous efficiency of radiation for the appropriate wavelength (Walsh, 1958).

Recording Methods Chlorided silver wires, well shielded from the light, made contact with the saline in the pipettes which went to the animal. Leads were taken from these wires to a gain-of-20 DC preamplifier and then to a DC-coupled Tektronix 502 oscilloscope. The DC drifts of the preamplifier and of the oscilloscope were negligible compared to the random drift originating at the preparation, and response averaging (see below) did much to reduce this latter drift. In some experiments the oscilloscope face was photographed with a Grass C-4 camera. The negatives were projected onto graph paper where the oscilloscope traces were traced and averaged by eye. For the most part, however, averaging was performed off-line with a LINC computer. A Honeywell 8100 FM tape recorder (Honeywell, Inc., Minneapolis, Minn.) was used to record simultaneously, from the vertical amplifier outputs of the oscilloscope, the stimulus waveform, the response waveform, and also a gate waveform which lasted for the duration of each oscilloscope sweep. The computer was then programmed to begin sampling the stimulus and response waveforms at the onset of the gate and to continue sampling as long as the gate was present. Recording and playback speeds of the tape recorder as well as sampling rates were adjusted to allow the computer to sample each waveform at about 200 points. In general, 32 to 128 or more successive waveforms were averaged, depending upon the signal-to-noise improvement required.

RESULTS

I. DC Responses

RESPONSES TO POSITIVE AND NEGATIVE STEPS The waveforms and features of nonlinear responses from light-adapted wolf spider eyes which are the subject of this paper are illustrated in Fig. 1. The stimuli for these responses were positive and negative incremental flashes superimposed upon a sustained background illumination. These flashes were always both rectangular shaped and longer than the portions of the response of interest. They were, in other words, equivalent to maintained step changes in background illumination and will be so designated. Each curve in Fig. 1 represents the average of from 32 to 128 recorded retinal action potentials; henceforth these curves will be called simply the step responses of the light-adapted wolf spider eye.

The step responses in Fig. 1 illustrate the features of light-adapted eyes previously discussed. First of all, there is a latent period before there is any detectable response. Within experimental error, this latent period is the same for all the responses. In the experiment illustrated in Fig. 1, the latent period was about 11 msec. A possible reason for the constant latency will be brought out later.

Second, there is overshoot in the responses to both positive and negative step changes in background illumination. However, whereas this overshoot increases with increasing positive step size, it decreases with increasing nega-

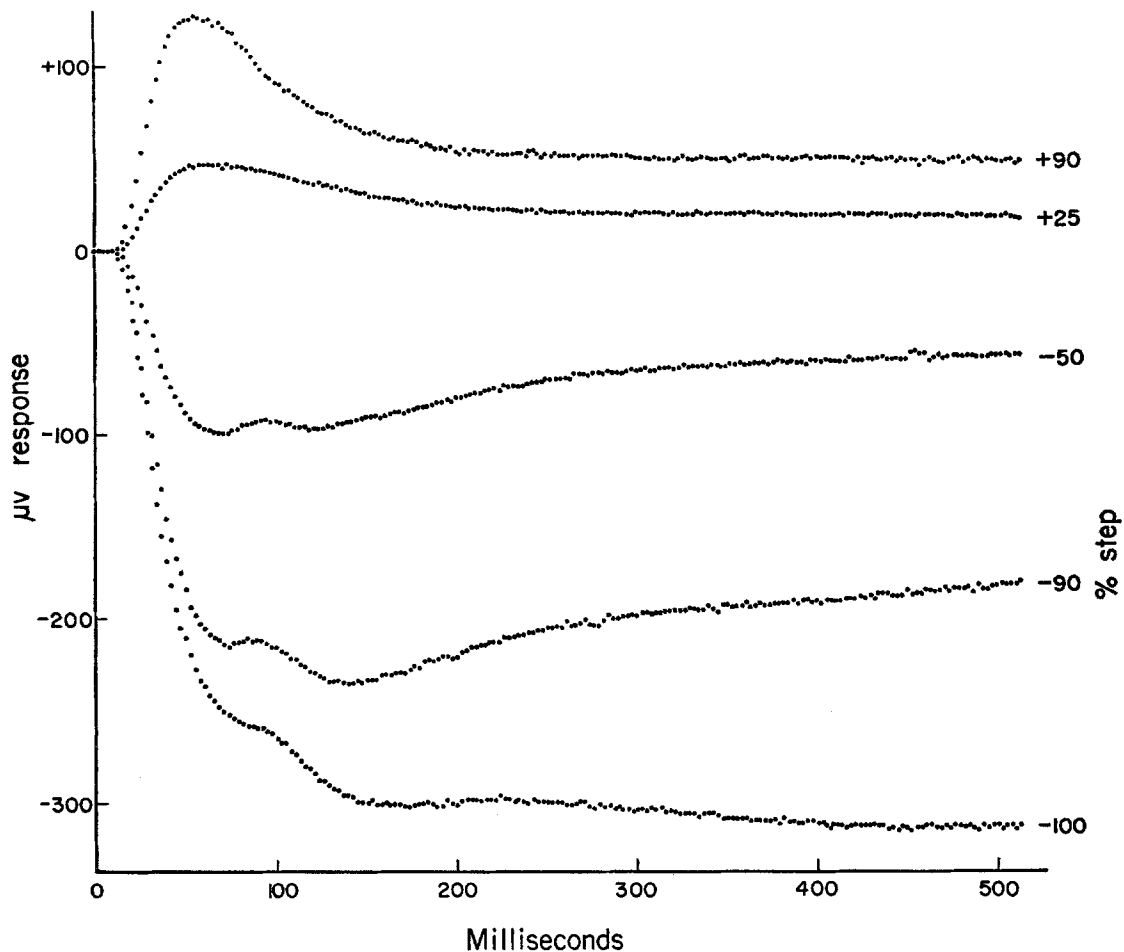


FIGURE 1. Averaged responses to positive and negative step changes in background illumination upon a light-adapted wolf spider eye. Each response is made up of from 32 to 128 retinal action potentials averaged at 195 points; the sampling time was 2.624 msec. Negativity of the cornea of the illuminated eye is upward in this and in the remaining figures. However, the convention will be that an upward deflection is a positive or increasing response and a downward deflection is a negative or decreasing response. The ordinate is labeled in this convention. The step stimulus sizes are given as per cents of the ambient background illumination of 12,100 lux.

tive step size. In the response to turning off the light (-100% step), there is no overshoot at all, and the response declines monotonically to a new potential.

Third, there are "notches" in the peaks of the negative step responses, but not in the peaks of the positive step responses. The origins of these notches are unknown. Finally, there are DC responses which may be measured about

one-half sec after the beginning of the step stimuli. There is also a persistent "creep" back towards base line superimposed upon all DC responses except those to turning off the light. This creep is especially evident in the responses to negative steps.

SHORT-TERM DC RESPONSES At the end of one-half sec, in the tails of the responses, the potentials appear to be approaching a DC value. In the responses illustrated in Fig. 1, these DC values are somewhat obscured by the superimposed creep, particularly in negative step responses. In other experiments, however (DeVoe, 1966), the creep has not been nearly so apparent. Where creep is present, it is nonetheless possible to see a rapid initial phase of decay from the peaks of responses. This rapid decay is assumed to end in a *short-term DC response*. Thus, in Fig. 1, there can be estimated the horizontal asymptotes which the rapid phases appear to be approaching, and these asymptotes are taken to be the short-term DC responses of the eye. At times it is difficult to estimate these asymptotes in responses to negative steps, and some scatter in plots to be presented may be due to this difficulty.

The magnitudes of the short-term DC responses from a different experiment are plotted in Fig. 2 as open circles vs. the per cent changes in background illumination. The cross marks the origin, which is the base line potential of the light-adapted eye. The asymmetry between positive and negative short-term DC responses, drawn as open circles, is evident. The solid line was fitted by a least squares method on theoretical grounds to be developed in the following paper (DeVoe, 1967). Basically, it is the DC stimulus-response relation of a nonlinear process whose dynamics, as will be explained later, are hypothesized to underlie the transients in step responses as well.

Over most of the range of incremental stimuli used, the short-term DC responses are in proportion to the logarithm of the total background illumination. To include both positive and negative steps in one logarithmic scale, the short-term DC responses are plotted vs. the logarithm of relative *total* background illumination in the inset of Fig. 2. A straight line fits well all experimental points for relative total background illuminations greater than 0.2 (for step stimuli between -80% and $+90\%$). Similar logarithmic relations between total illumination and DC responses were originally found by Kirschfeld (1961) for incremental step responses of light-adapted beetle eyes. However, the inset in Fig. 2 shows that for relative total background illuminations of less than 0.2, the stimulus-response relation plotted on these semilogarithmic coordinates bends towards a horizontal asymptote. The value of this asymptote is, of course, the same as the DC response to a -100% flash, which is the bottom point in the main part of Fig. 2. This bending is too abrupt to be ac-

counted for by the $k \cdot \log \left(1 + \frac{I}{I_b} \right)$ function proposed by Rushton (1959).

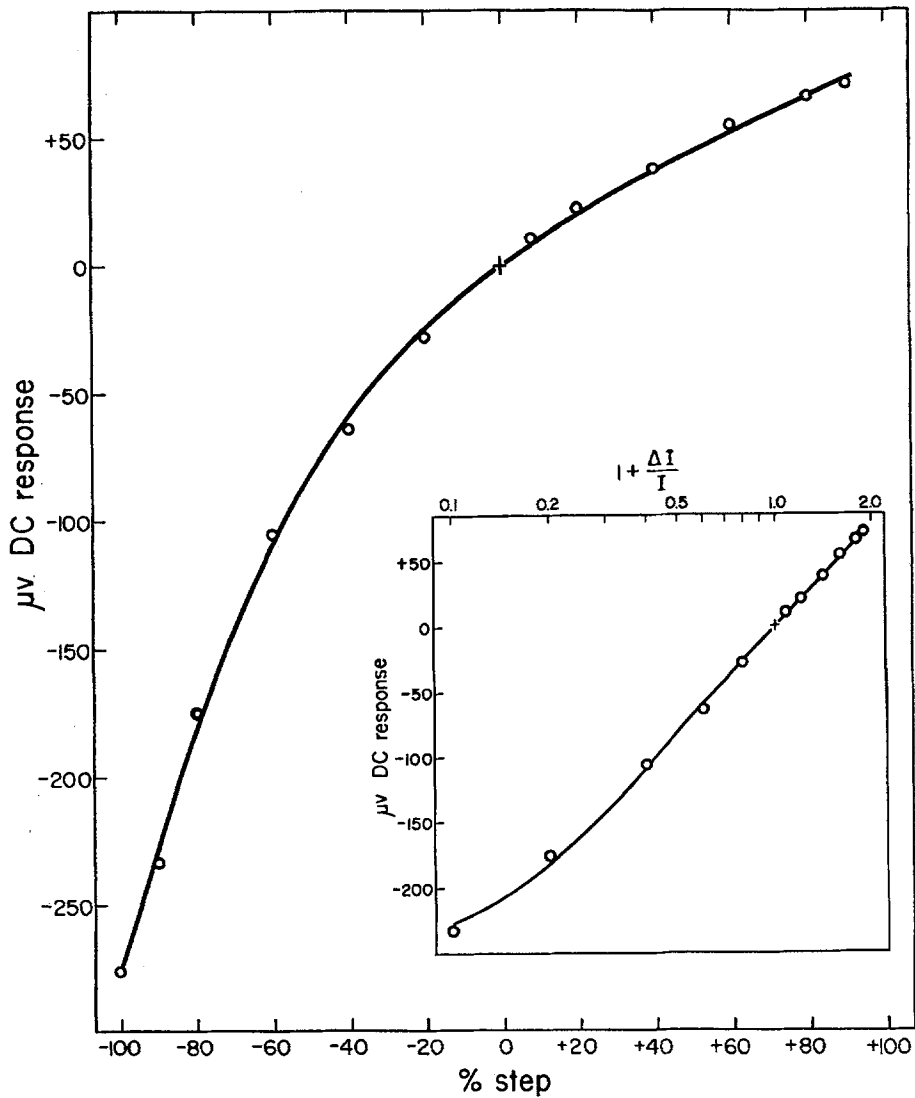


FIGURE 2. Short-term DC responses of the light-adapted wolf spider eye in microvolts relative to the base line in the light vs. per cent changes in the ambient background illumination of 14,600 lux. The open circles represent the incremental DC responses measured one-half sec after presentation of the step stimuli, and the solid line is a curve fitted on theoretical grounds by a least squares method (DeVoe, 1967). Inset, the same data points and solid line as in the main part of the figure are drawn vs. the logarithm of the total relative illumination. $\Delta I/I$ is the fractional step change in ambient background illumination.

Likewise, the points are not well fitted by a power function. The theoretical curve provides a good fit to all points, however. Indeed, as will be evident in the following paper (DeVoe, 1967), the theoretical curve is anchored to and depends upon just those bottom points in the figure which the logarithmic and power functions cannot encompass.

BACKGROUND POTENTIALS The short-term DC responses of the light-adapted eye, although having the quasi-logarithmic dependence upon total illumination shown in the inset of Fig. 2, are different from the DC responses of initially dark-adapted eyes, which in general also have a quasi-logarithmic dependence on intensity of illumination (Hartline, 1928). This difference will be brought out more strongly shortly. The DC responses of the initially dark-adapted eye can, however, be compared with the background potentials of the light-adapted eye. These background potentials, as stated above, are the DC responses of the eye to the ambient background illuminations.

The background potential can be measured as the DC response to turning off the background illumination. In many arthropods, the response of the initially dark-adapted eye to the end of a long flash is simply the return from the DC response to the original base line in the dark. This return is usually monotonic, even when the response at "on" or the responses to superimposed flashes are not (Hartline, Wagner, and MacNichol, 1952). In addition, there may be a fast and a slow phase of return to base line (Bernhard, 1942). In Fig. 1, the response of the light-adapted spider eye to turning off the background illumination (the response to the -100% step) likewise has a monotonic time course towards a new potential, and this time course appears to be divided into a fast and a slow phase. In one experiment, such responses to -100% steps were compared with the DC responses of the initially dark-adapted eye to the onsets of the same background illuminations. The DC responses to turning on the background illuminations were the same, within experimental error, as the DC responses to turning them off minutes or hours later.

In other experiments, however, the responses to the onset and termination of light continued to change slowly over seconds so that determinations of DC responses could not be made. These slow changes were not due to drifts in the recording apparatus. Magni and Strata (1965) observed similar slow changes in retinal action potentials elicited from dark-adapted eyes of the wolf spider *Lycosa tarentula* and found that these slow changes could be reversibly abolished by ether, leaving only a DC response to long flashes. Moreover, they found that this remaining DC response and the "off" response superimposed upon the slowly changing response of the unanesthetized spider were of the same magnitude. If the same thing is true for the spiders used in the present study, then in experiments in which there are the slow

initial changes in response to the onset of background illumination itself, the DC or background potential elicited by this background illumination can still be measured as the change in DC response to a -100% step.

The background potentials measured in four experiments in which more than one background illumination was used are shown in Fig. 3. The experimental data are given by the symbols, and the solid curves have been drawn

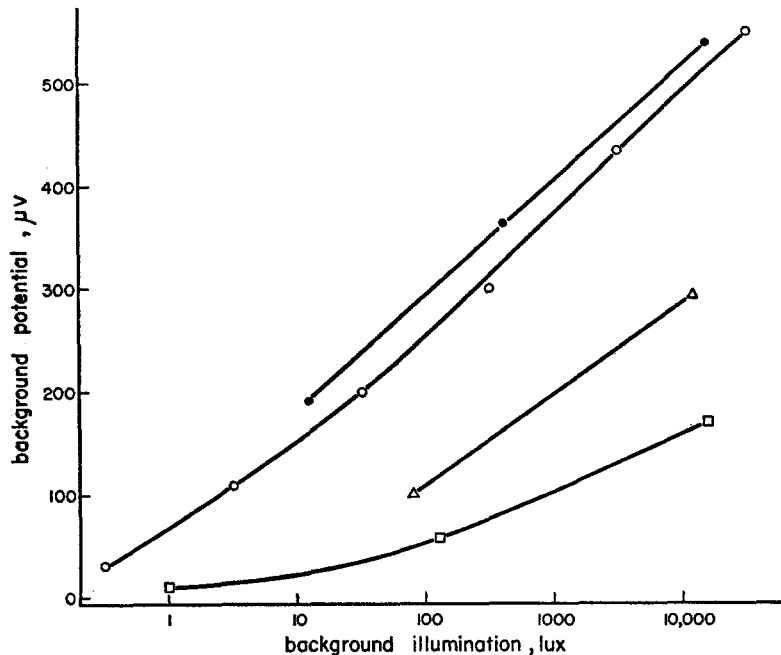


FIGURE 3. Background potentials relative to the base line in the dark, measured as the DC responses to turning off the background illuminations upon light-adapted wolf spider eyes. The next-to-top curve was obtained with light of wavelength $535\text{ m}\mu$ using fiber optics; all other curves were obtained with white light using projection optics. Each curve is from an experiment on a different spider. The solid lines were drawn by eye.

by eye. These curves are linear functions of the logarithms of high illuminations but not of low illuminations.

It can be seen that the amount of background potential actually elicited by any given background illumination varies from experiment to experiment, but these variations can presumably be ascribed to differences in stimulating or recording conditions. Thus, the next-to-top curve (open circles) was obtained using the fiber optic stimulator (see Methods) but is parallel to the topmost curve (closed circles), obtained with projection optics. Likewise, the bottom two curves have, roughly, scaled down ordinates from the top two curves, and can be taken to represent different preparation sensitivities.

In other words, the general progression of background potential with background illumination is nearly the same in all experiments.

DEPENDENCE OF SHORT-TERM DC RESPONSES ON AMBIENT BACKGROUND ILLUMINATION Reductions in background illuminations reduce not only background potentials, but also short-term DC responses to equivalent per cent step stimuli as well. This is to be seen in Fig. 4, where responses to positive and negative 80% steps at two different background illuminations are illustrated. These responses have been drawn with approximately equal peak

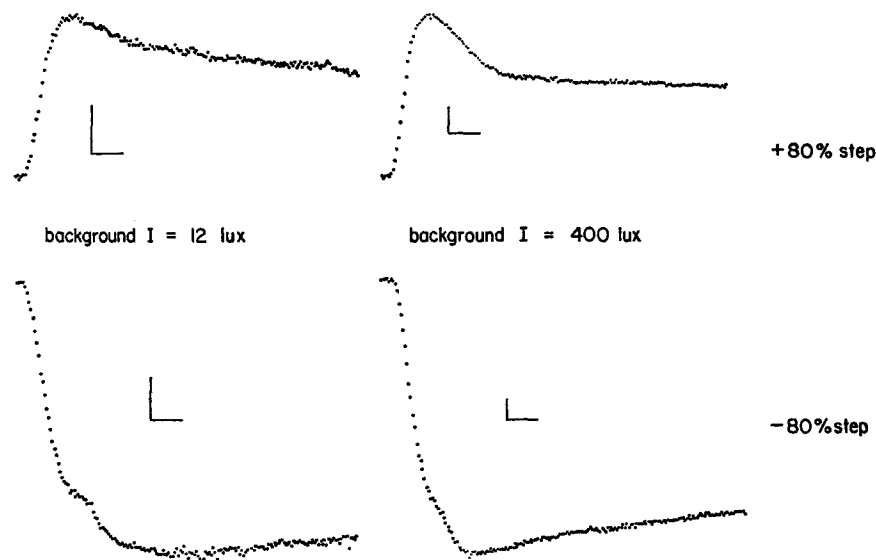


FIGURE 4. Averaged retinal action potentials recorded at two different background illuminations from a light-adapted wolf spider eye in response to positive and negative 80% step changes in illumination. Vertical calibration lines represent $20 \mu\text{v}$; horizontal calibration lines represent 50 msec. Sampling time per point was 3.136 msec.

amplitudes to emphasize that decreased light adaptation decreases both rise times and amount of overshoot. These points will be taken up again later in this paper. At the dimmer adapting backgrounds, the asymmetry between positive and negative step responses remains, however.

From the $20 \mu\text{v}$ vertical calibrations in Fig. 4, it can be seen that the same per cent step stimulus does not give the same number of microvolts of short term DC response at different background illuminations. The maximum negative DC step response which can be recorded is that to a -100% step, and as was shown in Fig. 3, this decreases with reductions in background illumination. Hence if the maximum negative DC step response (the background potential) decreases, so too must at least some other negative step

responses. In fact, *all* short-term DC responses change in proportion to the background potential, and this is true whether the changes in background potential are due to changes in illumination or merely to changes in recording conditions in different experiments at the same background illumination. This can be seen by plotting 100 times the ratios of short-term DC responses to background potentials (*per cent DC response*) vs. per cent change in background illumination. One such plot is given in Fig. 5, where the per cent

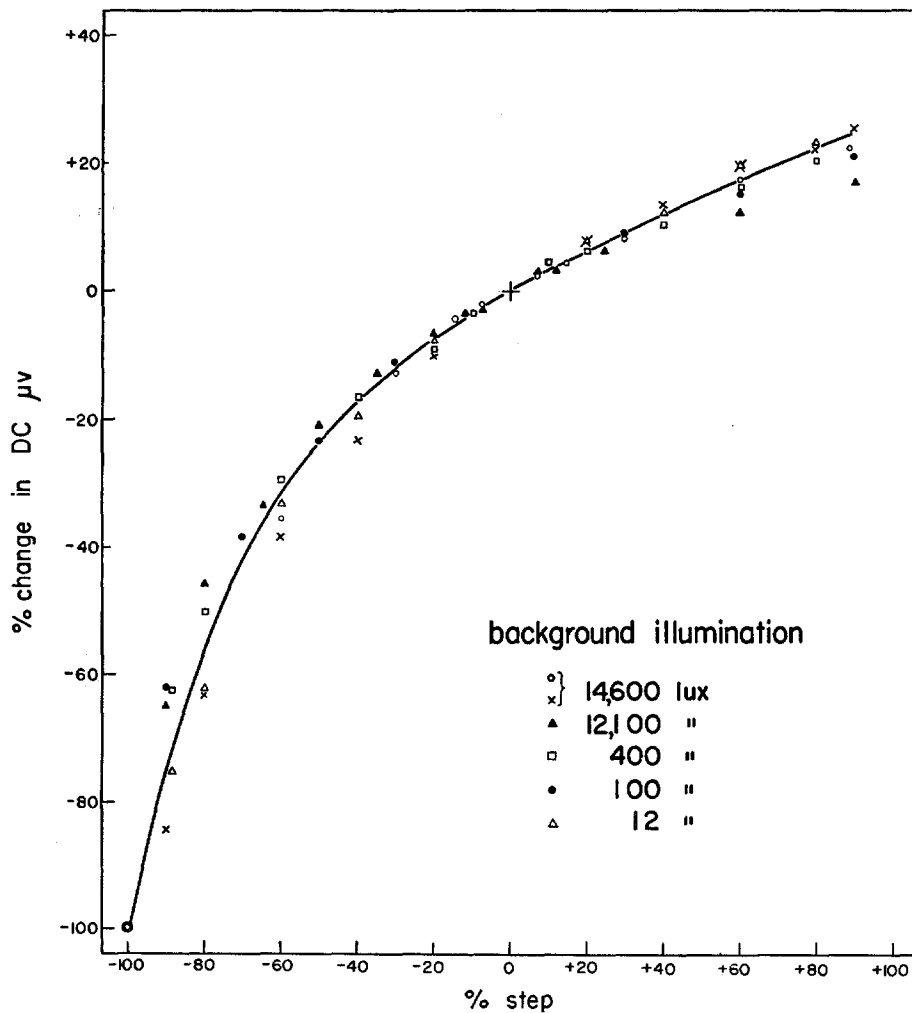


FIGURE 5. Per cent DC responses from light-adapted wolf spider eyes, defined as 100 times the incremental short-term DC responses to per cent step changes in illumination, given on the abscissa, divided by the background potentials, given by the short-term DC responses to -100% steps. The solid line is theoretical and was fitted to the points by a least squares method (DeVoe, 1967); it is formally equivalent to the DC voltage-current characteristic of a thermistor.

DC responses recorded in three experiments at five different background illuminations in the two different species all fall very nearly upon the same curve. As in Fig. 2, the solid line is a theoretical one fitted by a least squares method (DeVoe, 1967). There is some scatter in the data, particularly for negative step responses, in which it may reflect the difficulties in estimating the short term "dc" responses of waveforms which have creep superimposed upon them. Nonetheless, the reproducibility of per cent DC responses as functions of per cent step stimuli is good from experiment to experiment and from adaptation level to adaptation level.

The data in Fig. 5 extend at most over an incremental stimulus range of 19:1 and it is conceivable that over a larger stimulus range, the per cent DC responses recorded at different background illuminations might not be the same function of per cent step, as they appear to be in Fig. 5. To test this point, one experiment was performed with the dual channel stimulator using positive stimuli much larger than could be obtained from the glow modulator tube alone. The results were much the same as in Fig. 5. Within experimental error, a given per cent DC response was elicited by a given per cent step even when the step increased the background illumination as much as 1000-fold.

It is not possible at present to say whether these findings are applicable to the short-term responses of the light-adapted eyes of other arthropods, because the background potential has rarely been recorded in experiments with arthropod retinal action potentials. Even when it has been recorded (Kirschfeld, 1961), insufficient data have been given to permit determination of per cent DC responses. However, in the light-adapted fly's eye, Kirschfeld (1959) found that if a constant per cent incremental stimulus was presented, the (peak) response amplitude varied in proportion to the logarithm of the increment itself. This would follow from the results shown in Figs. 3 and 5 of this paper. The background potential V_o in the spider eye varies (over a range) in proportion to the logarithm of the background illumination I_o . A given stimulus change $\Delta I/I_o$ elicits a given response change $\Delta V/V_o$. Hence this ΔV must vary as the logarithm of this ΔI .

STEADY-STATE VS. SHORT-TERM DC RESPONSES In addition to the results in Fig. 5, another relation between the background potentials and the short-term DC responses is illustrated in Fig. 6. There, background potentials (open circles) and superimposed short term DC responses (filled circles) are plotted against the logarithm of the total background illuminations. It is clear that the background potentials are steady-state DC responses of the eye, since they were measured after many minutes or even hours of continuous illumination of the eye. The dot-dashed line drawn (by eye) through the background potentials thus defines the steady-state DC response of this eye as a function of the total background illumination. Since the short-term DC responses do

not lie upon this dot-dashed line, it is equally clear that they are not steady-state responses.

The differences between the dot-dashed line and the solid lines in Fig. 6 represent the amounts of further change in response which must occur before the eye becomes completely adapted to the changed background illumina-

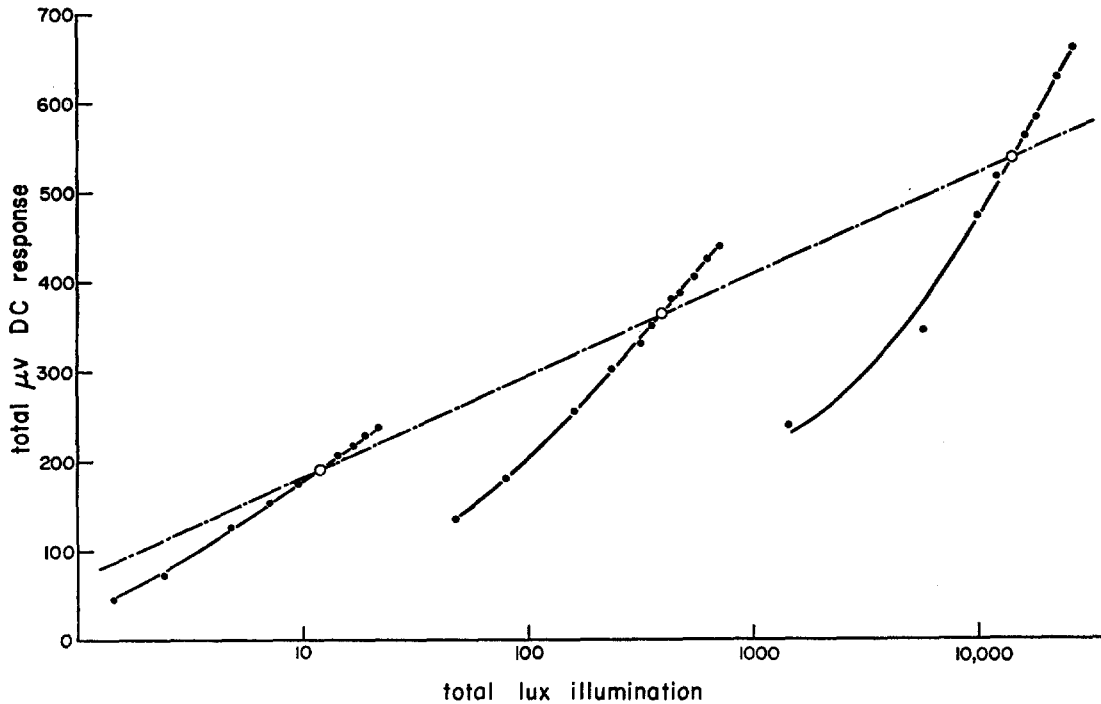


FIGURE 6. Short-term DC responses and background potentials on absolute coordinates. The filled circles represent short-term DC responses measured with respect to the open circles; the solid lines were drawn by eye. The open circles represent the background potentials measured as the DC responses to -100% steps; the dot-dashed line connecting these open circles was drawn by eye and was extended past the two end points only for purposes of clarity. The ordiates give the sum of incremental short-term DC responses and these background potentials. The abscissa gives the sum of ambient background illuminations and the step changes in these illuminations. The ambient background illuminations for the three curves were, left to right, 12, 400, and 14,600 lux. Results from one experiment.

tions. The beginnings of such changes were observed in Fig. 1 as creep. Creep is better illustrated on a slower time scale. In Fig. 7, creep in responses to positive and negative, 90% , 5 sec long flashes is shown. (The shapes of these responses during the first half-second are not strictly comparable to those in Fig. 1 because of slightly different recording conditions. In the experiment illustrated in Fig. 7, the indifferent electrode was on an unilluminated eye

shielded from stray light. In other experiments with the indifferent electrode on the carapace, creep has also been recorded on a long time scale and appeared similar to that in Fig. 7. These other experiments were not as fully analyzed, however.)

The responses in Fig. 7 do not appear to have reached the steady-state level by the end of 5 sec, and when they do has not been measured (for technical reasons). However, as shown in semilogarithmic plots in the insets, creep has an approximately exponential time course. The time constants are about $2\frac{1}{2}$ sec for the creep following the +90% step and about 3 sec for the creep following the -90% step. The difference between these time constants is probably not significant. Therefore, it may be estimated that in this experiment, it would have taken about 15 sec or so (four to five time constants) for the eye to completely adapt to the changed background illuminations and come to a new steady state.

One way to look at these long-term transients is in terms of changing sensitivity of the eye. For example, since only 10% of the original background illumination remains after a -90% step, it is to be expected that the eye will partially dark adapt to this new illumination. If the eye partially dark adapts, its sensitivity ought to increase. If the sensitivity increases, the potential elicited by the remaining background illumination likewise should increase. Thus the rise in potential seen during the prolonged -90% step response is just what would be expected if the sensitivity were simultaneously increasing. These increases in sensitivity may have something in common with fast, "neural" (i.e., nonphotochemical) dark adaptation (Dowling, 1963). Complete dark adaptation of the spider eye takes only about 2 min following termination of the background illumination used here (unpublished observations of the author). The origins of such fast dark adaptation remain unknown, however.

On the other hand, it is difficult to see why sensitivity changes to an increase in background illumination should take as long as sensitivity changes to a decrease in background illumination. As mentioned above, the steady-state DC response of the initially dark-adapted eye to light is reached in 1 or 2 sec at most (Magni and Strata, 1965). As Fig. 7 shows, the steady-state DC response of the initially light-adapted eye to an increase in illumination is not reached in 2 sec. Rather, the time course of creep after an increase in background illumination is about the same as after a decrease in background illumination. From this it may be supposed that creep in light-adapted eyes has a single origin. Likewise, it would appear that the process responsible for creep is either absent in dark-adapted eyes or is very much faster. Were this process not absent or faster, DC responses from initially dark-adapted eyes would not be reached in 2 sec.

One possible explanation for the slow or later changes in sensitivity which

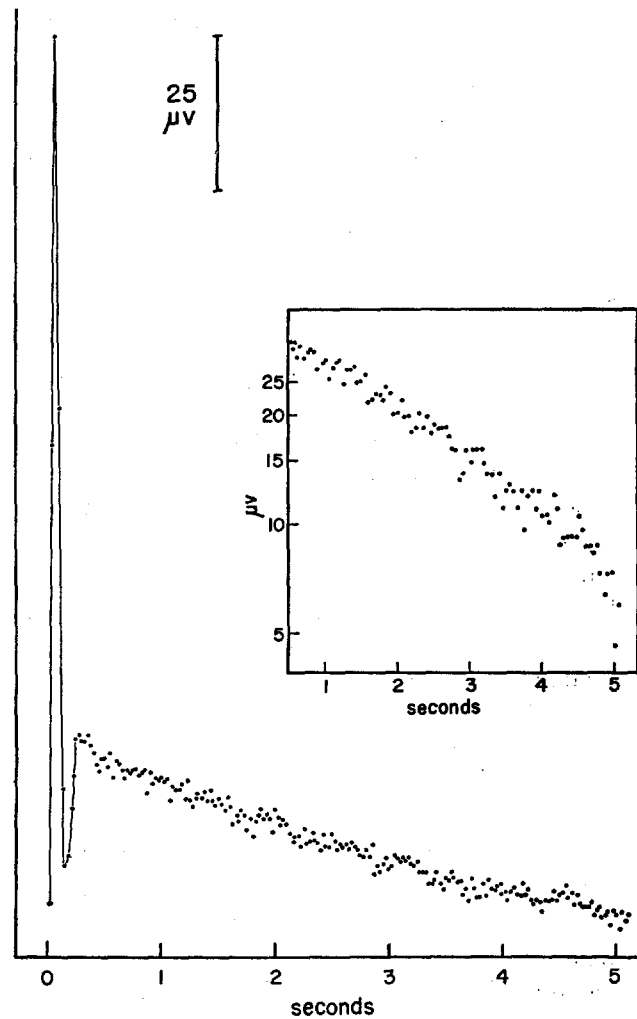
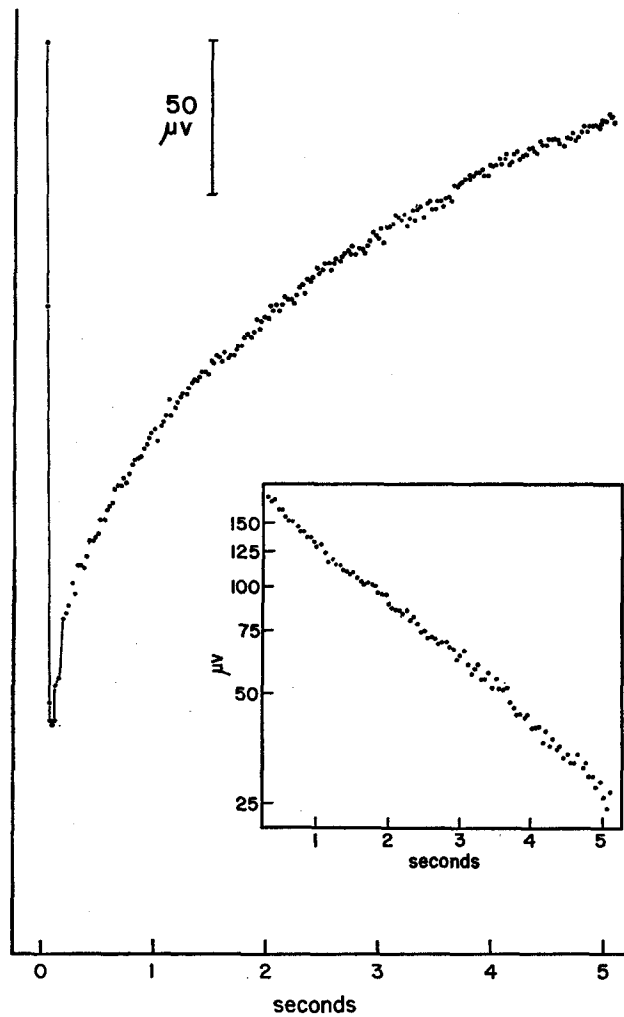


FIGURE 7. Long-term transient responses. Each response made up of points is the average of four retinal action potentials elicited by 5 sec long, 90% positive (left) and negative (right) step changes in the background illumination of 14,600 lux. The sampling time per point was 24.8 msec. Solid lines drawn by eye connect the first 9 or 10 points in each response to make evident these initial portions. Because of the slow sampling rate, the base line for each response is not shown. The base line for the +90% step response (left) lies about 15 μV below the first point, while the base line for the -90% step response (right) lies about 25 μV above the first point. Insets, the approximately exponential decays



during the last 4.5 sec of these responses towards estimated new background potentials (not measured in this experiment) are illustrated by these semilogarithmic plots. For the left-hand inset, the new background potential was estimated to be at the bottom of the graph and, for the right-hand inset, at the vertical position of the initial point drawn. Ordinates of both insets are the differences, on a log scale, between the recorded responses and the estimated new background potentials. The time constants of decay are, for the left-hand inset, about 3 sec, and for the right-hand inset, about 2.5 sec.

presumably underlie creep will be given in connection with the model in the following paper (DeVoe, 1967). Another explanation might possibly lie in movements of shielding pigments. In posterior median eyes of wolf spiders, these are in a position proximal to the tapetum in the dark and move to a position between the rhabdomes in the light. It takes 10-20 min for the pigment to move forward between the rhabdomes and 15-25 min for the pigment to retract to the dark-adapted position (Scheuring, 1914). These times are much too long to account for the creep illustrated in Fig. 7. On the other hand, they represent the time pigment movements take when the spider is moved into direct sunlight from darkness, or vice versa. It is not known how long such pigment movements would take when the moderate illuminations used in the present experiments were changed only $\pm 90\%$, but evidence from studies on pigment movements in insect compound eyes indicates that these movements might be considerably faster than those reported by Scheuring (1914). Bernhard and Ottoson (1964) have found that whereas there may be a lag in pigment movement upon turning off a bright adapting light upon the eye of the nocturnal moth, *Cerapteryx graminis*, this lag is "inappreciable" in pigment movements which follow extinction of a dim adapting light. Likewise, Demoll (1909) claimed that in certain forest dwelling butterflies, proximal pigment movements might take only 4-6 sec. Since pigment position in light-adapted eyes of Lepidoptera appears to bear a direct relation to log threshold (Bernhard and Ottoson, 1964), it is possible that similar pigment movements in wolf spider eyes might similarly affect sensitivity and, if fast enough, account for the creep illustrated in Fig. 7. At present nothing is known, however, about the relation between extent of pigment migration and sensitivity to light in wolf spider eyes.

Finally, others too have observed very slow changes in responses of light-adapted arthropod eyes. Thorson (1966) found decreases in incremental sensitivity at low frequencies (less than 0.1 cps) in isometric head-torque responses of locusts which were looking at small sinusoidal motions of a striped drum. The less the illumination, the less the low frequency sensitivity decrease. This is consistent with the data in Fig. 6, where the incremental sensitivity decrease on going from the short-term to the steady-state DC response is given by the ratios of the slopes of the dot-dashed and solid lines at their intersections. There, the less the original background illumination, the smaller the differences between steady-state and short-term responses and the less the ratio between the slopes of the lines. It was argued by Thorson that the fractional power law kinetics of the low frequency sensitivity decreases might be explained by a diffusion process somewhere in the locust visual system.

Similarly, Pinter (1966) found that the incremental sensitivity of light-adapted *Limulus* ommatidia also decreased below 1 cps of sinusoidal stimula-

tion. He found that this equivalent of creep could be described with a 3.6 sec time constant linear lead network, but no physiological basis for the network was advanced. More recently, however, Knight, Toyoda, and Dodge (1967) have asserted that the decrease due to light adaptation in size of quantal bumps from *Limulus* ommatidia (Adolph, 1964) can be made formally identical with the low frequency responses of Pinter's (1966) linear lead network.

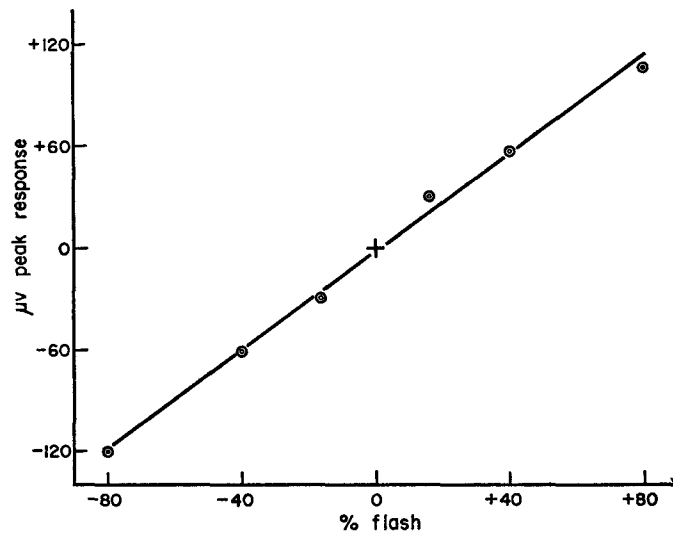


FIGURE 8. Peak amplitudes of responses of a light-adapted wolf spider eye to positive and negative 20 msec flashes whose intensities are given as per cents of the background illumination of 14,600 lux. The straight line was fitted by least squares.

II. *Short-Term Transient Responses*

DELAYED ONSET OF ASYMMETRIES IN STEP RESPONSES Although the short-term DC responses to large step stimuli show asymmetries, the responses to equally large flash stimuli do not. This is illustrated in Fig. 8, where there are shown peak amplitudes of responses to positive and negative 20 msec flashes. These peak amplitudes are proportional to the flash sizes, as indeed are any other amplitudes, for the responses upon which Fig. 8 is based were all versions of one another scaled up or down. Similar results were found previously (Kirschfeld, 1961; DeVoe, 1963). The linearity of response demonstrated in Fig. 8 can be taken to mean that asymmetries seen in short-term DC responses are not instantaneous, but are delayed.

Comparison of Figs. 2 and 8 shows that the asymmetries must have begun sometime after 20 msec and sometime before one-half sec. One way to find out when they did begin is to compare recorded responses to large positive

and negative steps with responses to small steps. Responses to steps which are as small as $\pm 8\%$ are linear responses (DeVoe, 1962). Hence, in these there are no asymmetries at all. To compare the linear step response to a small step with the nonlinear response to a large step, linear step responses are scaled up in the ratio of the two stimuli. Two such comparisons are shown in Fig. 9. The recorded response to a $+60\%$ step (solid line on the left) is superimposed upon the scaled-up response to a $+8\%$ step (open circles), and the recorded response to a -90% step (solid line on the right) is superimposed upon the scaled-up response to a -8% step. A similar comparison of recorded and scaled-up responses to flashes and steps from dark-adapted *Limulus* ommatidia has been made by Fuortes and Hodgkin (1964), although

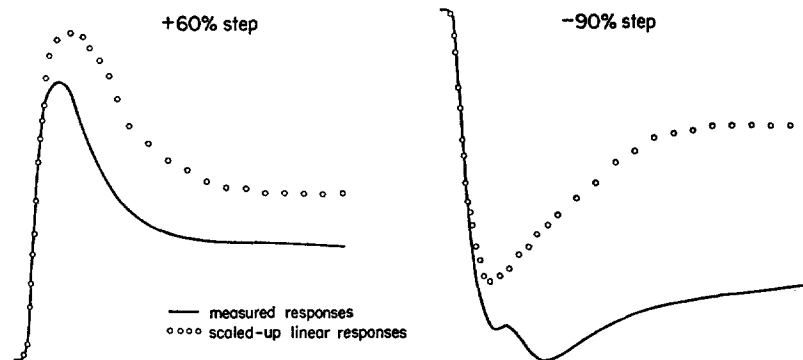


FIGURE 9. Comparisons of scaled-up linear step response and nonlinear step responses from a light-adapted wolf spider eye. The solid lines are averaged retinal action potentials recorded in response to the given sizes of step changes in the background illumination of 12,100 lux. The open circles on the left represent the averaged linear response to a $+8\%$ step scaled up $7\frac{1}{2}$ times; the open circles on the right represent the averaged linear response to a -8% step scaled up $11\frac{1}{4}$ times. The duration of each response is one-half sec.

the linear responses they scaled up were theoretical and not measured responses.

What is seen in Fig. 9 is that the initial portions of the recorded and scaled-up responses are the same, but that the later portions diverge from each other. This is why the peak amplitudes of flash responses in Fig. 8 were proportional to the flash sizes, for in terms of the results in Fig. 9 the stimuli were shorter than the time it took for the nonlinearities in response to be evident. Fig. 9 also helps to explain why all response latencies in Fig. 1 were the same, for the initial portions of all responses are appropriately scaled versions of one another and so must have the same latency.

The points at which recorded nonlinear responses and scaled-up linear responses diverge from each other depend upon the sizes of the responses, for if the responses are small enough they are linear and do not diverge from

each other at all. Some values for the points of divergence are given in Table I for the experiment illustrated in Fig. 9. These values are only approximate, since noise remaining in the averaged responses makes it difficult at times to decide just where recorded and scaled-up responses diverge. The trend in Table I is clear, however; the smaller the amplitude of response at which divergence occurs, the longer this divergence takes. It will be seen too that there is a large increase in time of divergence upon decreasing the step size from -65% to -50% or less. The reason for this is that for these smaller negative step responses, the point of divergencies is no longer upon the falling part of the response, as it is for the -90% step response in Fig. 9. Rather, the peak of the scaled-up -8% step response coincides in time and amplitude with the first peaks of the recorded nonlinear negative step responses. Divergence occurs in the notch between the two peaks. (These two peaks can be

TABLE I
POINTS OF DIVERGENCE OF MEASURED NONLINEAR STEP
RESPONSES AND SCALED-UP LINEAR STEP RESPONSES

Recorded nonlinear responses to positive steps were compared with scaled-up responses to $+8\%$ steps, while recorded responses to negative steps were compared with scaled-up responses to -8% steps. The points of divergence between recorded and scaled-up responses can be seen in Fig. 9 for two step amplitudes; points of divergence for responses to other amplitudes of steps were determined from similar plots.

Divergence point	Per cent step									
	+90	+60	+25	-20	-35	-50	-65	-80	-90	-100
Microvolts	103	88	47	-30	-63	-95	-103	-115	-128	-118
Milliseconds	33	42	74	92	100	95	39	37	37	32

clearly seen in the responses to -50 and -80% steps in Fig. 1.) Moreover, in all comparisons of nonlinear negative step responses with the scaled-up -8% linear step response, the time to peak in the scaled-up linear response coincided with the time to the first peak of the nonlinear responses, as for example is illustrated in Fig. 9, and with the inflection in the initial phase of the -100% step response. (The initial phase may be seen in the -100% step response illustrated in Fig. 1.) This might be interpreted to mean that negative step responses are the sums of two processes. One generates the waveform of the linear step response, and one adds on to this waveform, but only after a delay, thereby putting a notch into the composite response. On the other hand, notches do not appear in the positive step responses illustrated in this paper, but this may be only because such notches are too small to see. Notches do appear in responses to positive steps which are several orders of magnitude greater than the background illumination (unpublished observations of the author).

PEAK RESPONSES TO STEPS Except in the responses to turning off the background illumination, there is an incremental peak response which is greater than the short-term DC response to a step, whether this step is large or small, negative or positive. A single peak is present in the responses of wolf spider eyes to positive flashes which are longer than about 40 to 50 msec (Magni, Papi, Savely, and Tongiorgi, 1965). This is to say that the peak amplitude of response does not increase further when flashes are made longer than this. Responses to negative flashes behave differently, however. First of all, there may be two peaks in responses; for small negative stimuli, the first peak is usually the larger, whereas for large negative stimuli, the second peak may exceed the first. (Compare the responses to -50% and -90% steps in Fig. 1.) Second, it may take a longer negative than positive flash to elicit a peak response. For example, in one experiment, a positive, 50 msec, 80% flash was almost long enough to elicit the same peak response as did a 100 msec, 80% flash. However, both peaks in the response to -80% flashes were elicited only when the flashes were 100 msec long, and neither was elicited when the flashes were 50 msec long.

As was stated above in connection with Fig. 9, the peak amplitudes of positive or negative step responses may be smaller or larger, respectively, than the scaled-up linear step responses, but they may also coincide with the peak amplitudes of the scaled-up responses. In the experiment illustrated in Fig. 9, they coincide for responses to steps between about $+25\%$ to -50% . Since it can be seen from Fig. 9 that the ratios of peaks of scaled-up and nonlinear responses never differed by as much as did the ratios of short-term DC responses, asymmetries in peak responses ought to be less than for short-term DC responses and absent for sufficiently small steps. This is shown in Fig. 10. In order to include data from experiments at a number of different background illuminations, they have been plotted as 100 times the ratios of peak amplitudes to background potentials. For negative step responses, the larger of the two peak amplitudes was used. As was true for the per cent DC responses shown in Fig. 5, the per cent peak responses shown in Fig. 10 likewise appear to vary as one function of the per cent step stimulus. The solid line in Fig. 9 is a third order polynomial fitted to the data by least squares to show the course of the data; otherwise, it has no special significance. As predicted above, this solid line is a straighter, steeper curve than the one describing per cent DC responses (shown as the dotted line in Fig. 10).

The solid curve in Fig. 10 does tend to obscure the nearly linear relation between step size and per cent peak response noted above for the smaller steps. It is only in responses to these smaller steps that the peak times are nearly the same; for the rest, the peak times are not the same. The peaks in large positive step responses tend to come earlier, the second and larger peaks

in large negative step responses tend to come later. Such changes in peak times are presumably related to the time course of delayed asymmetries.

BACKGROUND ILLUMINATION AND AMOUNT OF OVERSHOOT From the frequency responses of human eyes (deLange, 1958; Kelly, 1961), *Limulus*

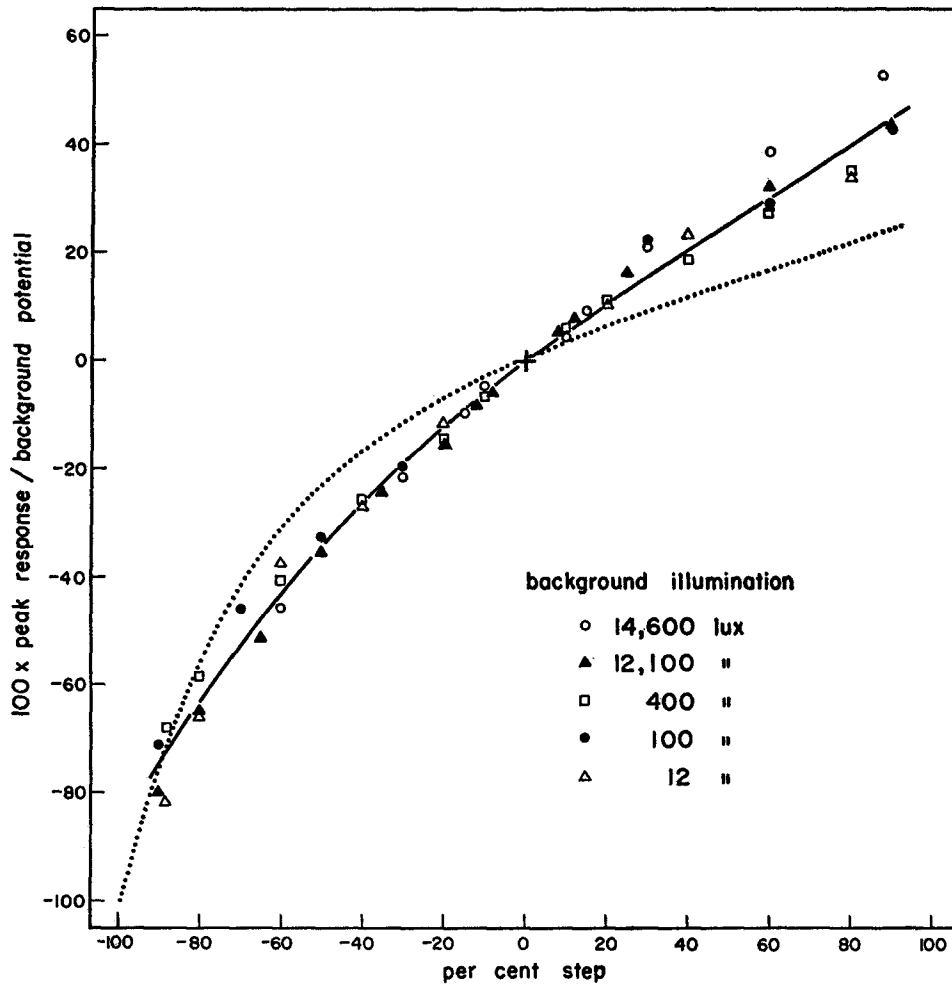


FIGURE 10. Per cent peak response to step changes in background illumination upon light-adapted wolf spider eyes. Per cent peak responses are defined as 100 times the amplitudes of the peaks in short-term step responses, measured from the base line in the light, divided by the background potentials, measured as the dc responses to -100% steps. Step stimulus sizes on the abscissa are given as per cents of the ambient background illuminations listed. The solid line is a third order polynomial fitted by least squares to the data points and is drawn solely to show the course of these points; otherwise, it has no theoretical significance. The dotted line represents, for comparison, per cent dc responses and is taken from Fig. 5.

ommatidia (Pinter, 1966), and wolf spider eyes (DeVoe, 1967), it appears that there is a decreasing amount of overshoot as the background illumination is decreased until, at the limit, which is dark adaptation, linear responses at least may possess no overshoot at all (Fuortes and Hodgkin, 1964; Pinter, 1966). In the light-adapted wolf spider eye, the progression from greater to lesser overshoot may be seen in step responses both when the stimulus varies

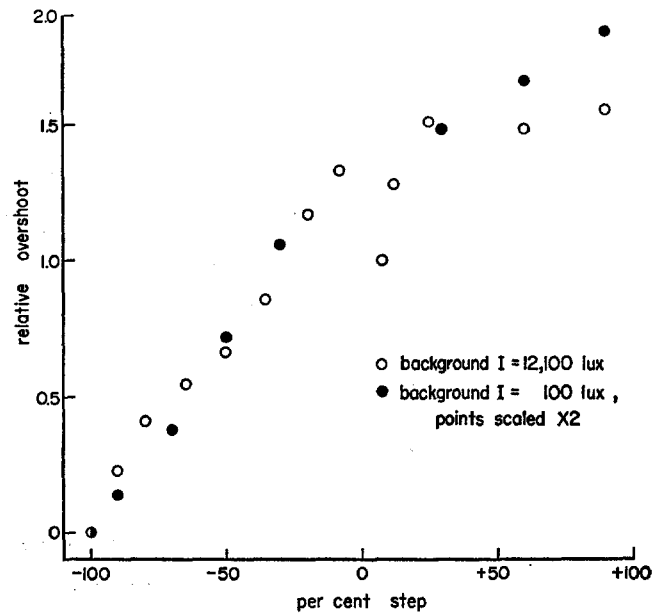


FIGURE 11. Relative overshoot in step responses of a light-adapted wolf spider eye. Overshoot in short-term responses is given by the quotient $(PK-DC)/DC$, where PK is the peak amplitude of response and DC is the short-term DC response, both being measured from the base line in the light. The amount of overshoot in the eye adapted to the background illumination of 12,100 lux (open circles) is given directly by the ordinate; the amount of overshoot in the eye adapted to the background illumination of 100 lux (filled circles) has been scaled up 2 times. In a similar experiment, the overshoot in an eye adapted to 400 lux had to be scaled 1.5 times to match the overshoot at 14,600 lux, while at a background illumination of 12 lux, the overshoot had to be scaled 2.5 times. In the responses to -100% steps, there was no overshoot. The sizes of the step stimuli are given on the abscissa as per cents of the ambient background illuminations.

from large positive to large negative step changes in ambient background illumination as well as when the ambient background illumination itself is decreased. These progressions are observable in the step responses which are illustrated in Figs. 1 and 4. On the other hand, the amount of overshoot which is observed in step responses recorded at any one background illumination seems to bear an approximately constant ratio to the overshoot in the step responses recorded at another background illumination when responses

to the same step stimulus size are compared. This may be seen in Fig. 11. The open circles represent the measured overshoot in responses recorded at a background illumination of 12,100 lux, while the filled circles represent the overshoot, multiplied two times, in the responses recorded at a background illumination of 100 lux. Similar results have been obtained in other experiments (see caption to Fig. 11).

There is a good deal of scatter in calculated overshoots, and this makes it hard to judge how well the overshoots found at different background illuminations may be matched up by the scaling procedure illustrated in Fig. 11. In addition, on the basis of the results in Figs. 5 and 10, no differences in amounts of overshoot with changes in background illumination would be predicted at

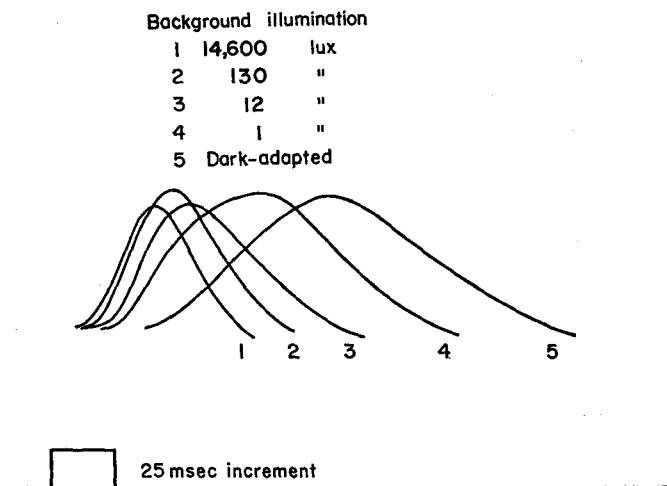


FIGURE 12. Responses to 25 msec flashes recorded at different states of adaptation. The flash intensity at each indicated state of adaptation is (1) 1650 lux, (2) 42 lux, (3) 16 lux, (4) 10 lux, and (5) 1.8 lux. The largest response (2) is 29 μ v. Results are from three successive experiments upon one animal.

all. According to those figures, at any given per cent step stimulus, there ought to be but one per cent DC response, but one per cent peak response, and hence but one amount of overshoot (which is the ratio $(PK-DC)/DC$; see caption to Fig. 11). Presumably the explanation why the variations of overshoot with background illumination are not evident from Figs 5 and 10 lies in the scatter of points.

SPEED OF RESPONSE, SENSITIVITY, AND DEGREE OF ADAPTATION Two other response features change when background illumination is changed. One of these, of course, is sensitivity. The other, as noted above in connection with Fig. 4, is speed of response. The relationship of this speed of response to sensitivity with changes in background illumination upon the wolf spider eye may be seen in Fig. 12. There, small (less than 30 μ v), linear responses

to 25 msec flashes have been selected to be of approximately equal amplitude so as to bring out the differences in latencies and rise times. The more light-adapted the eye, the more rapid this rise time and the sooner the peak of the response occurs, but, of course, the less sensitive is the eye. What Fuortes and Hodgkin (1964) found to occur upon light-adapting *Limulus* ommatidia also occurs here, however; the sensitivity changes far more than does the speed of response. Thus upon going from the dark-adapted eye to one exposed to a background illumination of 6600 lux, an approximately thousandfold larger flash must be used to get the same amplitude of response, but the peak time of this response has decreased only $2\frac{1}{2}$ times. Similarly, upon changing the background illumination from 52 lux to 6600 lux, the sensitivity decreased about 44 times but the peak times differed only by a factor of 1.2 times.

One inference may be drawn from the results in Fig. 12. Over the range of 14,600 to 12 lux background illumination, the differences in latency are small compared to the latencies at 1 lux and in the dark-adapted eye. This may explain why, in Figs. 1 and 4, there is so little change in step response latency. (These latencies are 11 and 16 msec at 12,100 and 12 lux background illuminations, respectively.) On the other hand, the decay times from the peaks of the responses in Fig. 4 appear to be quite different at 12 lux from those in the responses recorded at 400 lux background illumination. This could mean that the processes responsible for the changes in latency are different from the processes responsible for the time course of delayed asymmetries. The schema to be presented next and the results of the following paper support this inference.

DISCUSSION

The following discussion will be limited to short-term step responses only; that is, to responses lasting up to one-half sec following a step stimulus. The long duration creep of the eye's responses towards steady-state values was considered in detail earlier and will not be taken up again here.

The four features of the step responses of the light-adapted wolf spider eye to be explained are the following:

1. There is a response latency; this latency does not change much between background illuminations of from 14,000 to 12 lux.
2. Initial portions of responses to steps are in proportion to the step sizes.
3. All step responses (except those to -100% steps), linear and nonlinear, positive and negative, have overshoot. This overshoot increases monotonically from zero in -100% step responses to its largest value in the largest positive step responses.
4. There are asymmetries in short-term DC responses, except those to small steps.

These features may be explained by a schema based on delayed asym-

metries in response. In its simplest (and incomplete) form, the schema may be illustrated by Fig. 13. The curved line there represents asymmetries in short-term DC responses and is taken from the experiment illustrated in Fig. 1. The straight line connects the bottom point of the curve, the base line potential in the dark, with the background potential V_o , the base line at the

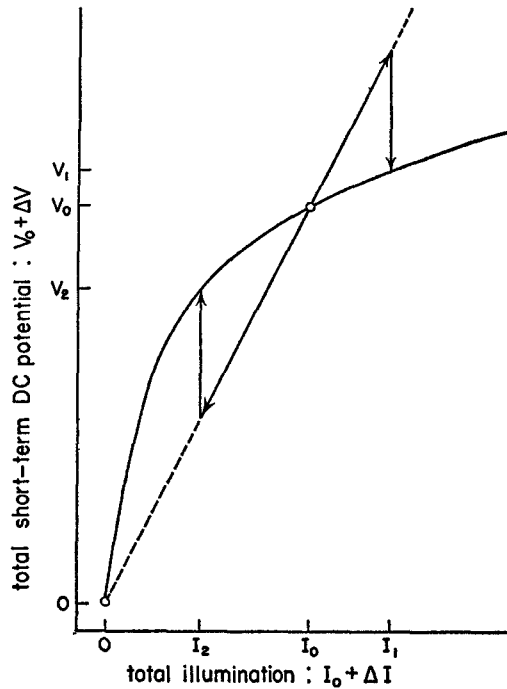


FIGURE 13. Schematic representation of short-term DC response plotted on absolute coordinates. The open circle at the bottom represents the potential in the dark, while the open circle in the middle represents the background potential V_o (the base line in the light) elicited by the ambient background illumination I_o . The slope of the chord joining these two circles gives the initial absolute sensitivity of the eye. The curve is similar to that in Fig. 2. Were there to be no immediate change in absolute sensitivity upon changing I_o to I_1 or I_2 , the response would first follow the arrows on the chord. Then, as the sensitivity of the eye changed, the response would move along the vertical arrows to V_1 or V_2 , respectively. See text for further descriptions.

background illumination I_o . The slope of this straight line is the absolute sensitivity V_o/I_o at the particular background illumination I_o .

Suppose now for the moment that the eye's response could change instantaneously upon an instantaneous change in background illumination, but that the eye's sensitivity could not, as can be inferred from Figs. 8 and 9. Then the immediate response of the eye to a positive or negative change in background illumination would be given by a point on the straight line in

Fig. 13, as shown by the solid arrows drawn upon this straight line. If now the sensitivity decreased (or increased) with time, the responses would decrease (or increase) from the initial peaks (which for all stimuli would be in proportion to the stimuli) down (or up) to the curved lines, as displayed in Fig. 13 by the vertical arrows. In other words, the cause of delays in asymmetries would be delayed changes in sensitivity.

The waveforms of response which could result from this delayed asymmetries schema are illustrated in Fig. 14 A. A monotonic time course for development of delayed asymmetries has been assumed. From the way these schematic responses are obtained, it is obvious that they will have overshoot. Even very small, incremental changes in I_o will result in response overshoot.

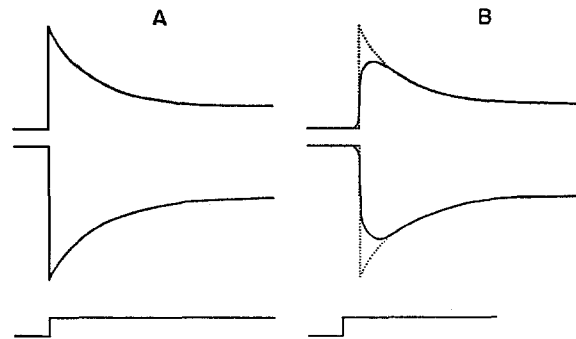


FIGURE 14. Schematic responses to positive and negative step stimuli, based on the schema in Fig. 13. The bottom line shows the timing of the step stimuli. A, the peak values for the top and bottom responses were obtained from the tips of the arrows along the chord in Fig. 13 and correspond to the instantaneous responses to stimuli I_1 and I_2 , respectively. The DC values of the top and bottom responses correspond to V_1 and V_2 , respectively. The monotonic decays from the peaks are hypothetical and were drawn by eye. B, the same responses as in A have been shifted to the right with respect to the stimuli to correspond to the latent period, and the peaks of the responses have been rounded.

For such stimuli, the responses will be linear, because the very small portions of the asymmetry curve around the point (V_o , I_o) in Fig. 13 can be considered to be straight. The schema is thus consistent with the overshoot observed in both linear and nonlinear responses of light-adapted eyes.

The schema is also consistent with the observed dependence of overshoot upon step size and sign. In Fig. 15, the solid line gives the overshoot predicted from Fig. 13 alone. For comparison, the points in Fig. 11 are superimposed. The right-hand ordinate gives the scale for these points. The satisfactory correspondence between the points and the curve when they are thus scaled to match each other may be taken to mean that overshoot due to delayed asymmetries can indeed provide an underlying basis for the variations in overshoot measured.

Although the schema in Fig. 13 is consistent with the observed overshoots, it is, as was stated above, incomplete. The recorded responses (Fig. 1) do not look precisely like those in Fig. 14 A. The recorded responses have a latent period, their peaks do not rise as abruptly as those shown, and the peak amplitudes are not linear functions of step sizes. However, the latent period can be added to the schema by simply delaying the beginning of the response, perhaps giving it an S-shaped rise as well. Likewise, the smooth peaks in response could be obtained from the schema by supposing that some-

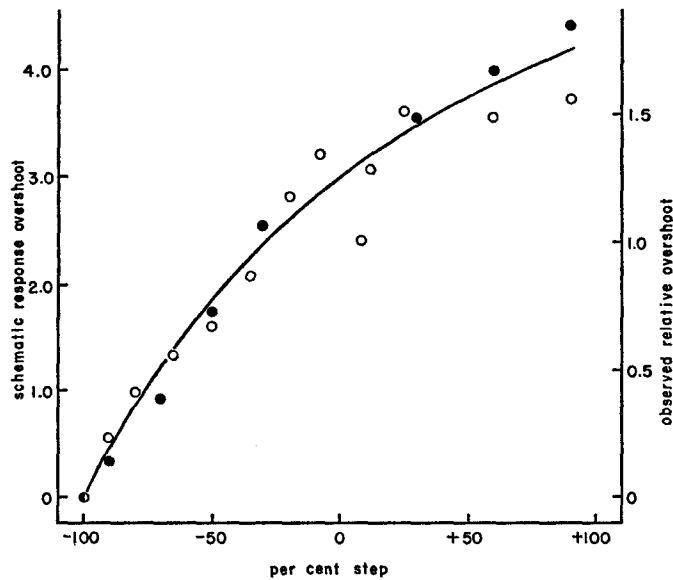


FIGURE 15. Schematic and measured overshoots in positive and negative step responses. The solid line was obtained from the schema in Fig. 13; its values are given on the left-hand ordinate. The open and filled circles are the data points from Fig. 11; their scale is given on the right-hand ordinate. As in Fig. 11, overshoot is defined as $\frac{(PK-DC)}{DC}$, where PK = peak incremental amplitude and DC = short-term incremental DC amplitude. For the schematic overshoots, the peak and DC amplitudes look like those in Fig. 14 A.

thing like the membrane capacity in the receptor cells limits the rate of rise and fall of the responses. The resulting smoothing might result in the peak responses falling at differing times upon the development of asymmetries as in Fig. 14 B. Further speculations along these lines can be better made by considering an actual quantitative model, and this will be done in the following paper (DeVoe, 1967).

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