

TEMPORAL INFORMATION PROCESSING IN CONES: EFFECTS OF LIGHT ADAPTATION ON TEMPORAL SUMMATION AND MODULATION

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Abstract—We have studied the temporal information processing of turtle cones in steady states of light adaptation using intracellular recording techniques. We measured the linear range incremental sensitivity of cones as a function of the stimulus duration. Linear range incremental sensitivity is a function of the background intensity. It is also proportional to the duration of short duration stimuli but is independent of duration for long duration stimuli. The plot of log sensitivity versus log stimulus duration displays two straight line asymptotes; a slope of one for short durations and a slope of zero for long durations. These asymptotes intersect at a time, the critical duration, which decreases with increasing background intensity. Linear systems theory was used to predict these results in addition to the interdependence of critical duration, response kinetics, and sensitivity for any state of adaptation. We have also calculated cone sensitivity as a function of sinusoidal frequency for a variety of background intensities. Correlations between these results and psychophysical studies suggest that the limits on temporal summation established by the cones appear not to be substantially altered by the rest of the retina.

Photoreceptors Cones Light adaptation Intracellular retinal recordings Temporal summation
Bloch's law

INTRODUCTION

Two of the main approaches used to study psychophysical and physiological temporal information processing by the visual system are time domain analysis using flashed stimuli and frequency domain analysis using sinusoidally modulated intensities. The most thoroughly studied time domain approach, the temporal summation relationship, describes visual thresholds as a function of stimulus duration. The early psychophysical work of Bloch (1885) demonstrated that for brief duration stimuli, visual thresholds were determined by the number of quanta in the stimulus (given by the product of the stimulus intensity and its duration). For these brief stimuli, the effects of each quanta are summed by the visual system and lead to threshold detection, a result termed temporal summation. For longer duration stimuli, Graham and Kemp (1938) determined that visual thresholds were a function only of intensity, and were independent of duration. If visual sensitivities (defined as the reciprocal of the threshold intensities) are logarithmically plotted as a function of the log of the stimulus duration, these regions of behavior approach two straight line asymptotes. For short durations, the asymptote has a slope of one, indicating complete temporal summation, while the asymptotic slope for long durations is zero, indicating zero temporal summation. The intersection of the

two asymptotes occurs for a duration called the critical duration (Roufs, 1972) which decreases with light adaptation (Graham and Kemp, 1938; Roufs, 1972). Light adaptation also produces an overall reduction in visual system sensitivity.

Early physiological studies of temporal summation in the electroretinogram (ERG) have indicated that much of the temporal summation relationship observed psychophysically may have origins in the photoreceptors (Hartline, 1928; Wulff *et al.*, 1955; Alpern and Faris, 1956; Johnson and Bartlett, 1956; Cone, 1964). A recent study (Hood and Grover, 1974) used aspartate perfusion to isolate photoreceptor activity in the frog ERG. Based on response amplitude matching in the dark and in one light adapted state, their results suggested that the photoreceptors may represent the limiting element in temporal summation. They also found that the critical duration decreased with light adaptation. Granda (1978) has studied temporal summation in the turtle using behavioral techniques. His observations in the dark and one light adapted state showed a dependence of threshold on pulse duration which was very similar to that measured psychophysically in humans, including the shortening of critical duration with background intensity. These results can be used to make correlations between psychophysics and physiology.

deLange (1952) used a frequency domain approach to study human psychophysical detection of sinusoidal stimuli of different temporal frequencies and

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was able to show that the threshold region of vision is linear and time-invariant. The relationship between psychophysical sensitivity (the reciprocal of the amplitude of the sinusoidal modulation at threshold) and sinusoidal frequency has been referred to as the temporal modulation relationship, deLange characteristic, or transfer function; in this paper it will be referred as the temporal modulation relationship. The psychophysical temporal modulation relationship shows a lowpass behavior for the dark adapted state, and an increasing bandpass nature for increasing background illumination (deLange, 1952; Kelly, 1961; Roufs, 1972). These studies have also indicated that visual sensitivity decreases with increasing background intensity. However, the desensitization observed using low frequency sinusoids is greater than that observed using high frequency sinusoids where the data points for different adaptation states superpose closely (Kelly, 1961).

Early physiological studies of temporal modulation include response matching in the spider photoreceptor (DeVoe, 1964), spike counting in cat ganglion cells (Hughes and Maffei, 1966), and analysis of the late receptor potential (primarily due to cones) in the cat retina (Maffei and Poppele, 1967). Pasino and Marchiafava (1976) used intracellular techniques in rods and cones of the salamander and found that the temporal modulation relationship was lowpass. Graf (1973) used behavioral responses to study temporal modulation in the turtle and pigeon, which can be used for correlating psychophysical and physiological data. All of these studies were limited to a single state of adaptation, generally dark adapted.

We report here the effects of steady state light adaptation on temporal information processing in the cone photoreceptor. Intracellular recording techniques were used to record small amplitude, linear range responses (Baylor and Hodgkin, 1973) from red cone photoreceptors in the turtle. Predictions of time and frequency domain behavior can be made for these responses using linear systems theory and these predictions have been tested experimentally.

METHODS

Standard intracellular recording techniques (Baylor and Hodgkin, 1973; Normann and Perlman, 1979a) have been used to obtain cone photoresponses in *Pseudemys scripta elegans*. The photostimulator was a narrow beam, high intensity light emitting diode (LED) which was filtered with a 633 nm interference filter to allow for exact quantal flux determinations. In addition this filter served to isolate the red cone system and helped eliminate coupling effects from green cones which may cause possible nonlinearities (Normann *et al.*, 1984).

The stimulus, centered over the impaled cone, was a circle of 320 μm diameter, which fully illuminated the cone's entire receptive field. These small area stimuli were used to minimize horizontal cell re-

sponses, which may lead to nonlinearities through negative feedback onto the cone (Baylor *et al.*, 1971). The background illumination was 2600 μm in diameter and was filtered with a 650 nm interference filter. The cone hyperpolarized in the presence of backgrounds but reached a steady state within 1–3 min (Normann and Perlman, 1979a) at which time sensitivity measurements were begun. All impalements were made on the dorsal side of the retina at least 1000 μm away from the visual streak to minimize variations in cone size (Ives *et al.*, 1983).

Averaging techniques were used to improve the signal to noise ratio in these small responses, which were generally less than 1 mV in amplitude. Only cones with maximum hyperpolarizations of 12 mV or greater have been included in this report. To ensure the responses used for analysis were in the linear range of the cone, the homogeneity, or scaling, aspect of linearity was tested during the experiment. This test consisted of summing from 5 to 10 digitized responses, reducing the stimulus intensity by 1/2 with a 0.3 log unit neutral density filter, and subtracting twice as many responses from the previous sum. If no net response resulted from this operation (indistinguishable from the baseline noise), both responses were in the cone's "linear" range, and the neutral density filter was removed as more responses were accumulated (usually an additional 5–10) to enhance the signal to noise ratio of the recording. When impulse responses were being recorded, a higher number of responses (usually >40) were accumulated, since these responses were used extensively in subsequent analysis.

Linear range incremental sensitivities of these recorded responses were calculated by dividing the response's peak amplitude by the intensity of the stimulus used to evoke the response [$r(t)_{\text{max}}/I$]. These sensitivities allow us the freedom to perform the temporal summation and modulation studies without requiring us to match response amplitudes, as has been done in the nonlinear response ranges by Hood with ERG's (1974) or DeVoe (1964) with spider photoreceptor responses. This is an important feature of our work since the linear range of cone responses is extremely noisy, and signal averaging techniques must be used. Matching responses would be very difficult, if not impossible to the accuracy that we can achieve with linear sensitivities.

RESULTS

(a) Theoretical

Although most of the dynamic range of the cone is a highly nonlinear function of intensity, it has been demonstrated that small cone responses (with amplitudes less than 1–2 mV) in the dark adapted turtle retina are linear and time-invariant (Baylor and Hodgkin, 1973). Based on this notion, we have made theoretical predictions of the dependence of these responses on stimulus duration using some basic

assumptions on the nature of the cone's impulse response. With the assumption that the dark adapted cone impulse response is monophasic, finite in area, and contains no singularities, we have shown in the Appendix that cone sensitivity based on peak amplitude (defined as response amplitude/stimulus intensity) must exhibit the temporal summation relationship, with complete summation for short durations and zero summation for long durations. We have also shown that critical duration (the intersection of the short and long duration asymptotes) is equivalent to the integration time of the cone, defined as the integral of the impulse response divided by its peak amplitude (Baylor and Hodgkin, 1973). If linearity and time-invariance also hold for the light adapted states as well, we can make similar predictions for the light adapted temporal summation relationship. Our assumptions on the light adapted impulse response must be modified, however, for it is known that the light adapted cone response becomes biphasic (Baylor and Hodgkin, 1974; Normann and Anderton, 1983). For impulse responses of this shape, we have shown that the temporal summation relationship must still occur. Here the critical duration will be equivalent to the peak integration time, defined as the integral of the initial hyperpolarizing lobe divided by its maximum amplitude (as opposed to the integral of the entire response). Peak integration time can be used to describe both light and dark adapted impulse responses since the peak integration time and integration time are equivalent for the monophasic dark adapted impulse response. We will consequently use the term peak integration time for any state of light adaptation.

We have also considered a sensitivity measurement based on the parameter of response area (as opposed to peak response amplitude), but we have shown in the Appendix that this will result in complete temporal summation for all durations.

(b) *Experimental*

In theory, one should be able to compute the response of a linear, time-invariant system to any stimulus by convolving the stimulus with the system's impulse response. To test the concept of linearity and time-invariance of small amplitude cone responses, we have convolved the cone's impulse response with pulses of various durations and compared these results with actual responses. These comparisons are shown in Fig. 1 where responses to pulses of from 1.2 to 578 msec duration were recorded for three states of adaptation (background intensities listed in legend). As a result of temporal summation, it was necessary to reduce the intensities of the stimuli as the durations were increased in order to maintain the responses within the linear range.

Although we cannot deliver an "impulse" to record the impulse response of a cone, we can approximate the impulse with a short duration pulse. If the kinetics of the responses to two brief but widely different

duration pulses are indistinguishable, these responses will both be excellent approximations to the impulse response. The response to the shortest stimulus (top response in each column of Fig. 1) was compared to the response of an approximately 10 times longer duration pulse stimulus (second response in each column) to ensure it was in fact the impulse response. By using a variety of short duration pulses (not all of which are shown in Fig. 1), we have determined that the maximum duration which will still evoke an impulse response varies from 10 to 20 msec, depending on the state of light adaptation. The impulse response at each state of adaptation was then smoothed and baseline noise was set to zero as shown in the smooth responses superposed on these impulse responses. The smooth impulse responses were then convolved with the stimuli used to generate the actual responses for each state. The results of the convolutions are shown as the smooth curves superposed on the remaining responses. The close agreement between the convolved and measured responses provides strong evidence that linearity and time invariance applies to this range of cone responses in both the dark and light adapted states.

We have used the data in Fig. 1 to determine the linear range incremental sensitivity for each stimulus duration by dividing the incremental peak amplitude of the response by the intensity of the stimulus. Figure 2 plots log sensitivity vs log duration of the stimulus pulse for the dark adapted (curve A) and two light adapted states (curves B and C). Data plotted in this format have a short duration asymptote (dashed) with a slope of one, a transition region of partial summation and a zero slope asymptote (also dashed) for the longer durations. Thus the temporal summation relationship is manifest in the cone for both the dark and light adapted states. In addition, as the background illumination is increased the critical duration decreases from 145 to 35 msec while the overall sensitivity decreases by several log units. The smooth curves in Fig. 2 show the predicted temporal summation relationship determined by convolving the impulse response for each state of adaptation with a variety of stimulus durations.

In the dark adapted state, the critical duration was 145 msec while the peak integration time measured from the impulse response was 142 msec. For the intermediate state of light adaptation, the critical duration was 60 msec and the peak integration time was 56 msec, while for the strongest background the critical duration was 35 msec and the peak integration time was 34 msec. As predicted from linear systems theory, this equivalence between the critical duration and peak integration time further strengthens the notion of linearity and time-invariance for these small amplitude responses.

The results shown in Figs 1 and 2 are typical of results seen in 14 other cones studied in two states of adaptation. The data are summarized in Fig. 3 and Table 1. Since the critical duration of each cone

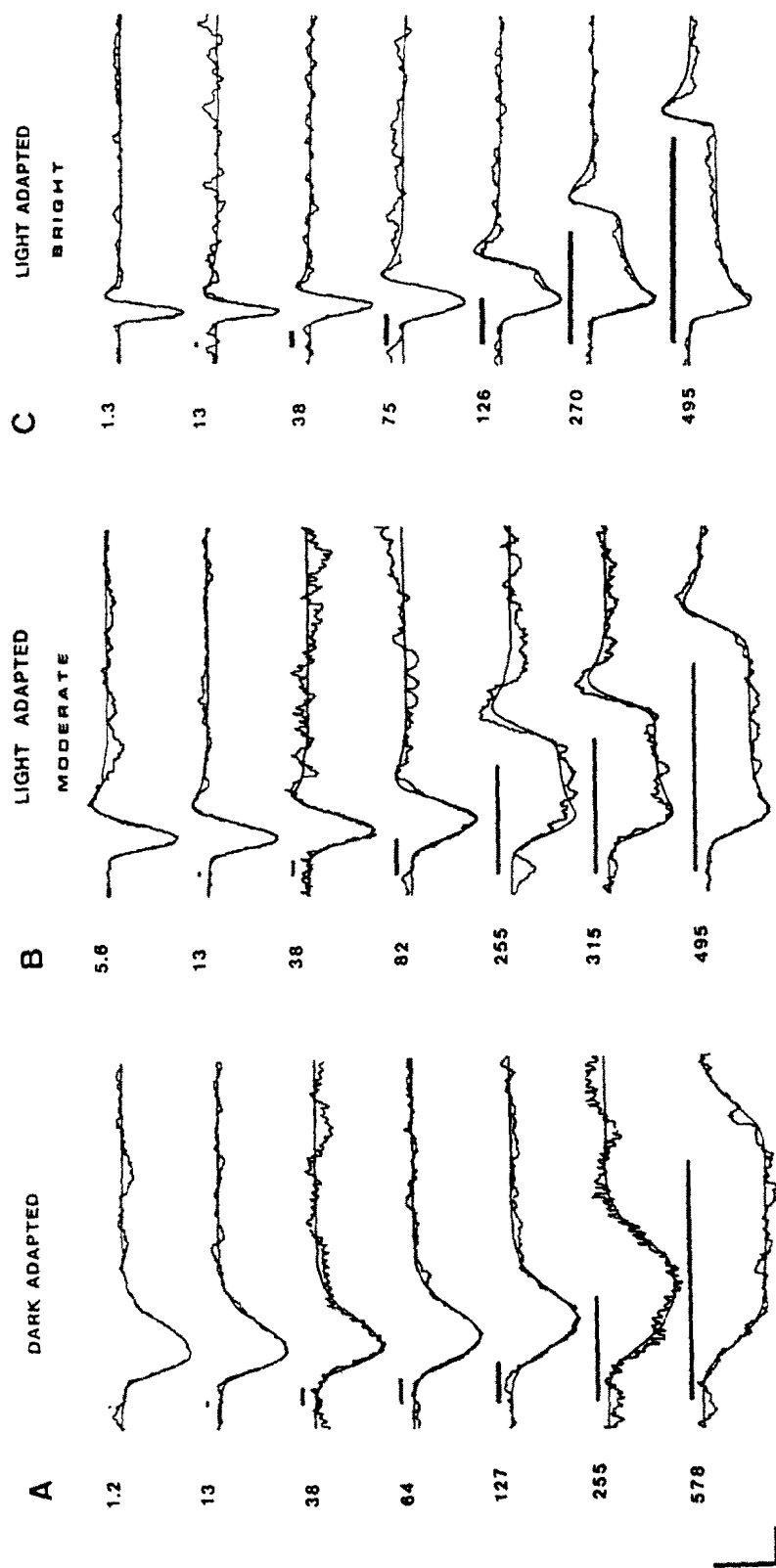


Fig. 1. Measured and convolved responses. Responses to varying duration rectangular pulse stimuli are shown for states of adaptation resulting from the following background intensities: (A) = dark adapted, (B) = 6.12×10^4 Q(650 nm)/sec/ μm^2 , (C) = 6.76×10^5 Q(650 nm)/sec/ μm^2 . Smooth responses, computed by convolution of the stimulus with the impulse response, are superposed over the measured responses. Scale bars in lower left corner are 0.5 mV and 100 msec, while the stimulus durations are listed to the left of the response and shown as the bars over each response.

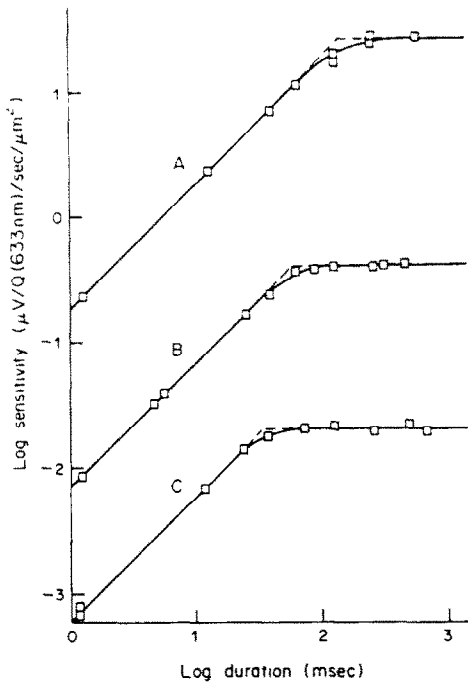


Fig. 2. Temporal summation relationship. Sensitivities determined from the responses in Fig. 1 (plus additional responses not shown) are plotted in the temporal summation format (log sensitivity versus log stimulus duration). As in Fig. 1, background intensities are: (A) = dark adapted, (B) = 6.12×10^4 Q(650 nm)/sec/ μm^2 , and (C) = 6.76×10^5 Q(650 nm)/sec/ μm^2 .

varied, each data set has been shifted horizontally to the mean critical duration for all 14 cones at each adapted state. Further, since the sensitivity of each cone also varied, each data set was shifted vertically

to the mean sensitivity of the zero summation asymptote for each state. The mean dark adapted critical duration was 152 msec while the mean peak integration time was 148 msec. Other means and their standard deviations are listed in Table 1.

These results show that the critical duration can be determined from a single response, the impulse response, by measuring its peak integration time. By recording impulse responses in numerous states of adaptation, the entire temporal summation relationship can be described for each state from the kinetics and sensitivity of the impulse response. If the details of the transition region are neglected, we can characterize the temporal summation relationship for any state of adaptation with just two parameters, the cone's sensitivity and the peak integration time of the impulse response. To investigate critical duration as a function of background intensity in greater detail, we have recorded impulse responses at nine different background intensities in one cell (eight of which are shown in Fig. 4) and at four different background intensities in another. For these two cones, the critical durations were calculated and the values are plotted vs log background intensity in Fig. 5. The critical duration decreases monotonically with increasing background illumination as a result of the faster kinetics exhibited in the impulse responses. A smooth curve has been drawn through the data for cell 2, and has been shifted vertically to fit the data of cell 1. In addition, the same smooth curve has been drawn through human psychophysical critical durations (Roufs, 1972; observer R.K.). In this figure we have converted our background illumination into the units of trolands.

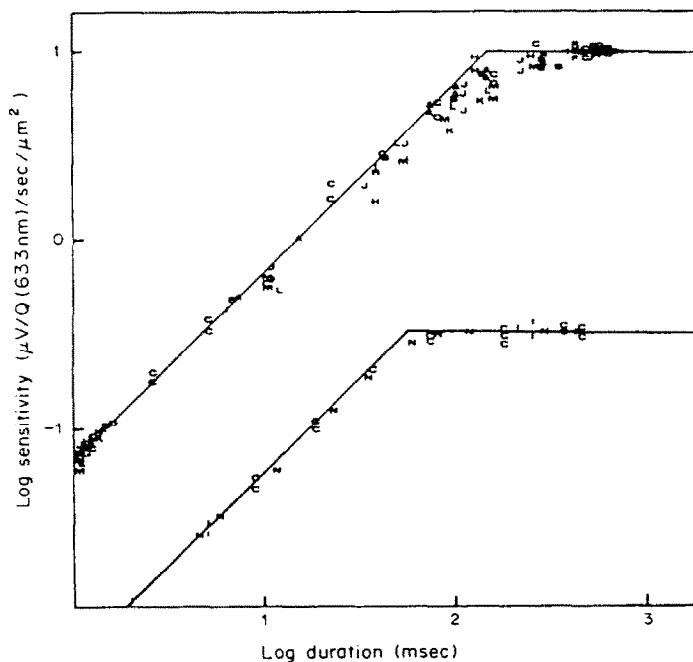


Fig. 3. Data summary of temporal summation relationship. Data from 15 cells in two states of adaptation [upper curve = DA, lower curve = 6.12×10^4 Q(650 nm)/sec/ μm^2] are shown in the temporal summation format, where each cell is designated as a letter A–Z.

Table 1. Data summary

Parameter	Units	DA mean	DA SD	LA mean	LA SD
T_c	msec	152	20.2	57	15.0
T_i	msec	148	14.8	50	6.9
T_c/T_i	—	1.04	0.14	1.13	0.25
S	$\mu V/Q \text{ sec } \mu m^2$	13.0	10.4	0.33	0.12
V_{max}	mV	15.2	3.2	17.3	2.5

T_c = critical duration.

T_i = peak integration time.

S = sensitivity.

DA = dark adapted.

LA = light adapted ($6.1 \times 10^4 Q(650 \text{ nm})/\text{sec}/\mu m^2$).

SD = standard deviation.

Just as the temporal summation relationship can accurately be described solely from impulse responses, we can predict the temporal modulation relationship by taking Fourier transforms of the impulse responses. The temporal modulation relationships (log sensitivity versus log frequency) shown in Fig. 6 for nine states of adaptation were obtained from the smooth responses in Fig. 4. As predicted from theoretical considerations, the dark adapted curve is strictly lowpass while increasing background illumination results in a more bandpass relationship. Similar results were seen in two other cells studied. As indicated by the close superposition of the high frequency regions of these curves (with the possible exceptions of the two highest background

intensities, curves H and I), background mediated cone desensitizations as would be revealed by responses to high frequency sinusoids do not appear to be as extensive as the desensitizations which would be revealed by low frequency sinusoids. The asymptotic value of these high frequency sensitivities falls off with a slope of approximately -6 . The lower frequencies, however, do show pronounced desensitization with light adaptation, best indicated by the zero frequency sensitivities. Because the desensitizing effects of backgrounds are a function of the frequencies used to measure the effects, Fig. 6 also shows an apparent increase in temporal resolution of the light adapted cone. One way to quantify this is to measure cutoff frequencies (the frequency at which

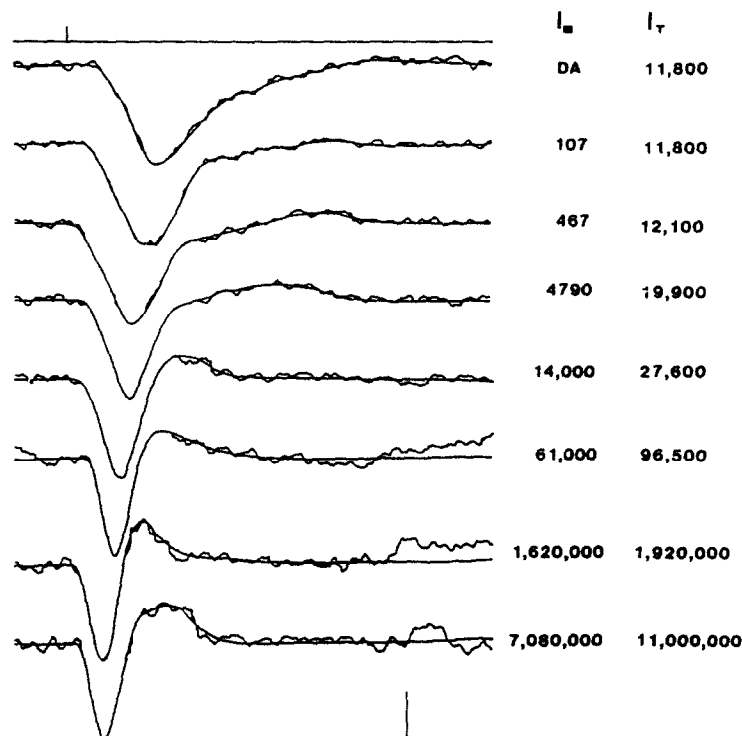


Fig. 4. Impulse responses as a function of background intensity. These eight responses were recorded from a red cone studied under ten backgrounds (only eight are shown for clarity). The stimulus of 1.3 msec is shown at the top of the figure while the scale bars at the bottom of the figure indicate 0.25 mV and 100 msec. The numbers to the right of each response are the background intensities and test flash intensities in units of $Q(650 \text{ nm})/\text{sec}/\mu m^2$ and $Q(633 \text{ nm})/\text{sec}/\mu m^2$, respectively. The smooth responses superposed on the measured responses were used to compute the peak integration times and temporal modulation curves for each state.

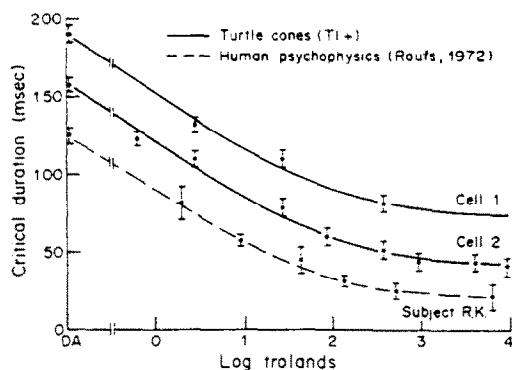


Fig. 5. Critical duration vs background illumination. Critical durations calculated as the peak integration time from the impulse responses of two red cones are plotted against the log of the background intensity. The critical durations from subject R.K. of Roufs (1972) study are also shown, while our background intensities have been converted to photopic trolands according to Wyszecki and Stiles (Chap. 2, 1967). The same curve drawn through cell 2 is fitted to the data of cell 1 and the psychophysical observer by vertical shifting.

the sensitivity is reduced by 1/2 of its maximum value, Roufs, 1972). For this cone, the cutoff frequency increased from 2.9 to 12 Hz as the background was increased.

DISCUSSION

(a) The effect of critical duration on sensitivity

The overall desensitization by backgrounds can be described by the psychophysical Weber-Fechner relationship which has been found to occur in the cone

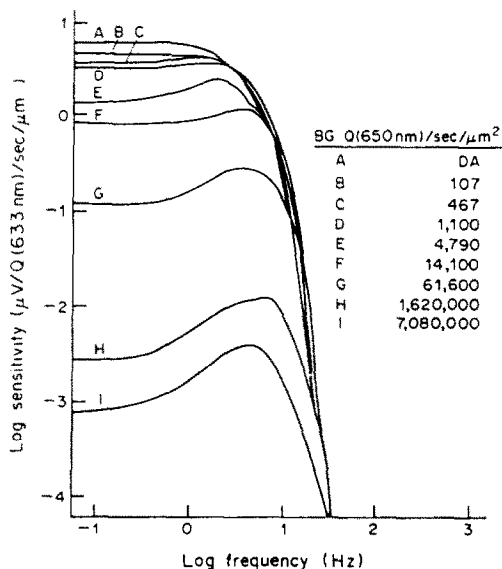


Fig. 6. Temporal modulation relationship. The smooth impulse responses illustrated in Fig. 4 (plus one impulse response not shown) were used to compute the temporal modulation curves for nine states of adaptation (backgrounds listed in inset). The impulse responses were scaled by their individual sensitivities prior to computing the Fourier transform.

(Normann and Werblin, 1974; Normann and Anderton, 1983). This desensitization is reflected in the temporal summation relationship as a downward vertical displacement in the curves of Figs 2 and 3. However, due to the changes in critical duration which accompany these changes in background intensity, the regions of the curves for short and long stimulus durations do not shift equally. A given change in background illumination will result in a greater shift in cone sensitivity for long duration pulses than for short duration pulses (if critical duration were to remain constant, these shifts would be equal). Clearly, when studying desensitization by backgrounds it is necessary to consider any changes which might occur in the critical duration.

If we reduce the temporal summation relationship of Figs 2 and 3 to their asymptotic behavior, the sensitivity for any duration stimulus can be determined solely from the critical duration and step sensitivity. For pulses longer than the critical duration, the sensitivity is simply the step sensitivity. Sensitivities for stimulus durations shorter than the critical duration can be determined from the equation, $\log S_d = \log S_s - \log (T_c/d)$, where S_d , S_s , T_c and d are the short duration sensitivity, step sensitivity, critical duration, and stimulus duration, respectively. Conversely, the step sensitivities can be calculated from short duration sensitivities using the equation, $\log S_s = \log S_d + \log (T_c/d)$.

(b) Correlations to other physiological and psychophysical studies

As discussed by Brindley (1970), the most general and "difficult to doubt" hypothesis which can be used to link physiological and psychophysical observations is that indistinguishable signals sent from the sense organs to the brain result in indistinguishable perceptions. Thus, one would expect that perceptual threshold detections will be associated with photoresponses within the cone's linear range.

The two most important temporal summation studies which can be used for correlations with our results are the behavioral studies in the turtle, *Pseudemys* (Granda, 1978) and the summation studies of *Pseudemys* ganglion cells (Maxwell, Granda and Fulbrook, personal communication). Granda observed the temporal summation relationship in his turtle behavioral data, with regions of complete, partial and zero temporal summation for various colored stimuli in the dark adapted state. Granda measured the dark adapted critical duration with red stimuli to be between 125 and 150 msec, similar to the mean critical duration of 150 msec we have measured. The ganglion cell study also demonstrated the temporal summation relationship, with critical durations for red on-center ganglion cells to be between 90 and 140 msec (their data is considerably noisy and their preparations might have been slightly light adapted), also similar to our data. Both of these studies support the notion that in the turtle, the behaviorally ob-

served temporal summation relationship may reflect mechanisms found in the cone. This suggests that the observed summation relationship in humans may also be a manifestation of cone temporal integration.

We can also compare the dependence of critical duration on background intensity. For Granda's (1978) turtle behavioral study we only have the dark and one (unspecified) light adapted state, but the light adapted critical duration was reduced by approximately one half. To quantitatively correlate critical duration as a function of background we must resort to interspecies data. The most complete descriptions are from human psychophysics and the data for observer R.K. (Roufs, 1972) has been shown in Fig. 5. The shape of this relationship is typical for other observers in his study and has been found in other studies (Graham and Kemp, 1938; Keller, 1941; and Herrick, 1956). The strong similarity between this psychophysical data and our cone data further supports the notion that the cone may be the main locus underlying the psychophysical results.

In correlating our temporal modulation data to turtle psychophysics, we have used the behavioral study of Graf (1973) in the turtle, *Chrysemys picta picta*. Unfortunately, only data from two turtles were presented, with six data points for each curve. The peak frequency occurred at roughly 8 Hz in these curves which were fairly bandpass in nature due to the state of adaptation. The sparsity of data points does not permit an estimation of the slope of the high frequency asymptote. An intracellular study (Pasino and Marchiafava, 1976) of temporal modulation in salamander rods and cones gave similar results to our dark adapted data. For the cone, the curves were strictly lowpass for small spot stimuli and displayed a high frequency asymptote of -6 and a cutoff frequency of 2.4 Hz. A recent study of the temporal modulation relationship in *Pseudemys* horizontal cells for several states of adaptation showed that these curves become more bandpass in nature with increasing background illumination (Tranchina, Gordon and Shapley, 1984). In addition, the high frequency data superposed on an asymptote with a slope of approximately -6 , as in our data, with the zero frequency sensitivities approximately displaying the Weber-Fechner law. The agreement between our cone data and these horizontal cell observations (Tranchina *et al.*, 1984) suggests that the cone to horizontal cell synapse does not produce a significant increase in temporal integration beyond that which occurs in the cones themselves (Normann and Perlman, 1979b; Schnapf and Copenhagen, 1982).

The correlations to the human psychophysical modulation data include the general shape characteristics, the high frequency asymptote of approximately -6 , and the approximate Weber-Fechner relationship for step sensitivities or peak frequency sensitivities. One further correlation that can be made is the product of the critical duration and the cutoff frequency, which was originally determined by

Roufs (1972) to be constant. This product for our cone data was also constant, at a value of 0.48, while the average for all of Roufs' observers was 0.49. These correlations suggest the possibility that the human cone is primarily responsible for the threshold temporal modulation relationship.

We conclude that in the turtle, temporal information processing and the associated effects of light adaptation are primarily determined by the cone. This suggests that the human cone may also play a large role in the observed effects of temporal information processing. It thus appears for threshold detections, the rest of the visual system acts to pass the cone signals as efficiently as possible to the perceptual centers.

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APPENDIX

Proofs

In these proofs, we assume that for any state of adaptation, the cone can be represented as a linear, time-invariant system (at least in its linear range). Further, linear range, incremental sensitivity is defined as the peak of the response divided by the intensity of the stimulus. The peak is measured as the incremental deviation from the baseline voltage. In the interest of simplification, these proofs are based on positive going responses and positive peak responses (although the cone photoresponse is a hyperpolarization).

Temporal Summation

Proof of monophasic temporal summation

This proof is based on the general assumption that the impulse response is causal, monophasic, with finite area and contains no singularities. If $h(t)$ is the impulse response of a system, the response $r(t)$ to stimulus $s(t)$ is

$$r(t) = \int_{-\infty}^{\infty} h(\tau) s(t - \tau) d\tau.$$

Short duration asymptote:

For the short duration asymptote the stimulus can be described as

$$s(t) = I[u(t) - u(t - D)]$$

where I is the intensity of a pulse with duration D , and $u(t)$ is a unit step function. Consequently

$$r(t) = I \int_{t-D}^t h(\tau) d\tau.$$

For durations, D , which are much shorter than changes in the impulse response $h(t)$

$$h(t - D) = h(t)$$

and the response can be described by

$$r(t) = Ih(t) \int_{t-D}^t d\tau = Ih(t)D$$

$$r(t)_{\max} = Ih(t)_{\max} D \quad (1)$$

where $r(t)_{\max}$ and $h(t)_{\max}$ refer to the peaks of the response and impulse response, respectively. The sensitivity will vary as a function of the duration for this asymptote in the following manner.

$$S = r(t)_{\max}/I = h(t)_{\max} D$$

$$\log S = \log h(t)_{\max} + \log D.$$

Since $h(t)_{\max}$ is a constant

$$\log S = \log D + \text{constant}.$$

Thus the log of sensitivity will display an asymptotic slope of one for short durations.

Long duration asymptote:

For long durations, consider a step stimulus $s(t) = Iu(t)$

$$r(t) = \int_{-\infty}^{\infty} h(\tau) Iu(t - \tau) d\tau = I \int_0^t h(\tau) d\tau. \quad (2)$$

Since $h(t)$ is monophasic with finite area

$$r(t)_{\max} = I \int_0^{\infty} h(\tau) d\tau. \quad (3)$$

The sensitivity as a function of duration for this asymptote will be

$$S = r(t)_{\max}/I = \int_0^{\infty} h(\tau) d\tau$$

$$\log S = \log \left[\int_0^{\infty} h(\tau) d\tau \right] = \text{constant}$$

exhibiting a slope of zero in the temporal summation format.

Critical duration:

The critical duration, T_c , will occur at a time when the sensitivities will be equivalent for both asymptotic behaviors. Equating (1) and (3)

$$\text{short duration } r(t)_{\max} = \text{long duration } r(t)_{\max}$$

$$Ih(t)_{\max} D = I \int_0^{\infty} h(\tau) d\tau$$

$$Ih(t)_{\max} T_c = I \int_0^{\infty} h(\tau) d\tau$$

$$T_c = \int_0^{\infty} h(\tau) d\tau / h(t)_{\max}.$$

Thus for a monophasic impulse response, the critical duration, T_c , will be equivalent to the integral of the impulse response divided by its peak amplitude (which is the integration time).

Proof of biphasic temporal summation

Consider a biphasic impulse response with an initial positive phase, followed by a single negative phase. The zero crossing between these two phases can be denoted as t_c . It is evident from equation (1) that for short durations the peak response is still given by

$$r(t)_{\max} = Ih(t)_{\max} D$$

and will result in a slope of one for sensitivity plotted logarithmically against the log of the duration, similar to the monophasic impulse response. For long durations,

$$r(t) = I \int_0^t h(\tau) d\tau.$$

However

$$\int_0^{t_c} h(\tau) d\tau > 0 \quad \text{and} \quad \int_{t_c}^{\infty} h(\tau) d\tau < 0.$$

Therefore

$$r(t)_{\max} = I \int_0^{t_c} h(\tau) d\tau. \quad (4)$$

To find the critical duration, T_c , we set the two peak responses equal

short duration $r(t)_{\max}$ = long duration $r(t)_{\max}$

$$Ih(t)_{\max} D = I \int_0^{t_c} h(\tau) d\tau$$

$$Ih(t)_{\max} T_c = I \int_0^{t_c} h(\tau) d\tau$$

$$T_c = \int_0^{t_c} h(\tau) d\tau / h(t)_{\max} = T_i +$$

which is the peak integration time as defined in the text.

Temporal summation for the parameter of area

As stated in the text, the temporal summation relationship for the parameter of area will exhibit a slope of one on a log-log plot. This can be alternatively stated as the response area will be constant for constant quanta stimuli, regardless of the duration. The areas of the response $r(t)$, stimulus $s(t)$, and impulse response $h(t)$ will be the zero frequency terms of their Fourier transforms, where multiplication is equivalent to convolution in the time domain

$$r(t) = h(t) * s(t)$$

$$R(\omega) = H(\omega)S(\omega)$$

and for the areas of these responses

$$R(0) = H(0)S(0)$$

Since $H(0)$ is constant for the steady state, the area of the response will be constant for stimuli of constant quanta $S(0)$, and a slope of one will occur for all durations in the temporal summation relationship for the parameter of area.