

ADAPTATION, BRIGHTNESS PERCEPTION AND THEIR
CORRELATION WITH PHOTORECEPTOR RESPONSES

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ABSTRACT

In psychophysics, the effects of light backgrounds and photopigment bleaching can be equated in a variety of situations involving sensitivity, flicker, and the subjective perception of brightness. We have investigated such possible equivalences at the single unit level through intracellular recordings from vertebrate rods. At a given level of background or bleaching adaptation, vertebrate rods respond with characteristic waveforms to brief flashes of light of increasing intensity. The peak responses can be plotted vs. flash intensity to give a response curve in each state of adaptation. Two consequences of light adaptation are a shift to higher light intensities and a compression of the response curve. We have been able to establish equivalences in single units between bleaching and backgrounds in terms of threshold elevation and response compression. Moreover, we have found that such equivalent (background, bleaching) pairs have similar response curves. But these response curves are direct measures of stimulus flash intensity. Based on the close parallels between the psychophysical and the neurophysiological equivalences of bleaching and backgrounds, we therefore propose that brightness perception is mediated by the peak responses of photoreceptors. It is not often that behavioral observations can be traced back to the neuronal machinery and the latter suggest psychophysical tests which can further clarify brightness equivalence relations. This approach is discussed in the light of our results.

Introduction:

A major aspiration of neuroscience is to relate psychophysical and behavioral observations to the underlying neuronal machinery. Correlations with complex functions, such as memory, are difficult to come by. We are better off with adaptation and brightness perception which are considered in this paper.

Light adaptation is a fascinating phenomenon. We can see the light from a faint star in the night sky and we can see

objects some 10^{12} times as bright in full sunlight. When the ambient light level changes it takes time to adapt to it and the bigger the change, the longer it takes. At any given level of background light our visual system only operates over some three orders of magnitude of light intensity. This is the operating range of the photoreceptors, as well as of the neurons at the various stages of the visual pathway. The neuronal input-output ranges can be modulated somewhat through biochemical changes and through the interplay of excitation and inhibition. But they cannot be shifted over the enormous intensity range over which light adaptation operates. Moreover, as a general principle, there cannot be responses at any one stage of a serial information system to responses outside the range of a preceding stage. We must therefore conclude, as the signal is transmitted from photoreceptors to ganglion cells, LGN and cortex, that the capability for shifting the operating range over the adaptive range must reside in the photoreceptors (Leibovic, 1971, Dowling & Ripps, 1972).

Hecht (1937) had proposed a chemical basis for visual transduction and adaptation. In agreement with his ideas, the state of photopigment bleaching does affect adaptation, but not in the way he had envisaged. Nor is adaptation determined solely by the bleached pigment. It also depends on a biochemical cycle mediating transduction and affecting membrane conductance in a series of steps involving Ca^{++} and cGMP which have yet to be fully elucidated.

Crawford (1947) showed how background light and pigment bleaching both affect the state of adaptation, and he introduced

the notion of an equivalence between backgrounds and bleaching in terms of threshold elevation. This equivalence has been amply confirmed in a variety of different experimental situations (Rushton 1962). In particular, it has been extended to the perception of brightness: Barlow and Sparrock (1964) have shown that the apparent brightness of a bleached retinal area is the same as that of the background which elevates the visual threshold by the same amount.

If light adaptation is indeed mediated by photoreceptors, how do their responses correlate with the psychophysical findings and what measure of these responses can be assigned to brightness perception? We have addressed these questions by recording the intracellular responses of the rods in the isolated retina of *Bufo marinus*. In particular we have investigated the effects of backgrounds and bleaching on thresholds and response amplitude. The stimulus was a 100 msec flash. A background of a given intensity could be projected onto the retina, and bleaching of the photopigment could be accomplished by exposing the retina to a timed, intense background light. The materials and methods have been described fully elsewhere (Leibovic, Dowling, Kim: in preparation).

Clearly there are species differences and we know that, for example, the rods of rats adapt differently from those of frogs. Nevertheless, there are similarities among all vertebrate rods and, as we shall see, the results on *Bufo* bear quite a resemblance to psychophysical data.

Bufo Rod Responses:

A typical series of intracellularly recorded rod responses to flashes of increasing intensity is shown in Figure 1. At high

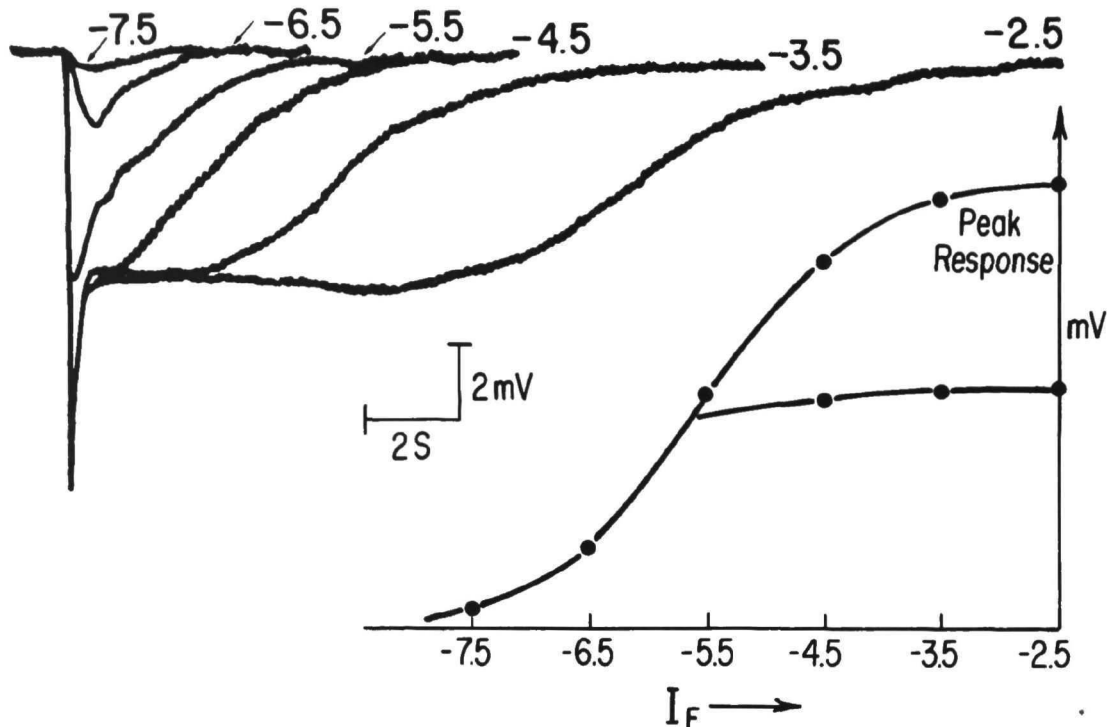


Figure 1: Responses of a dark adapted rod to 100msec flashes of increasing intensity.

Inset: The peak responses (mV) are plotted vs. relative flash intensity (I_F = neutral density of flash in log units). At high intensities the peak and plateau of the response give rise to two branches of the curve. This is the "operating curve".

intensities the response waveform develops a spike and a plateau before relaxing back to baseline. The response amplitude cannot increase indefinitely, but saturates at some level. The flash intensity producing the smallest detectable response (in practice, a criterion response of 1/2 mV or 1 mV) is the threshold intensity.

Both threshold and saturated response amplitude depend on the state of adaptation. Two consequences of either bleaching or background adaptation are a shift of the threshold to higher

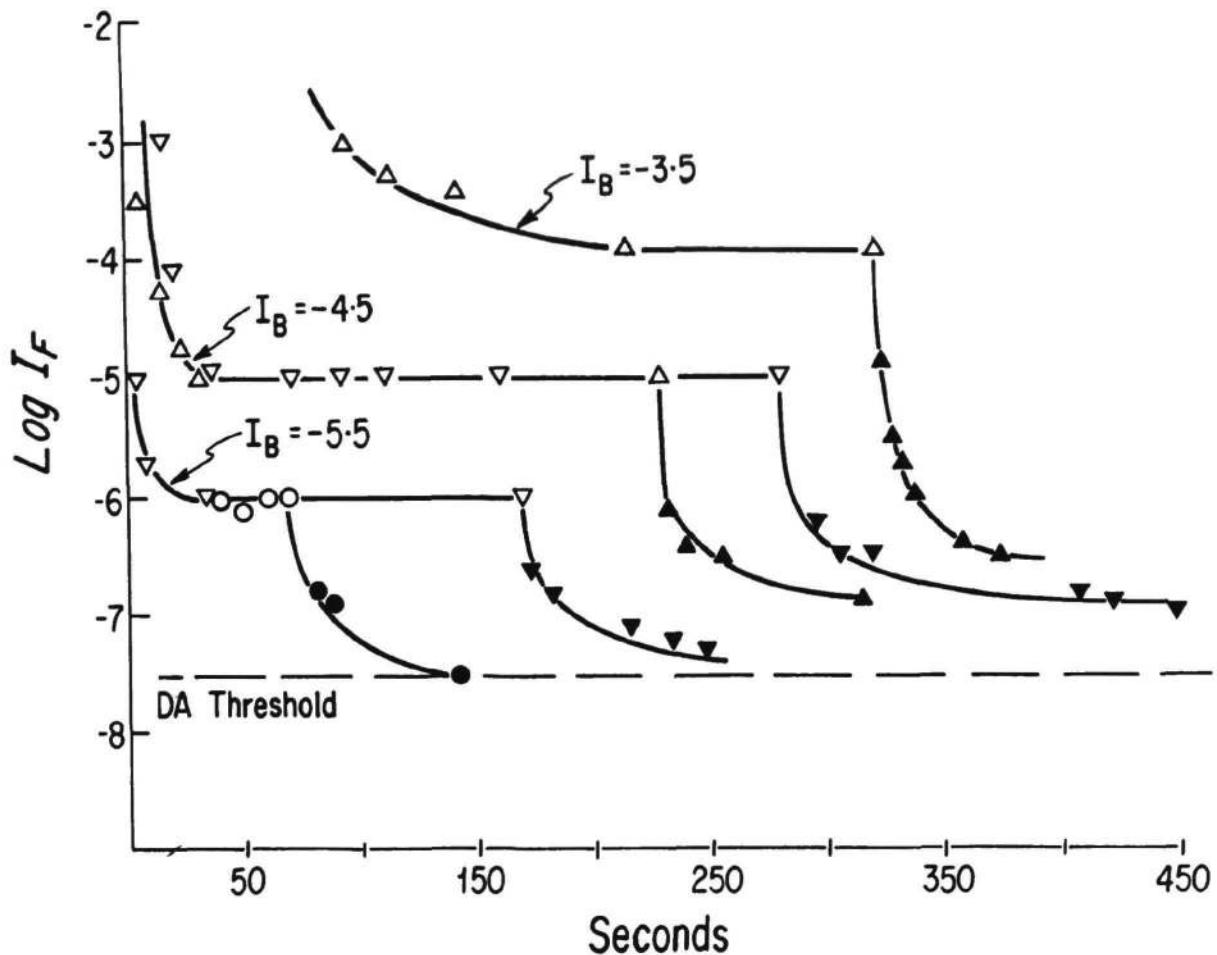


Figure 2: Threshold Recovery when a Background is turned ON and OFF:

A typical set of threshold recovery curves is shown, the lowest containing two experiments at a nominal background N.D. - 5.5, the middle ones two experiments at N.D. - 4.5, and the upper curve one experiment at N.D. - 3.5. The light was turned on at time 0 and, after a steady threshold was reached, the light was turned off. In the two experiments at N.D. - 5.5 the light was turned off after different exposure times and similarly at N.D. - 4.5. There was no measurable threshold recovery at backgrounds of N.D. - 2 or brighter. $\text{Log } I_f$ on the ordinate is the relative intensity in N.D. units of a 100 mS flash which elicits a 1/2 mV response.

The original, dark adapted threshold of the cells was $\text{Log } I_f = -7.5$. The estimated fraction of pigment bleached at the termination of light exposure was less than 0.02 up to $I_B = -4.5$ and about .07 at $I_B = -3.5$, where I_B is the N.D. of the background.

NOTE: N.D. is short for the logarithm of neutral density attenuation.

light intensities and a reduction of the saturated amplitude. In fact, all response amplitudes are reduced. This can be displayed in the "operating curve", a graph of peak amplitude versus flash intensity for stimuli from threshold to saturation at each level of adaptation, illustrated in the inset to Figure 1.

Effects of Backgrounds on Thresholds:

When a background is projected onto the retina the intracellular threshold response falls rapidly from an initially high level to a lower value. When the background is turned off the threshold again falls rapidly to the dark adapted value, unless some measurable fraction of the pigment has been bleached, in which case the final threshold is elevated, depending on the amount bleached. This is quite analogous to the psychophysical observations. Our data are shown on Figure 2 for three different backgrounds. The complete range of threshold elevations is about five orders of magnitude (5 log units) of light intensity. This is comparable to the range of some 6 orders of magnitude for the scotopic range of human vision.

The steady state threshold elevation of Bufo rods in the presence of a background is shown in Figure 3. Again there is a close parallel with psychophysical results. At low background intensities the threshold is close to the dark adapted value. As the intensity rises the threshold becomes proportional to the square root of the background. This is precisely what one would expect for the detection of a signal in the presence of noise (see e.g. Leibovic 1972 p. 114). At still higher intensities, threshold is proportional to background (Weber-Fechner rule in psychophysics).

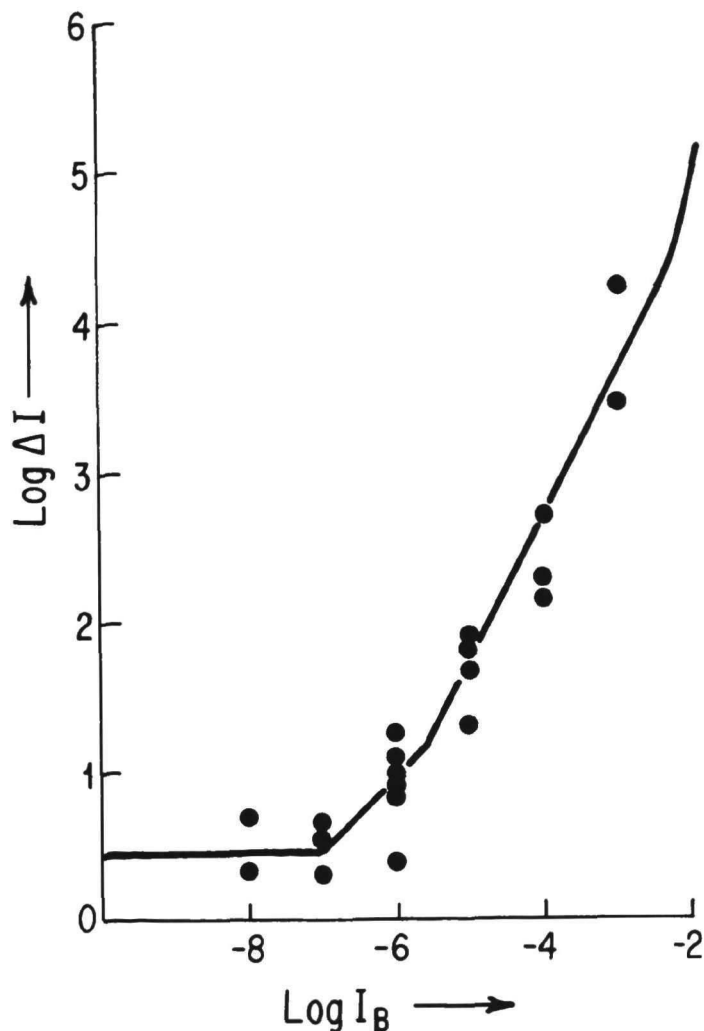


Figure 3: The ordinate is the threshold elevation above the dark adapted threshold in units of N.D. The abscissa is the relative background intensity in units of N.D.

We can see that there are close similarities between psychophysics and these single photoreceptor responses with regard to threshold elevation due to backgrounds.

Effects of Bleaching on Thresholds:

There is essentially no pigment regeneration in the isolated retina. Therefore it is an ideal preparation for studying bleaching. Our data for threshold elevation as a function of bleaching are shown in Figure 4. Up to almost 20% bleaching,

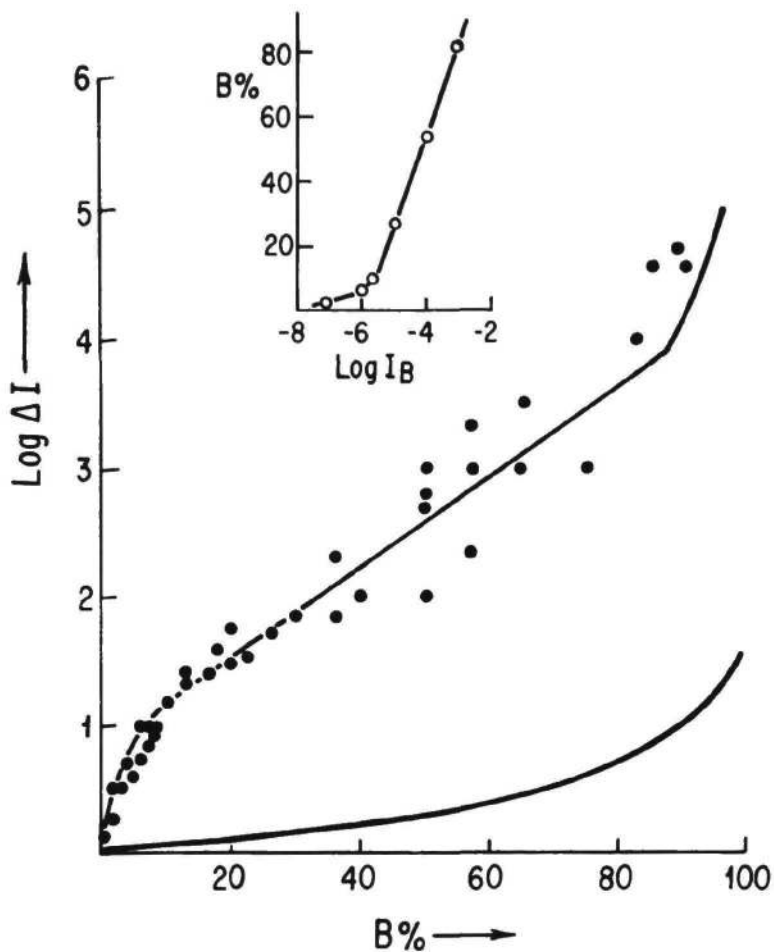


Figure 4: The ordinate is the same as in Figure 3. The abscissa is the bleached percentage. The lower curve is the threshold elevation due to the reduced photon absorptions in the presence of bleached pigment. In fact, the threshold elevation is much greater, showing that it is not simply due to the presence of bleached pigment. Inset: Threshold equivalent I_B and B . For each point on the curve, I_B and B have the same threshold.

the threshold rises linearly and thereafter it rises exponentially. The linear region has not been reported previously, perhaps due to the difficulties of accurate measurement and the scatter of the data points. If there were fewer data points in that region on our graph, one might have been tempted to simply draw a straight line through the points, which would have implied an exponential relationship over the whole range. The value of the exponent depends on the range of thresholds covered. Thus, Rushton (1962) used an exponent of 20 (see his Figure 3) on a graph that has a maximum threshold elevation of $\log 20$. But this is an extrapolation. The actual

thresholds he measured only went up to about log 7. Thus, the differences between our data and psychophysics may be more apparent than real. In any event, the qualitative similarities are close.

Effects of Background and Bleaching on Saturated Amplitude:

When we measure the saturated amplitudes, firstly in the dark adapted cell, secondly in the presence of a known background and thirdly after bleaching a given fraction of pigment, we can find the reduction of the saturated response in the last two conditions. Our data are shown in Figures 5 and 6. The points on these Figures are mean values obtained from the raw data. These Figures establish a relation between bleaching and backgrounds at the upper end of the operating curve, just as Figures 3 and 4 establish a relation at the lower end.

Is there any connection between these relations?

Equivalences between Backgrounds and Bleaching:

We can establish an equivalence between backgrounds and bleaching with respect to either thresholds or amplitudes: Given a threshold elevation ΔI_T we can find a background I_B and a bleached fraction B which produce this threshold elevation. We write this equivalence as:

$$I_B \overset{\Delta I}{\sim} B \quad (1)$$

We can similarly establish an equivalence

$$I_B \overset{A}{\sim} B \quad (2)$$

where A is the ratio of the saturated amplitude in the presence

of the background I_B or due to the bleached fraction B to the saturated amplitude of the dark adapted cell.

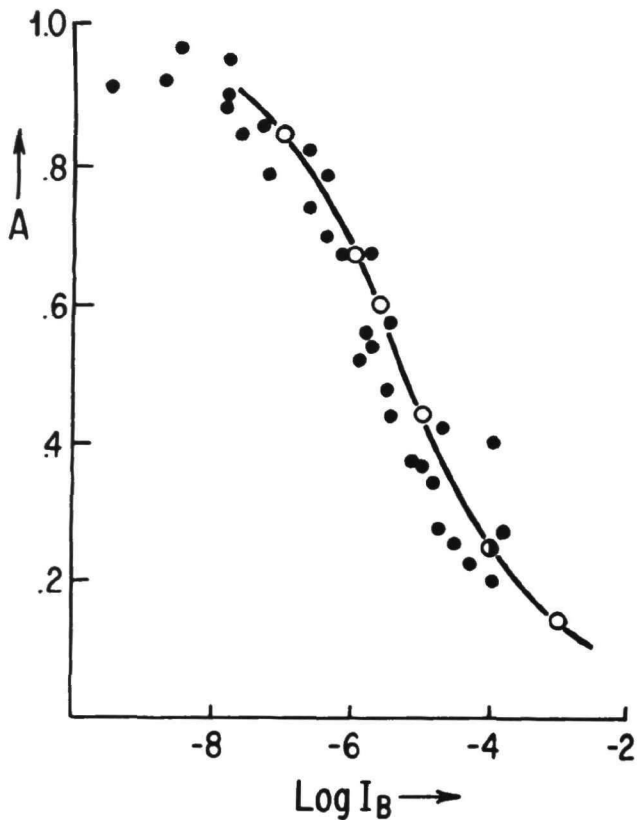


Figure 5: Amplitude reduction vs. background. See text for details.

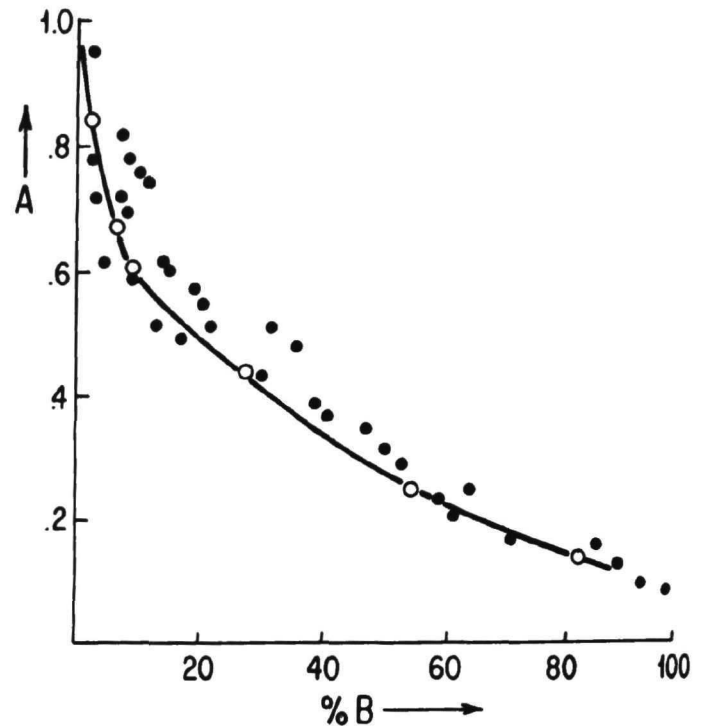


Figure 6: Amplitude reduction vs. bleaching. See text for details.

In the simplest case the two equivalences are the same. In other words, if I_{B1} and B_1 produce the same threshold elevation ΔI_1 then they also give rise to the same amplitude reduction A_1 .

The inset on Figure 4 plots the (I_B, B) equivalence with respect to threshold elevation derived from the curves of Figures 2 and 3. These points are replotted as the open circles on Figures 5 and 6 as follows: From the (I_B, B) equivalence, $\log I_B = -4$ corresponds to $B = 54\%$. The open circles on Figures 3 and 4 with abscissae -4 and 54 respectively are then positioned as closely as possible to the experimental data to yield the same

value of A in the two Figures, which is 0.25 in this case. The other open circles are obtained similarly. The curves on Figures 4 and 5 are drawn by hand and it can be seen that they are close to the open circles as well as to the experimental points. Thus, the (I_B, B) pair with the same value of ΔI also has the same value of A. This implies a close agreement between the equivalences (1) and (2).

The agreement between the equivalence relations can also be demonstrated by a statistical procedure (Leibovic et al., in preparation). The result is the same. We therefore accept the proposition that the two equivalences coincide. But, if this is the case, then do the equivalences at the beginning and end of the operating curves extend also to the complete curve? More precisely, suppose the thresholds and saturated amplitudes coincide on the operating curves for a given background I_B and a given bleached percentage B. Do the curves then coincide everywhere?

Figure 7 shows this to be the case. In view of the statistical variability of the data evident in Figures 2 to 5, the (I_B, B) pair with coincident operating curves will not necessarily correspond to the exact pair on the inset of Figure 4. The significant point is that if a particular (I_B, B) pair have the same threshold, they have the same saturated amplitude and the same operating curves.

Some Implications for Psychophysics:

Equivalent effects of bleaching and backgrounds were first established in psychophysics. It is now evident that there are equivalences operating at the cellular level as well. We have

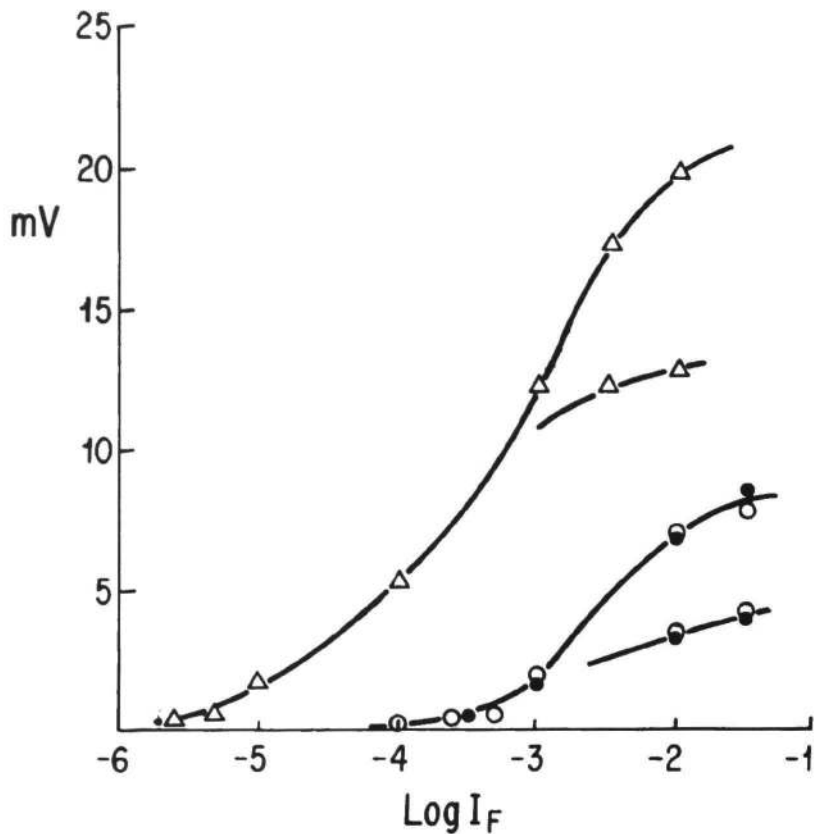


Figure 7: Operating curves for a cell in the dark adapted state (Δ), in the presence of a background of N.D. -5 (\bullet) and after bleaching approximately 15% (\circ). Note the coincidence of the curves for N.D. -5 and 15% bleaching. Similar results were obtained for other (I_B, B) pairs up to background N.D. -3.5 and 70% bleaching.

demonstrated that the rod threshold in Bufo can be elevated some 5 or 6 log units before rising to saturation. This is the same as the psychophysically measured range in scotopic vision. At low background intensities the rod threshold obeys the Rose-de Vries rule and at higher intensities the Weber-Fechner rule, just like psychophysical threshold. In bleaching adaptation the rod threshold varies exponentially with the bleached fraction just as the psychophysical threshold, although the value of the exponent is different, in part at least due to the treatment of the data: in psychophysics too the value of the exponent differs in different experimental situations.

The compression of the rod responses due to adaptation is analogous to the fading of rod vision under photopic conditions.

Finally the equivalence between bleaching and backgrounds extends to the complete rod operating curve at any level of

adaptation. This result is especially interesting. For, the operating curve plots the peak responses to flashes of light. Each flash intensity is associated with a given peak response at any level of adaptation. There is therefore a 1-1 correspondence between light intensity and peak response. A given (I_B, B) pair which is equivalent with respect to threshold also results in equal peak responses to a flash of light. This is the cellular counterpart of the equal apparent brightness of a threshold equivalent (I_B, B) pair.

Can there be another feature of the response which could signal equivalent brightness? If so, it would not be the time integral of the response waveform or any other time dependent feature. A look at the different response waveforms due to bleaching and backgrounds suffices to confirm this: The response kinetics are significantly faster with a background than for the equivalent level of bleaching. But there could be another point on the waveforms in 1-1 correspondence with the peak response which would serve equally well. That is possible. However, from the point of view of signal detection, the peak response is the easiest to detect and transmit. We therefore propose that brightness perception is mediated by the peak photoreceptor response.

Our proposal would receive additional support if it could be shown psychophysically that not only is the subjective brightness the same for equivalent bleaching and background, but also that the perceived brightness of flashes of increasing intensity is the same, when superimposed on retinal areas of equivalent bleaching and background.

If the peak photoreceptor response conveys brightness information, we may ask what information is contained in the rest of the complex response waveform? It is a long lasting response which generates a visual persistence, a form of short term memory, which may be responsible for the perceived temporal continuity of the visual world.

A final point concerns the significance of electrophysiological signals: The neural response waveform reflects underlying biophysical and biochemical mechanisms. Thus the various phases of the action potential are shaped by sodium and potassium conductance activation and sodium inactivation. Similarly photoreceptor responses reflect changes in the electrical parameters caused by light absorption and the transduction biochemistry of phosphodiesterase, transducin, cyclic GMP, calcium and other products. As we have seen here, certain features of the response waveform can also be correlated with psychophysical phenomena. Electrophysiology, therefore, occupies the interface between sensory and molecular events.

Acknowledgements:

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