VISUAL ADAPTATION AND INHIBITION

BY

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Abstract

Two key experiments, together with classical results, allow the development of a theoretical framework and a quantitative model of the effects of adaptation and lateral mechanisms on the brightness, discriminability, and absolute detectability of achromatic lights.

The first key experiment is the replication of an apparently forgotten study that determined the intensities of lights pulsed in the dark adapted eye that have the same brightnesses as steady lights to which the other eye has become adapted. It is confirmed that, as a function of intensity, the brightness of a steady (adapted) light increases more slowly than the brightness of a pulsed (unadapted) light. Furthermore, once the intensity of the steady light exceeds a certain level its brightness remains constant.

The second key experiment measures increment thresholds on pulsed backgrounds in the dark adapted eye, and on steady adapted backgrounds. The results show that thresholds on pulsed (unadapted) backgrounds are based upon afterimages at high background intensities, and that when the afterimages are masked, increment thresholds follow a continuously accelerating function. Weber's law is observed only when discriminations are based upon afterimages, or when the eye is allowed to adapt to each background before threshold is measured.

The theoretical development assumes that the adaptation process is composed of three components. The first is that light adaptation causes the depletion of photopigment, which has the effect of reducing the proportion of quanta in a stimulus that are absorbed by unbleached photopigment
molecules. Using the results of Rushton's densitometry measurements of the bleaching and regeneration of photopigment, the effects of photopigment depletion on dark adaptation thresholds, brightness, and intensity discrimination are analyzed.

The second component is the "dark light" signal, generated by bleached photopigment, that is equivalent to the neural signal produced by some continuous background light that is stabilized on the retina (Barlow, 1964). A new formula is derived that relates the intensity of this equivalent background to the proportion of bleached cone pigment.

The third component is an attenuator that is not governed by the current state of bleaching, but rather by the immediate history of visual responses. It is shown that this adaptation mechanism has the property of reducing neural responses to lights, as if approximately multiplying their intensities by some factor between 0 and 1.

It is also concluded that simple inhibitory mechanisms can simultaneously account for the lateral effects that continuous inducing fields exert on the brightness and discriminability of adjacent test fields.

Finally, a simple TSD (Theory of Signal Detectability) framework is proposed in order to analyze the relationship of brightness matching and increment threshold experiments.
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If the eye is suddenly exposed to a bright environment, after becoming accustomed to the dark, the visual field appears extremely bright and the discrimination of intensities within the visual field is relatively poor. However, over several minutes brightness decreases greatly and intensity discrimination improves. These two observations illustrate what is usually meant by the term light adaptation. The term dark adaptation refers to the reverse process which has a much slower time course -- after adapting to intense lights it may take an hour in darkness before the eyes regain maximum sensitivity.

In addition to direct adaptation effects that lights have on a given retinal area, they also effect brightnesses and intensity discriminations of lights falling on neighboring regions. These lateral (or spatial) interactions include, for example, the phenomena of simultaneous brightness contrast, Mach bands, and sensitization or desensitization effects on increment thresholds.

This paper is concerned with data and theory concerning many of these basic adaptation and lateral effects. In particular, it is mainly concerned with intensity discrimination and apparent brightness of achromatic (white) light.

The paper is divided into eight sections. The first five sections present both new and classical experimental results that form the foundation of the theory. In particular, Section I provides a brief discussion of the kinetics of photopigment bleaching and regeneration in the human retina. Section II presents some of the basic results of dark adaptation studies, and shows how these results are related to the bleaching kinetics discussed in the first section. The effects of adaptation on brightness and intensity discrimination are examined in Sections III and IV. Discussion of some
I. Photopigment Bleaching and Regeneration

Aside from effects due to the optical properties of the eye, the processing of visual stimuli begins with absorption of light by photopigment molecules in the receptors. This section describes some basic properties of this first stage of visual processing; subsequent sections describe how these properties manifest themselves perceptually.

Hecht (1934, 1937) proposed a simple photochemical theory of vision. Hecht's theory is now generally disregarded, but many of his ideas about the photochemistry of visual pigments still appear to be correct. Hecht assumed that as photopigment is being broken down (or bleached) by light, it is simultaneously being replaced (or regenerated). He described the bleaching and regeneration of receptor photopigments by the following equation:

\[
\frac{dx}{dt} = K_1 \cdot I \cdot (a - x) - K_2 \cdot x, \tag{1}
\]

where \(x\) is the concentration of bleached photopigments, \(a\) is the maximum possible concentration of regenerated photopigment, \(I\) is the intensity of light falling on the receptors, and \(K_1\) and \(K_2\) are the velocity constants of the bleaching and regeneration reactions, respectively. Equation (1) says that the rate of change of the concentration of bleached products is equal to the rate at which photopigment is bleached minus the rate at which it is regenerated; where the rate of bleaching is proportional to the rate at which quanta are absorbed, and the rate of regeneration is proportional to the concentration of bleached products. Actually, this is only a special case of Hecht's original formulation, but recent direct
measurements of photopigment density in both human rods and cones have verified equation (1) over a fairly broad range of conditions. These measurements were made possible with the development of reflection densitometry techniques (Campbell and Rushton, 1958; Weale, 1959). Roughly speaking, with these techniques changes in photopigment density are measured by changes in the intensity of a beam of light reflected back from the retina.

It is convenient to rewrite Hecht's equation in terms of the proportion of photopigment bleached, instead of in terms of concentration. This is done simply by dividing both sides of equation (1) by a. Also, the constants $K_1$ and $K_2$ are replaced by the more meaningful ones used by Rushton and Henry (1968). Thus,

$$\frac{dq}{dt} = I \cdot \frac{(1 - q)}{Q_e} - \frac{q}{t_o}$$

(2)

where $q$ is the proportion of pigment bleached, $Q_e$ is the energy (in troland seconds) of a brief stimulus needed to bleach a full complement of unbleached photopigment to proportion $1/e$, and $t_o$ is the time constant of regeneration (in seconds). Also, the symbol $p$ will be used here to denote $1 - q$, the proportion of pigment in the unbleached state.

Over a fairly wide range of conditions Rushton and Henry (1968) report that for cone pigments, $Q_e$ is about $2.4 \times 10^6$ td. sec, and $t_o$ is about 120 sec. However, following brief flashes (i.e., 1 msec up to several seconds) regeneration proceeds more quickly with a time constant of about 60 sec.²
There are several limitations to equation (2). First, according to equation (2) regeneration begins as soon as light is absorbed by photopigment molecules; however, the bleaching process itself apparently takes around 1 sec to complete (Rushton, 1964). Fortunately, since the regeneration process is slow relative to 1 sec, this simplification does not introduce appreciable error. Second, photopigment bleaching produced by extremely intense flashes is not described by equation (2). Under these conditions photopigment molecules often receive multiple quantum hits within a brief period of time. This apparently produces photoreversal, and possibly some other unusual effects on visual pigment molecules (Rushton, 1964). However, in none of the experiments described here are intensities high enough to produce these effects.

An important solution to equation (2) is that for the special case in which a light of intensity $I$ is left on for a long time. Under such steady state conditions photochemical equilibrium is reached, and thus the rate of bleaching and regeneration must be equal. Therefore, the solution to equation (2) is given by setting $\frac{dq}{dt} = 0$. This gives,

$$q = \frac{I}{I + \alpha}$$

where $\alpha = \frac{Q_e}{t_o}$. Also, the steady state proportion of unbleached photopigment is given by,

$$p = (1 - q) = \frac{\alpha}{\alpha + I}$$

Using the values of $Q_e$ and $t_o$ ($t_o = 120$ sec) given above, shows that $\alpha$, ...
which is the intensity of a steady light needed to bleach half the photopigment in cones, is about 20,000 td. (or 4.3 log td.).

Also note that according to equation (2) the regeneration of visual pigments in the dark (I = 0) is described by

$$\frac{dq}{dt} = -\frac{q}{t_0}.$$  \hspace{1cm} (4)

The important point of this section is that with equation (2) the proportion of photopigment available to respond to incoming light can be calculated at any point in time over a very wide range of conditions.
Footnotes

1 The troland (abbreviated td.) is a unit used to specify retinal illumination; in particular, 1 troland is the retinal illumination produced by viewing a surface of luminance 1 candle per square meter (cd/m²), through a pupil with an area of 1 mm². For example, a light colored object viewed under moderate indoor lighting produces retinal illumination levels in the range of 100 to 1,000 tds. (Le Grand, 1957). A troland second is the total energy falling on a unit area of the retina as a result of illuminating the retina with 1 troland for 1 second. The other luminance unit used in this paper is the millilambert (abbreviated mL) — 1 mL = 3.14 cd/m².

2 These estimates are based upon measurement of the density of all cone pigments together. However, blue cone pigment (cyanolabe) apparently is so scarce that the measurements primarily reflect the kinetics of the red (erythrolabe) and green (chlorolabe) cone pigments. Rushton has shown that these two pigments regenerate at the same rate, and furthermore that with the white (tungsten) light he used for bleaching, they also bleach at the same rate. Rushton's estimates of $Q_e$ and $t_o$ should also apply to the bleaching and regeneration of cone pigments in the experiments presented here, since all present stimuli were also comprised of white light from a tungsten source.
II. Dark Adaptation

This section examines the changes in absolute sensitivity of the eye that occur during dark adaptation. The next two sections examine the equally important effects of adaptation on the brightness and discriminability of lights.

The traditional method of measuring the recovery of sensitivity of the eye during dark adaptation has been to measure absolute thresholds at various times following offset of an intense preadaptation (or bleaching) light. For example, Hecht and Shlaer (1938) measured absolute threshold luminance for detection of a 2° test field flashed 7° in the periphery of the retina, after preadaptation for several minutes to a 1550 mL background field. Their results are given in Figure 1, which shows how log absolute threshold (in units of $10^{-9}$ mL) varies as a function of time after offset of the adaptation background. The data fall along two distinct segments or branches. The upper branch of the curve, which for more intense bleaches may extend for 10-12 minutes, reflects sensitivity of the cones; the lower branch reflects sensitivity of the rods. Thus, for example, when the test flash is confined to the rod free fovea only the upper branch appears, and dark adaptation is complete after no more than 7 to 10 minutes. On the other hand, for a rod monochromat (a rare individual whose eyes contain no cones) thresholds decline along a single continuously decelerating function that agrees with the lower branch in Figure 1 (Rushton, 1961). There is much other evidence for this duplistic interpretation of dark adaptation curves (Hecht, 1937).

One possible contributor to dark adaptation thresholds (as well as most of the other effects discussed here) is changes in pupil size; that is, as the pupil expands during dark adaptation, more light is admitted into
the eye and thresholds are reduced. However, since pupil area can vary by little more than a factor of 10, changes in pupil size can produce no more than 1 log unit changes in threshold. Furthermore, changes in pupil size are a rather uninteresting factor; so all experiments described (and most of those reviewed) here were carried out with appropriate control or correction for changes in pupil diameter.

A. Effects of Photopigment Depletion on Dark Adaptation Thresholds

As mentioned in the previous section, Hecht proposed a simple photochemical theory of vision. In his theory, absolute (or incremental) threshold at a given time is governed solely by the current photochemical state of the receptors, which he described with equation (1). In particular, Hecht assumed that a briefly presented light is detected when the number of quanta absorbed by unbleached photopigment molecules exceeds some fixed criterion; and therefore, that dark adaptation thresholds can be accounted for solely by the fact that prior adaptation depletes photopigment, thus reducing the proportion of quanta in the threshold flash that will be absorbed by unbleached photopigment molecules. In other words, threshold should be inversely proportional to the amount of pigment in the unbleached state. For example, if half the photopigment is bleached, then threshold should be twice what it is in the completely dark adapted eye.

It is highly likely that this sort of adaptation process should occur even though, as will be shown, it is not the only adaptation process. In fact, the theory presented later takes into account the idea that reducing the proportion of unbleached pigment has the same effect as reducing the intensity of lights falling on the retina. This type of adaptation process will be referred to as the "depletion effect."
The difficulty with Hecht's theory is that the depletion effect is not powerful enough to account for the very large elevations in threshold that are associated with small changes in photopigment concentration. Using the retinal densitometer, Rushton (1963, 1965a) has been able to measure both psychophysical thresholds and the density of cone pigments during the course of dark adaptation. The solid circles in Figure 2 show a foveal dark adaptation curve obtained after bleaching away 99% of all cone pigment with an intense background field of 2 min duration. These data are comparable to the upper segment of the dark adaptation curve in Figure 1. (Note, however, that in Figure 2 log relative threshold is plotted instead of log absolute threshold. Relative threshold is defined as the ratio of absolute threshold, \( \Delta I \), to absolute threshold in the dark adapted eye, \( \Delta I_0 \). Plotting the data in this way simply rescales the vertical axis so that threshold in the dark adapted eye has a value of 0.) The open circles in Figure 2 show the actual proportion, \( q \), of bleached cone pigment present during the course of dark adaptation. (Also note that the open circles are accurately described by equation (4) with \( t_0 = 120 \) sec.)

The results in Figure 2 are not at all what one would expect if the only effect of bleaching is to reduce the proportion of quanta absorbed by receptor photopigments. As mentioned above, bleaching half the photopigment should double threshold. Instead, the data show that threshold is elevated by a factor of 20. Worse yet, similar measurements for rods show that bleaching even 25% of the rodopsin increases threshold by a factor of around 100,000 (Rushton, 1965b). The dashed curve furthest to the left in Figure 2 shows the dark adaptation curve that would have been obtained if only the depletion effect were operating. As mentioned
Figure 2
earlier, the depletion effect predicts that threshold is inversely proportional to the proportion of unbleached pigment; thus, the dashed curve in Figure 2 was obtained from the relation,

\[
\frac{\Delta I}{\Delta I_0} = \frac{1}{1 - q}.
\]

Obviously, the dashed curve doesn't come close to predicting the results.

On the other hand, thresholds do show a systematic relationship to the proportion of bleached pigment. In fact, the correspondence of the solid and open circles in Figure 2 shows that log threshold is linearly related to the proportion of bleached pigment,

\[
\log \frac{\Delta I}{\Delta I_0} = 3q.
\]

In a certain sense, Figure 2 may be misleading in that the data have intentionally been plotted in a way that shows the linear relationship between log threshold and the proportion of bleached photopigment. It should be kept in mind that as long as both threshold and proportion of bleached pigment are decreasing functions of time then there always exist monotonic transformations of the vertical axes that will bring the open and solid circles into correspondence.

In any event, it appears that in addition to the depletion effect, photopigment bleaching has some other very large effects on threshold. How these additional effects vary with the proportion of bleached photopigment can be seen by partialling out the depletion effect. This is done simply
by replottting relative thresholds in terms of quantum absorptions per second rather than in terms of intensity, since this measure is independent of how much pigment is in the bleached state. This is shown by the dotted line in Figure 2, which was obtained by noting that the rate of quantum absorptions for threshold ($\Delta Q$) is proportional to threshold intensity ($\Delta I$), and to the proportion of unbleached pigment ($1 - q$). That is,

$$\Delta Q_0 = c \cdot \Delta I_0$$

and

$$\Delta Q = c \cdot \Delta I \cdot (1 - q),$$

where $\Delta Q_0$ is the dark adapted absolute threshold in quantum absorptions per second, and $c$ is a proportionality constant. Therefore we have,

$$\frac{\Delta Q}{\Delta Q_0} = \frac{\Delta I}{\Delta I_0} \cdot (1 - q) \quad (6)$$

Taking logs of both sides of equation (6) shows that the dotted curve in Figure 2 is simply the difference between the solid and dashed curves.

Comparison of the solid and dotted curves shows that the depletion effect has most significance for threshold if more than about half the photopigment is bleached. If less than about half the photopigment is bleached, threshold elevations are mostly the result of some other effects produced by bleached photopigments. These additional effects of bleaching are captured in the formula, obtained by combining equations (5) and (6), that relates relative threshold in quantum absorptions per second to the
proportion of photopigment bleached;

\[ \frac{\Delta Q}{\Delta Q_0} = (1 - q) \cdot e^{\gamma q} \]  \hspace{1cm} (7)

where \( \gamma \) is equal to about \( \frac{4}{3} \). Rushton (1961) has collected data indicating that equation (7) also holds for rods (that is, for the lower branch of the curve in Figure 1), but the value of \( \gamma \) is about 40.

In summary, dark adaptation thresholds can be accounted for only in part by the fact that bleaching depletes the photopigment available to catch quanta in the threshold flash. The bleached photopigments themselves seem to produce large additional effects on threshold, and these effects are described by equation (7).

B. Equivalent Backgrounds and Barlow's Hypothesis

Clearly, a complete account of the dark adaptation process must include an explanation of equation (7). Unfortunately, it appears that no reasonable explanations have been proposed. However, a number of important insights into the mechanisms responsible for equation (7) have grown out of the concept of the "equivalent background" introduced by Stiles and Crawford (1932), and later developed by Crawford and others.

Before defining the equivalent background a few words need to be said about classical increment threshold experiments. From these experiments it is known that threshold for detecting a briefly flashed increment field on a continuously presented background is a monotonically increasing function of the background field's intensity. Furthermore, unless small increment fields are used (Barlow, 1958), or unless special techniques are used to reduce cone sensitivity relatively to that of the rods (Aquilar and Stiles,
1954), these monotonic functions are described by the generalized Weber law:

\[ \Delta I = k(I + I_o) \]

where \( \Delta I \) is the intensity of the increment field, \( I \) is the intensity of the background field, and \( k \) and \( I_o \) are constants. Again absolute threshold in the dark adapted eye will be denoted by \( \Delta I_o \), which from equation (6) is seen to be equal to \( K \cdot I_o \).

The important point here is that dark adaptation thresholds and increment thresholds can be linked together, in the sense that there always exists a continuously presented background that produces exactly the same rise in threshold as that produced at time \( t \) after presentation of a given bleaching background. This continuous background is called the equivalent background. The importance of making this association between dark adaptation thresholds and increment thresholds is that it turns out that if a continuous background and a bleached background after some time have identical effects under one set of experimental conditions, then they also have identical effects under a variety of other experimental conditions. For example, Crawford (1937, 1947) and Blakemore and Rushton (1965) have shown that when a state of adaptation (at time \( t \) after bleaching), and a continuous background field have the same effect on threshold for detecting, say, a 6° increment field, then they also have identical effects on threshold for increment fields of any size (e.g., 5'). This correspondence is found to hold over the entire course of dark adaptation. Furthermore, the result is far from trivial since changing the size of the increment field, dramatically changes the shapes of both the increment threshold and
the dark adaptation threshold functions.

Primarily on the basis of the results of Crawford, and Blakemore and Rushton, Barlow (1964) proposed that bleached photopigment in the receptors produces signals in the visual system whose effects on threshold are indistinguishable from those produced by a continuous background illumination—the equivalent background. He calls these signals "dark light" since they arise from the bleached photopigment, and are therefore present even in the dark. This hypothesis can account for the results of Crawford, and Blakemore and Rushton, but at first glance it seems odd that these bleaching signals are not clearly visible since they supposedly affect threshold just like those signals generated by "real light."

However, Barlow and Sparrock (1964) suggest that indeed "dark light" can be visible—it is the afterimages that are seen intermittently throughout the course of dark adaptation. Furthermore, they propose that the reason afterimages appear so weak and intermittent is that unlike a "real light" background, a "dark light" background is stabilized on the retina. (It is well known that stabilized images quickly fade.) Barlow and Sparrock confirmed their hypothesis in an ingenious experiment in which they found the intensity of stabilized background lights that have the same apparent brightness as afterimages observed during dark adaptation. In particular, they found that afterimages and stabilized backgrounds that have the same apparent brightness produce exactly the same elevations in threshold.

Also, Burkhardt (1966) and Sparrock (1969) have shown that increment thresholds obtained on stabilized and unstabilized backgrounds (of the same intensity) are almost identical. This implies that the results of the earlier equivalent background studies of Crawford, and Blakemore and
Rushton, would have been unchanged if stabilized rather than unstabilized background fields were used.

All these results provide strong evidence that bleached photopigment generates "dark light" signals that are indistinguishable from those generated by a continuous (but stabilized) background light. (Some other supporting evidence is given in Barlow (1972).) However, it is important to note again that the "dark light" hypothesis itself does not account for thresholds observed during dark adaptation. In particular, it does not account for the elevations in threshold described by equation (7); it says only that they are the result of signals, arising from the bleached photopigments, which act just like those produced by "real light." On the other hand, if the "dark light" hypothesis is correct then the necessity of explaining equation (7) is circumvented, in the sense that any theory of visual processing that can deal with the effects of continuous background lights will also be able to deal with the effects of photopigment bleaching, simply by representing the effects of bleaching with an equivalent continuous background. Furthermore, since "dark light" is assumed to arise solely from bleached photopigment, the intensity of the equivalent background is dependent only upon the proportion of photopigment in the bleached state.

The relationship of the intensity of the equivalent background to the proportion of bleached photopigment is derived below. However, in order to do this a more precise definition of the equivalent background is needed: A continuous background, $I_x$, is the equivalent background associated with time $t$ after offset of a bleaching light, when increment threshold (in quantum absorptions per second) on $I_x$ is the same as absolute threshold at time $t$. In other words, $I_x$ must satisfy,
\[ \frac{\Delta Q(I_x)}{\Delta Q_o} = \frac{\Delta Q(t)}{\Delta Q_o} . \]

(The thresholds are divided by the dark adapted absolute threshold, \( \Delta Q_o \), since obviously, only relative thresholds are needed in order to determine equivalent backgrounds.)

This definition is slightly different than the one usually given (Crawford, 1947; Blakemore and Rushton, 1965), which is that \( I_x \) should satisfy,

\[ \frac{\Delta I(I_x)}{\Delta I_o} = \frac{\Delta I(t)}{\Delta I_o} . \]

The two definitions are equivalent except when a substantial proportion of pigment is bleached. Under these conditions the old definition overestimates the effect of "dark light" on threshold, since it does not take into account the fact that part of the elevation in threshold is due to the depletion effect, as discussed in connection with Figure 2. Fortunately, most previous equivalent background analyses have been carried out for experiments in which the proportion of bleached pigment remained relatively low. In particular, this is true for the experiments upon which Barlow's "dark light" hypothesis has been founded. We now derive the relationship of \( I_x \) to \( q \) for cone bleaching. (Similar calculations can be carried out for bleaching in rods.)

At any given time \( t \) after bleaching there is a certain proportion \( q \) of pigment in the bleached state. Thus, the equivalent background associated with time \( t \) after bleaching is obviously the same one that is
associated with proportion $q$ of bleached pigment. Furthermore, the relative threshold, in quantum absorptions per second, associated with $q$ is given by equation (7), and therefore, by the definition of the equivalent background, $I_x$ must satisfy,

$$\frac{\Delta Q(I_x)}{\Delta Q_o} = (1 - q) \cdot e^{\gamma q} . \quad (9)$$

Now, as pointed out earlier in deriving equation (6),

$$\Delta Q(I_x) = c \cdot (1 - q) \cdot \Delta I(I_x)$$

and

$$\Delta Q_o = c \cdot \Delta I_o .$$

(Note, this is not the same value of $q$ as in equation (9).) It turns out that equivalent backgrounds are themselves never intense enough to bleach an appreciable proportion of pigment; therefore,

$$\Delta Q(I_x) = c \cdot \Delta I(I_x) .$$

Furthermore, cone increment thresholds obey the generalized Weber law (equation (8)) over a wide range of background intensities. Therefore,

$$\frac{\Delta Q(I_x)}{\Delta Q_o} = \frac{c \cdot K \cdot (I_x + I_o)}{c \cdot K \cdot I_o} = \frac{I_x + I_o}{I_o} . \quad (10)$$
Combining equations (9) and (10) gives,

\[ \frac{I_x + I_o}{I_o} = (1 - q) \cdot e^{\gamma \cdot q} \]

or,

\[ I_x = I_o \cdot (1 - q) \cdot e^{\gamma \cdot q} - I_o \quad (11) \]

(This expression differs from the one derived by Barlow (1964) since he did not take the depletion effect into account.)

Theoretically, once it is determined how the visual system processes real light backgrounds then, with equations (2) and (11), the effects of bleaching are also determined over a wide range of conditions. Equation (2) gives, at any point in time, the current proportion of bleached pigment, and thus the magnitude of the depletion effect can easily be determined. Furthermore, equation (11) gives the equivalent background of real light, \( I_x \), that is of the same effective intensity as the "dark light" generated by the bleached pigment.

In order to keep things relatively simple, it will be assumed in the theory developed later, in Section VII, that this analysis (equations (2) and (11)) is correct; however, there are some limitations and potential difficulties. To begin with, aside from accepting the densitometry measurements of Rushton, there are two important assumptions upon which equation (11) is built. First, absolute thresholds are assumed to depend only upon the proportion of photopigment in the bleached state, independent of how this state of bleaching was reached. The fact that during dark adaptation, the
proportion of bleached pigment and threshold decline together, as shown in Figure 2, suggests that this assumption is correct; however, it has not yet been adequately tested. The second main assumption is, of course, that the bleached photopigment molecules produce "dark light" signals that are indistinguishable from stabilized "real light." Although there are a number of experiments that support this assumption (some of these were reviewed above), there are a few that do not (Rushton and Westheimer, 1962; Westheimer, 1968). However, at present the implications of these "negative" experiments for the "dark light" hypothesis is a controversial issue (Barlow and Andrews, 1973; Barlow and Sakitt, 1973). (Note, that the first assumption described above may be correct even if the "dark light" hypothesis is proven incorrect.)

 Another limitation to equation (11) is that it does not apply to short-term dark adaptation effects. During the first couple of seconds after offset of a background field threshold drops precipitously--much too quickly to be accounted for by equation (11). The thresholds observed during these first few seconds are probably, in large part, the result of neural (as opposed to photochemical) aftereffects of the background field. Neural adaptation effects are examined in later sections; however, we will not be primarily concerned with analyzing short-term dark adaptation thresholds.

 This section has focused exclusively on experiments that measure absolute thresholds during dark adaptation; however, this is only part of the picture. At least from a naive point of view, the effects of adaptation on the brightness and discriminability of lights are equally important. Unfortunately, they have received very little study. In particular, it appears that only Wright (1947) has carried out any systematic studies of the time
course of brightness changes during dark adaptation. Similarly, there appear to be few systematic studies of the time course of changes in intensity discrimination during dark adaptation. No doubt, part of the difficulty is that these types of studies are technically difficult, since unless the stimuli following the bleaching light are near absolute threshold, or are well spaced out in time, they will alter the state of adaptation; making measurement of the "time course" hazardous.

Despite technical difficulties, adaptation effects on brightness and discriminability require detailed experimental analysis. However, rather than attempting a complete systematic study of the time course of brightness and discriminability changes during light and dark adaptation, the next two sections begin more modestly by examining, in detail, the two endpoints of the light/dark adaptation continuum. In particular, the focus is on measuring the apparent brightness and the discriminability of lights presented to the dark adapted eye, versus measuring the brightness and the discriminability of lights to which the eye has become completely adapted.

In studying the effects of adaptation on brightness and intensity discrimination, it is important to ask to what extent the observed effects are due to either photopigment depletion, or the "dark light" signals generated by the bleached photopigment. In order to answer these questions, equations (2) and (11) can be used to partial out the effects of "dark light" and photopigment depletion. (Note, equation (2) has already been used to analyze the role of depletion effect in dark adaptation thresholds.) It will be shown that photopigment depletion almost always plays an important role when large amounts of photopigment are bleached.

On the other hand, the effects of "dark light" are almost always
negligible. There are two reasons for this. First, since "dark light" is stabilized on the retina, its brightness is greatly reduced. Therefore, "dark light" signals should add little to the brightness of lights. Second, the experiments described in later sections almost always concern the effects of adaptation on stimuli whose intensities far exceed the intensity of the "dark light." For example, consider the relative contributions of "dark light" and "real light," for continuous backgrounds at photochemical equilibrium. A continuous background will bleach all but proportion $p$ of photopigment, where $p$ is given by equation (3) in section I; and the bleached photopigment will generate a "dark light" background whose intensity is given by equation (11). Calculating the ratio of the "dark light" to the "real light" (i.e., $I_x / (p \cdot I)$), with parameter values in equation (3) and (11) that apply for cone bleaching, shows that the intensity of the "dark light" never exceeds 3% of the "real light" intensity. Therefore, the contribution of "dark light" should be negligible, since under most conditions subjects cannot even detect a 3% change in the intensity of a continuous light.
Footnotes

3 The subscript in $I_x$ indicates that the "dark light" is dependent on the concentration of bleached products as given earlier in Hecht's equation (equation (1)).

$\Delta Q$ on both sides of this equation is used to designate two different functions; $\Delta Q (t)$ is a dark adaptation threshold function, and $\Delta Q (I_x)$ is an increment threshold function. However, this should not lead to any confusion since the arguments, $t$ and $I_x$, indicate which function applies.

4 On the other hand, rod increment thresholds do not obey Weber's law at high background intensities; therefore a different function must be used at this step.
III. Adaptation: Brightness

Perhaps the most salient aspect of light adaptation is the dramatic brightness changes that lights undergo during the first few minutes after presenting them to the dark adapted eye. This section begins with the investigation of this effect.

A. Brightness in the Unadapted and the Steady State Adapted Eye

A natural starting point in the study of these brightness changes is to compare the brightness of lights presented to the dark adapted eye with their brightness after they have been viewed for a long time. This important experiment was carried out by Craik in 1940 (although apparently it has since been forgotten). Craik used the successive binocular matching procedure shown at the top of Figure 3. He first had subjects view a large field (45° of visual angle) continuously with the right eye until adaptation to it was complete. Also, during this time the left eye was kept dark adapted. The stimulus presentation sequence consisted of turning off the adapting light and simultaneously pulsing the matching field (also 45°) for one second, in the dark adapted left eye. After this, the adapting field was also flashed on and off for one second, and then turned on until the next trial. (Trials were spaced far enough apart to insure that the left eye remained relatively dark adapted.) The intensity of the light pulsed to the dark adapted eye was adjusted until it had the same apparent brightness as the adapted light. However, it should be noted that light adaptation produces color differences between the adapted and matching fields, and this made it more difficult for subjects to decide when the two fields matched in brightness.

Craik's results, for the condition just described, are given in the lower curve (solid circles) in Figure 4. (The other curves will be described
Figure 3
shortly.) Now, if there were no adaptation effects on brightness then the continuously adapted light and a pulsed matching light of the same intensity would have the same brightness; therefore, the data would fall along the diagonal line of slope one drawn in the figure. What Craik finds is that for low to moderate intensities of the adapted light, the intensity of a light pulsed to the dark adapted eye, that is needed to match it, increases linearly on this log-log plot. But, at high intensities the function takes a sharp break so that little increase in brightness of the adapted light occurs with further increases in its intensity.

The range of intensities over which brightness remains constant roughly corresponds to the range of normal daylight intensities obtained out-of-doors. According to LeGrand (1957), the retinal illumination produced by a light colored object, viewed in daylight, will vary roughly from 3.5 to 5 log trolands — 5 log td. if viewed in direct sunlight.

The difference between the diagonal line and Craik’s curve is a measure of the change in brightness due to adaptation. At the break in the curve, the difference is about 2 log units. In other words, adapting to a light of 3.5 log td. is equivalent to reducing its intensity by a factor of 100.

In addition to the experimental condition just described, Craik also carried out exactly the same experiment but with the pulsed matching field presented not to a dark adapted eye, but to a partially light adapted eye. This was accomplished by filling the gap between successive presentations of the matching field with an adapting background field whose intensity was fixed throughout the experiment. Craik obtained curves for several adapting field intensities. The open circles in Figure 4 were obtained with a
1.1 log td. preadaptation field. The obvious feature of these data, and the other conditions not shown, is that they fall along a curve of approximately the same shape as before, but now the entire curve is shifted vertically.

Experiment 1: As will be seen, Craik's experiment is very important, but it has never been fully replicated or extended. (However, some of the data obtained by Onley and Boynton (1962) provide a partial replication of one of Craik's conditions in which the matching eye was preadapted to a fixed level. Their experiment will be described later.) Furthermore, Craik mentioned in his paper that he had some problems with apparatus stray light, with intensity control, and with variations in pupil size. In any event, before drawing conclusions from his results, we decided to replicate the base condition (the lower curve in Figure 4). However, in order that this experiment might be more comparable to the increment threshold experiments described later, a slightly different stimulus configuration and procedure were used. Instead of using a successive brightness matching technique with large $45^\circ$ fields, small adjacent fields were simultaneously presented for comparison.

Method. The stimulus configuration, as seen by the subject in maxwellian view, is shown at the top of Figure 3b. It was comprised of two semicircles, one presented to the left eye and the other to the right eye, and a pattern of 5 dim red fixation lights which were presented to both eyes to help maintain binocular fusion. Together, the semicircles subtended a visual angle of $5^\circ$, and were composed of white light (color temp. 3000$^\circ$ K). Subjects were instructed to fixate the center fixation light.
The stimulus presentation sequence, which was computer controlled, is shown in the bottom half of Figure 3b. After dark adapting for 10 min, the right eye field was turned on and the subject adapted to it for 2 min. This was followed by presentation of a series of trials that consisted of turning off the continuous right eye field for $\frac{1}{2}$ sec, pulsing the left and right eye fields on and off together for $\frac{1}{2}$ sec, and then $\frac{1}{2}$ sec later, turning the right eye field back on until the next trial.

The interval between trials was 10 sec. It was hoped that this was enough time between presentations for the left eye to remain relatively dark adapted. (In fact, results of threshold studies (e.g., Crawford, 1947) suggest that at least for the intensities of the left eye field reached in this study, this is approximately true.)

Subjects controlled the intensity of the field pulsed to the dark adapted left eye, and adjusted it to have the same brightness as the field simultaneously pulsed in the right eye. The computer recorded the subject's final setting, and then the subject began adapting to the next right eye field intensity. In all experimental sessions, subjects started with the lowest right eye field intensity and worked upward to the highest. Therefore, as in Craik's experiment, for each continuous adapted light presented to the right eye, we find the intensity of a light pulsed in the dark adapted left eye that has the same brightness. However, as in Craik's experiment, slight color differences developed between the lights presented to the adapted and unadapted eyes.

Results. Two practiced observers served as subjects, and both produced similar results. (The data for both subjects are given in Table 1 of the Appendix.) The solid circles in Figure 5 are the data from two experimental sessions, for subject W.G.
Despite the differences in procedure and stimuli, these results are very similar to Craik's, shown in Figure 4. The slope of the linear portion of the curve is .70, as compared with Craik's slope of .65. Furthermore, both curves begin to flatten out for adapted field intensities above 3 to 3.5 log td.

B. Effects of Photopigment Depletion on Brightness

What produces the large changes in apparent brightness shown in Figures 4 and 5? To begin with, it is necessary to ask how much of the effect is due simply to the depletion effect. Clearly, the light pulsed to the relatively dark adapted left eye will always fall on nearly a full complement of unbleached photopigment, but the continuous light in the right eye will bleach all but proportion $p$ of the photopigment in the receptors, where $p$ is given by equation (3) in Section I. Thus, the depletion effect has the potential of producing changes in brightness.

Suppose the depletion effect is the only adaptation process in operation. In this case, a matching field of intensity $I'$, and an adapted field of intensity $I$, would have the same brightness, if the quantum absorptions per second for each field were the same; that is, if

$$Q' = Q.$$ 

For lights falling on a relatively dark adapted retina, $p = 1.0$, but in general this is not true for the adapted eye; therefore

$$Q' = c \cdot I'$$

and

$$Q = c \cdot I \cdot p.$$
Using equation (3) to replace $p$, shows that according to the depletion effect, the two fields should match when,

$$I' = \frac{I \cdot \alpha}{I + \alpha}$$

(12)

where $\alpha = 20,000$ tds. for cone bleaching. (Throughout this paper, $\alpha$ is taken to be 20,000 td.) The dashed line in Figure 5 shows the predictions of equation (12). Again, as was the case for dark adaptation thresholds, it is seen that most of the observed changes in brightness are due to some adaptation process other than the simple depletion of photopigment. For the reasons given at the end of Section II, these brightness effects are probably not due to "dark light" signals, but to the relatively much stronger "real light" signals, that apparently tune down visual responding when a light is left on continuously.\(^7\)

An interesting aspect of the depletion effect is its prediction that the brightness matching function should break over sharply in the neighborhood of 3.5 to 4.5 log td. Is this, in fact, the reason that the data show a similar flattening out for adapted lights above 3.5 log tds? One way to test this hypothesis is to partial out the depletion effect, as before, by plotting the data in terms of quantum absorptions per second. However, it is more instructive to assume instead, that without the depletion effect the data would have continued along the straight line that describes the data at low intensities. Then, the depletion effect can be added back in, to see how well the resultant function agrees with the actual data.

First, note that the data in Figure 5 are approximately linear on a log-log plot for intensities below 3.5 log td. In other words, the data are described by a function of the form,
\[ \log I' = a \cdot \log I + b \]  

(13)

The "depletion effect alone" curve, shows that the depletion effect plays essentially no role at these lower intensities; therefore, equation (13) is totally the result of other adaptation processes. Suppose equation (13) also describes the effect of these other adaptation processes at higher intensities. In other words, suppose that the data would be described by equation (13) at all intensities if there were no depletion effect. This is shown by the dotted line in Figure 5, that was obtained by setting \( a = .70 \) and \( b = -.70 \) in equation (13). Now, as shown earlier, depleting all but proportion \( p \) of the available photopigment is equivalent to reducing a light of intensity \( I \) to \( p \cdot I \). Therefore, the predicted relationship between a light pulsed in the dark adapted eye and a light to which the other eye has become completely adapted is given by eq. (14);

\[ \log I' = a \cdot \log(p \cdot I) + b \]  

(14)

where,

\[ p = \frac{a}{a + I} \].

The dotted/dashed line in Figure 5 is a plot of this function for \( a = 20,000 \) td. The same analysis was carried out for Craik's data, and the predicted functions are plotted in Figure 4.

The depletion effect does correctly predict the shape of the data, but the asymptotic brightness of the adapted lights is over predicted by
about 1/3 log unit. There are two possible reasons for this. One possibility is that the effect of the other adaptation processes alone is not described by eq. (13) at high adapted light intensities. If in fact the dotted function in Figure 5 were to decelerate some at high intensities, then the combined processes would more accurately account for the results. The other possibility is that densitometry measurements are in error; that is, that $\alpha$ is really smaller than 4.3 log td. If it is assumed that eq. (14) is correct, then the half bleaching constant, $\alpha$, can be estimated from the data by forcing eq. (14) to predict the correct asymptotic brightness. Doing this gives an average value, for $\alpha$, of about 3.8 log td. which is 1/2 log unit lower than Rushton & Henry's (1968) estimate. It should be added that Rushton's estimates of $\alpha$ in fact vary from experiment to experiment, and are sometimes as low as 3.8 log td. (Rushton, 1965a).

In any event, the analysis presented here shows that for daylight intensity levels, the depletion effect plays an important role in visual perception — it is probably the primary reason brightness remains constant for all steady state retinal illumination levels above 4 log td.

C. Brightness After Preadaptation to a Fixed Level

Another important aspect of Craik's data, that was mentioned earlier, is that the effect of adapting the matching eye to a fixed level is to shift the entire curve vertically by some fixed amount (see open circles in Figure 4). Interestingly, this is exactly the result one would expect if the effect of adapting to a fixed level was to reduce visual response to all lights as if multiplying their intensities by a factor between 0 and 1. In other words, Craik would have gotten the same results if he simply ran the dark adapted condition (solid circles) with an appropriate filter over the subjects left eye (i.e. matching eye).
Similar results are found in the binocular brightness matching experiment carried out by Onley and Boynton (1962). The data obtained from subject J. O. are shown in Figure 6. The vertical axis shows the intensity of one half of a 5° bipartite field pulsed for 300 msec to the right eye, that has the same apparent brightness as the other half which was presented simultaneously to the left eye, and whose intensity is given along the horizontal axis. The bipartite field was presented once every 6 sec, but between presentations each eye viewed a 10° preadapting field. The preadaptation field in the right eye (i.e., matching eye) was always fixed at 0 log mL (i.e., about 1 log td.). However, the preadapting field in the other eye was not -- each set of points connected by solid lines in Figure 6 was obtained with the preadaptation field whose intensity is indicated at the base of the function. Thus, each solid line curve was obtained with a fixed state of adaptation in the test eye. (Of course, the state of adaptation in the matching eye is also fixed.)

If these data agreed exactly with Craik's finding that adaptation to a fixed level reduced all lights by a fixed factor, then all the curves in the figure would be parallel. This seems to be approximately correct, although there is some tendency for the functions to come together at high test field intensities.

Also from Figure 6, a replication of one of Craik's curves can be extracted; the one obtained with a 1 log td. level of preadaptation in the matching eye. (However, since in Onley & Boynton's study the matching eye was always adapted to 1 log td., none of their data provides a replication of Craik's dark adapted condition that was replicated in Exp. 1.) The X's in Figure 6 are the points that should fall along a Craik function, since they are the points for which the preadapting and test field
luminances are the same. The Craik function formed by the $X$s seems to be most similar in shape to the data from Exp. 1. This can be seen from the dotted line, which is the same curve that is drawn through the data in Figure 5, but shifted vertically by an appropriate amount.\footnote{6} Finally, $\alpha$, the half bleaching constant, can also be estimated from the $X$s in the same way as before. The value obtained is about 4.0 log td. which agrees well with the other estimates. Thus, despite differences in procedure, Onley and Boynton's results agree fairly well with those of Craik and Experiment 1.

In summary, the Craik function (e.g., the solid circles in Figure 5) shows the effects of adaptation on the brightness of lights, over the whole range of intensities that the visual system normally encounters. For any intensity light along the horizontal axis, the difference between the diagonal line of slope 1, and the Craik function gives a measure of the total change in apparent brightness that the light undergoes, from when it is first presented to the dark adapted until the eye has become completely adapted to it. The reduction in the brightness of lights for intensities up to 3.5 log td. (the linear part of the Craik function) is primarily the result of adaptation processes other than the depletion effect. However, these other adaptation processes seem to behave in a simple fashion — they reduce the brightness of lights as if multiplying their intensities by a factor between 0 and 1. For adapted light intensities above 3.5 log td. the depletion effect becomes important, and is probably the primary reason the Craik function flattens out.

Clearly, the results of Craik’s experiment (and Onley & Boynton’s) form a basic set of data that adequate models of adaptation should be able to predict. However, it should be emphasized again that Craik’s experiment only measures the relative brightnesses of lights at the end-
points of the light/dark adaptation continuum. Presumably, if brightness matches were obtained at various times after the onset of continuously presented lights, a family of curves would be obtained (indexed by time since onset of the continuous light), lying between the diagonal line and Craik's function. Similarly, another, although probably somewhat different, family of curves would be obtained if brightness matches were made at various times after the offset of lights to which the eye has become completely adapted (i.e., during dark adaptation). Obviously, all these data would provide a much more complete picture of the effects of adaptation on apparent brightness; however, Craik's experiment does set the limits within which all these data must lie.
Footnotes

6. The vertical position of the dotted curve was determined as follows. From Figure 5 it is seen that adapting to a 1 log td. light is equivalent to reducing its intensity by a factor of 10. But, since preadapting to a fixed level has approximately the effect of reducing the intensity of all lights by the same factor, then preadapting to 1 log td. in the matching eye would shift the solid curve in Figure 5 vertically by 1 log unit. This is the dotted curve plotted in Figure 6.

7. This conclusion is based upon the assumption that the adaptation effects produced by the "real light" signals from a continuous background will not dissipate during the 1/2 sec (or 1 sec in Craik’s experiment) that the continuous background is turned off. Since "dark light" and "real light" signals supposedly affect the visual system in the same manner, then both types of signals must be able to trigger adaptation mechanisms that produce reductions in brightness. The analysis presented earlier (at the end of Section II) simply showed that for continuous adapted lights, the "dark light" signal is negligible relative to that of the "real light;" therefore, its contribution can be ignored. On the other hand, if the effects of the "real light" signals were to decay during the 1/2 sec of darkness, then it would be the effects of the persisting "dark light" (plus the depletion effect) that are being observed in Experiment 1. We are currently testing this hypothesis experimentally, and very preliminary results suggest that the "dark light" effects are relatively small under the present conditions. Throughout this paper, it will be assumed that a 1/2 sec gap in a continuous background field is not large enough for the adaptation effects of the "real light" signals
to decay to the point where the "dark light" signals make a significant contribution. However, depending on the results of current experiments this assumption may have to be altered.
IV. Adaptation: Intensity Discrimination

Brightness is largely dependent upon the current state of adaptation; to what extent is this also true of our ability to discriminate lights on the basis of intensity? Craik's experiment provides a natural starting point in the study of brightness effects. This section begins by considering the analogous experiment for intensity discrimination.

A. Intensity Discrimination in the Unadapted and the Steady State

Adapted Eye

Intensity discrimination is usually measured with the increment threshold experiment. In other words, it is measured by finding out how much light must be added to a background light in order for the addition to be just detectable. Therefore, an intensity discrimination experiment analogous to Craik's is to obtain increment thresholds on lights flashed in the dark adapted eye, and compare these to increment thresholds obtained on lights after they have been viewed for a long time. The second case, that is measuring increment thresholds on continuously presented backgrounds, is simply the well known classical increment threshold experiment, which under most circumstances yields the generalized Weber's law (eq. (8), Section II). There have also been a number of studies that have measured increment thresholds on pulsed backgrounds (Bartlett, 1942; Brindley, 1959; Cornsweet and Pinsker, 1965; Sperling, 1965; Leshowitz, Taub and Raab, 1968; Alpern, Rushton, and Torii, 1970). However, only two of these studies obtained both the continuous and the pulsed increment thresholds functions within the same experiment, and then only over a limited range of background intensities. In Experiment 2 this range is extended and it is found, in agreement with these earlier studies, that Weber's law describes intensity discrimination in both the adapted and the unadapted eye. (However, Alpern, Rushton, and Torii report deviations from Weber's law at high background
intensities; the reason for this will be explained later.) In addition, it is shown that adaptation produces an overall improvement in intensity discrimination (i.e., a smaller Weber fraction).

Perhaps the most important point of this paper, however, is that these increment threshold functions, obtained in the dark adapted eye, are composite functions reflecting the sensitivity of two different underlying processes. In particular, short-term positive afterimages mediate intensity discrimination at high background intensities in the unadapted eye. In Experiments 3 and 4 a simple technique is used to eliminate the afterimages, and it is found that intensity discrimination, under any fixed state of light adaptation, is not described by Weber's law, but by a continuously accelerating function whose slope exceeds 2 at high background intensities.

Experiment 2.

Method. The stimulus configuration used in all the increment threshold experiments described in this section is shown at the top of Figure 7. The display was comprised of a 45' increment field centered in a 5° circular background field, that in turn, was surrounded by 4 dim red fixation lights. Subjects viewed the entire display with the right eye, in maxwellian view, and were instructed to fixate the center of the imaginary cross formed by the fixation lights. Before presenting any stimuli, the subjects first dark adapted for 10 minutes.

The stimulus presentation sequences for the pulsed and continuous conditions are shown in the top two lines of Figure 7. In the pulsed (dark adapted) condition (line 2), the background and increment fields were flashed on and off together for 50 msec once every 10 sec. Thresholds were measured by having subjects adjust the intensity of the increment field until it was just at the threshold of being detectable. Increment thresholds in the
continuous (adapted) condition (line 1) were measured in exactly the same way except the background field remained on continuously, and subjects first viewed the background field alone (every time its intensity was changed) for at least two minutes before adjusting the 50 msec increment field to threshold. Experimental sessions always began with the lowest background intensity and worked upwards to the highest.

Results. The data for subject W. G. are shown in Figure 8. (Measurements under these conditions were also made for three other subjects as part of Exp. 3; all subjects produced results very similar to those in Figure 8.) The data plotted in Figure 8 are increment threshold functions; that is, the vertical axis gives log intensity of the increment flash needed for threshold as a function of log background intensity, given on the horizontal axis. The open circles are the increment threshold function obtained with the continuous background, and the solid circles the increment threshold function obtained with the pulsed background. Both increment threshold functions approximately obey Weber's law for moderate to high intensities; in other words, the data points roughly fall along a diagonal line of slope one. However, over the range where they obey Weber's law, threshold is about 10 times (1 log unit) lower in the continuous (or light adapted) case than in the pulsed (or dark adapted) case. Also note that the functions must come together at low intensities, since when the background is turned all the way off the two conditions are identically the same.

Discussion. On the basis of the previous studies listed above, it was expected that the increment threshold functions for pulsed and continuous backgrounds would obey Weber's law for moderate through high intensities. However, the two previous studies that measured increment threshold functions under both conditions (Cornsweet & Pinsker, 1965; Leshowitz et. al., 1968) were not primarily interested in the effects of adaptation on intensity
discrimination so their results had to be replotted, under appropriate assumptions, in order to be compared with those in Figure 8; however, doing this shows that they agree with the present finding that adaptation reduces threshold by a constant factor at all but the lowest background intensities.

On the basis of all these data, it would seem that intensity discrimination is described by Weber's law regardless of the state of adaptation, since obviously there is little room for deviation from Weber's law between the two Weber functions that define the endpoints. Furthermore, it appears that the effect of adaptation is to improve intensity discrimination by a constant factor for all but the lowest background intensities.

Unfortunately, this simple picture is deceptive. In 1959, Brindley noted that at high background intensities, intensity discrimination in the dark adapted eye (measured under conditions similar to those in Experiment 2) seems, subjectively, to be based upon afterimages of the background and increment flashes, and not upon the initial appearance of the stimuli when they were flashed. Subjects in Exp. 2 made similar observations.

If afterimages are mediating detection at high intensities, then what would intensity discrimination be like if afterimages were not present? The straightforward approach is to use Brindley's technique, which is to ask subjects to ignore the afterimages and base their judgments upon initial appearances. This technique does not work. The reason is that the increment field is seen so immediately in the quickly decaying positive afterimage that subjects cannot decide if it was present in the initial flash. (The subjective appearance of these afterimages will be discussed shortly.)
Experiment 3. The solution to the problem was found in the simple experimental procedure of extending the duration of the background field. That is, the increment field is still flashed on and off for 50 msec once every 10 sec, and its onset is simultaneous with that of the background field, but now the background field is not turned off until some time after offset of the increment field. The effect of this procedure is to mask the afterimages, preventing them from mediating detection, so that intensity discrimination on the basis of initial appearances can be measured over a wider range of background intensities.

Method. The stimulus configuration and the method of obtaining increment thresholds were exactly the same as in Experiment 2. Increment threshold functions were obtained for the six conditions shown in Figure 7. That is, in addition to the 50 msec, and continuous background conditions of Experiment 2, increment thresholds were measured for 100, 200 and 500 msec backgrounds. Also included was a continuous condition with a 500 msec gap just before presentation of the increment field. This condition was included in order to provide an increment threshold condition that might be more comparable to the brightness matching experiments; Craik's, and Experiment 1.

As in Experiment 2, the duration of the increment field was always 50 msec, and its onset was simultaneous with that of the background field (except, of course, in the without-gap continuous condition).

In a given session, increment thresholds were obtained at all background intensities for one of the six conditions. Each of the four practiced subjects that participated in the experiment went through the six conditions three times.
For the 500 msec background condition, two separate increment threshold functions can be obtained; one by asking the subject to base his judgments upon whether the increment field was seen in the afterimage, and the other upon whether it is seen at the onset of the background field. These additional increment threshold functions were obtained from two of the four subjects.

**Results.** Consider first the increment threshold functions obtained with the 500 msec background. This is a particularly important condition since with 1/2 sec between initial appearance and afterimage, subjects have no difficulty deciding which cue is mediating detection. This means that thresholds for detecting the increment can be obtained either on the basis of initial appearances, at the onset of the 500 msec background, or on the basis of the appearance of the afterimage.

Surprisingly, at high background intensities, with the 500 msec background, detection is still most sensitive when based upon afterimages. That is, even though the increment field is flashed simultaneously with the onset of the background field, it is not until a half second later, when the afterimage appears, that the increment field is seen. Figure 9 is meant to give an idea of the appearance of these stimuli at high background intensities. The white rectangular areas show stimulus intensity over time; the upper one for the 100 msec background condition, and the lower one for the 500 msec background condition. The circles above the rectangular areas give the corresponding subjective appearance of the stimuli at various times during and after presentation. As the figure shows, the increment field, at high background intensities, is not seen until after the background is turned off. If the increment field is slightly above threshold, the positive afterimage of the background and increment fields persists for about a second or so. As the intensity of the increment
field approaches threshold, the afterimage fades more and more quickly. These effects are particularly dramatic if chromatic increment fields are used, since then it seems all the more paradoxical when a vividly colored increment is not seen until a 1/2 sec after it was presented. Use of colored increment fields also shows that the afterimages are homochromatic (i.e., are the same color as the original stimulus).

The increment threshold functions obtained with the 500 msec background, as well as one obtained for the continuous background (without a gap) are shown in Figure 10. The triangles that fall along the solid line are thresholds for detecting the increment at the onset of the background (that is, on the basis of initial appearances). Clearly, intensity discriminations made on the basis of initial appearance, in the dark adapted eye, do not at all obey Weber's law (compare with the lower most curve which is the increment threshold function for continuous adapted backgrounds), rather they follow a continuously accelerating function whose slope exceeds 2 at high background intensities.

The triangles that fall along the dotted line are thresholds for detecting the increment in the afterimage. Intensity discriminations made on the basis of afterimages approximately obey Weber's law, except that the slope is slightly less than 1.0 (about .9).

The "afterimage" and the "initial appearance" increment threshold functions cross around 4.3 log td. Above 4.3 log td., threshold (in the usual sense) is mediated by afterimages. However, even though the afterimage remains clearly visible, the intensity of the increment field can be turned up to the point where the increment is just detectable at the onset of the background field. This is how the data point on the solid line at 4.5 log td. was obtained. ("Initial appearance" thresholds at the higher background levels could not be measured since they exceeded
the range of the apparatus -- 6.20 log td.)

Below 4.3 log td. detection is more sensitive on the basis of initial appearance. However, the triangles along the dotted line below 4.3 log td. were obtained by turning up the intensity of the increment field until it was just detectable in the afterimage.

Figure 11 shows, for subject W. G., a replication of the 500 msec and continuous background conditions, plus the increment threshold curves obtained with the shorter duration backgrounds. Figure 12 shows the data for subject S. J. (The other subjects produced very similar results, and their data are given in Table 2 of the Appendix). It is seen that the increment threshold functions obtained with the shorter duration backgrounds show the same pattern as that for the 500 msec background. In fact, all the increment threshold functions (for pulsed backgrounds) agree up to a certain point, then there are breaks in the functions, and from then on they approximately obey Weber's law. The longer the duration of the background, the higher the background intensity before a curve begins to follow Weber's law.

The solid triangles in Figure 13 are the increment thresholds obtained on the background that was continuous except for a 500 msec gap just before the increment flash was presented. (The increment threshold functions for the 500 msec and continuous background conditions from Figure 10 are also shown for comparison.) With the 500 msec gap, increment thresholds still obey Weber's law for moderate through high intensities. However, over the range where Weber's law holds, threshold is raised by a constant factor over the without gap continuous condition (lower most curve in Figure 13).

Discussion. The initial reason for trying to mask the afterimages by extending the duration of the background was that when the background and increment fields were of equal duration, subjects could not decide whether
Figure 11
detection was based upon initial appearances, or upon afterimages. As mentioned earlier, subjects had no trouble deciding which cue was mediating detection, when the background was at 500 msec duration, but, they had much more difficulty with the shorter duration backgrounds. However, independent of subjective reports, the form of the data in Figures 11 and 12 is extremely suggestive -- intensity discrimination is based upon initial appearances up to the breaks in the functions; and for background intensities above this point, discrimination is based upon afterimages.

Another important aspect of the data is that the increment threshold functions all agree up to the point where the afterimages take over. This means that the procedure of extending the duration of the background to mask the afterimages does not introduce any unwanted backward masking effects on detection of the increment at the onset of the background field. The data show that for all background durations there is only one increment threshold function that describes intensity discrimination on the basis of initial appearances. Extending the duration of the background has exactly the effect intended; it masks the afterimages so that the "initial appearance" increment threshold function can be traced up to higher background intensities.

The two lower most curves in Figures 11 and 12 are the increment threshold functions for the 50 msec background, and for the continuous adapted background. In fact, the lower two curves in Figure 11 are exactly those of Exp. 2, shown in Figure 8. However, in the context of Figure 11, a slight kink becomes apparent in the 50 msec background function, at around 2.9 log td. (or 1.6 log td. sec). This kink can also be found in the increment threshold functions obtained in many of the studies listed earlier. Brindley (1959), Bartlett (1944) and Sperling (1965) all show
kinks around 1.6 log td. sec. (Thresholds in two of the remaining three studies were obtained only for background energies below 1.6 log td. sec.) It is interesting to note that on the basis of subjective reports, Brindley reported that detection is based upon initial appearances for background energies up to somewhere between 3 and 4 log td. sec -- a value 1 1/2 to 2 1/2 log units higher than that obtained by the objective procedure of Experiment 3.

The original problem that motivated this experiment, and the previous one, was to measure intensity discrimination at the endpoints of light adaptation. Previous work suggested that Weber's law describes intensity discrimination at both endpoints. However, this is only because discriminations on pulsed backgrounds, in the dark adapted eye, are based upon afterimages at high background intensities. The true picture is given in Figures 10, 11, and 12.

It is important to realize that under most real life circumstances afterimages do not mediate intensity discrimination, since background illumination levels change in a step like fashion; rather than in a pulsed fashion. Thus, when one steps out into the sunlight, the "background" remains on; therefore afterimages are masked. Under normal circumstances, it is the continuously accelerating function and the generalized Weber's law that describe the endpoints of the light/dark adaptation continuum for intensity discrimination, just as Craik's function does for brightness.

B. Effects of Photopigment Depletion on Intensity Discrimination

As with brightness matching and absolute threshold, it is appropriate to ask to what extent the depletion effect can account for the effects of adaptation on increment threshold. Consider the changes in threshold predicted by the depletion effect alone. In the dark adapted eye, increment thresholds are described by some function;
\[ \log \Delta I = f(\log I) \quad \text{(15)} \]

(In particular, this function is the continuously accelerating one shown in Figure 13). Now, the effect of depleting all but proportion \( p \) of the available photopigment in the receptors is equivalent to reducing a light of intensity \( I \) to \( p \cdot I \). Therefore, after adapting to a background light (long enough for photochemical equilibrium to be reached), the depletion effect predicts that increment thresholds should be described by,

\[ \log p \cdot \Delta I = f(\log p \cdot I) \]

or,

\[ \log \Delta I = f(\log p \cdot I) - \log p \quad \text{(16)} \]

where,

\[ p = \frac{\alpha}{\alpha + I} \]

The predictions of eq. (16) for \( \alpha = 20,000 \) td. are shown by the dashed line in Figure 13. As expected, the depletion effect cannot account for the large decreases in threshold observed. However, it does predict that light adapted thresholds obey Weber's law at high background intensities (i.e., above about 4 1/3 log td.). This prediction holds almost independently of the function \( f \), since when \( I \) is very large \( p \cdot I \) approaches the half bleaching constant, \( \alpha \). This means that increment thresholds at high intensities are approximately given by,
\[ \log \Delta I = f(\lambda) - \log \frac{\alpha}{(\alpha + I)} \]

Combining terms and taking antilogs shows that,

\[ \Delta I = K \cdot (\alpha + I) \]

where \( K \) is a constant. This last equation is the generalized Weber's law. It is not unlikely that this property of the depletion effect is responsible for the Weber's law behavior observed for cone threshold, at background intensities above 4 1/3 log tds.\(^9\)

As with the brightness results, it is unlikely that "dark light" signals are responsible, to any significant extent, for the observed adaptation effects on increment threshold, since the intensity of the "dark light" produced by the continuous adapted background, is always less than 3% of the intensity of the "real light." Neither increasing nor decreasing the intensity of the continuous background by 3% would produce a noticeable change in the results of Experiment 3 (see footnote 7).

C. Short-term Afterimages and Bloch's Law

One curious aspect of the data in Figures 11 and 12 is that the afterimage increment threshold functions are all parallel. Why should afterimage discrimination obey Weber's law regardless of background duration? Part of the answer to this question is given by the simple relationship between the afterimage increment threshold functions shown in Figure 14. In this figure, all of subject S. J.'s data, except those obtained with continuous backgrounds, are replotted as a function of the total energy (intensity x duration) of the background, rather than as a function of background intensity. As can be seen, all the afterimage increment threshold functions now collapse onto one function (the heavy black line). For the
other subjects, the afterimage threshold function for the 500 msec background falls somewhat above the afterimage threshold function for all the shorter duration backgrounds. Therefore, intensity discrimination on the basis of afterimages appears to be a function of the total energy of the background, for durations up to somewhere between 200 and 500 msec. This suggests that whatever process is giving rise to the afterimages integrates energy (that is, obeys Bloch's law) over about 1/4 sec. Put another way, all the afterimage increment threshold functions shown in Figure 12 are expected to be parallel, and shifted vertically by the amounts shown, if the magnitude of afterimage signals is a function only of the total energy of the stimulus.

The long-term afterimages that are seen throughout the course of dark adaptation also have long integration times. Brindley (1959), for example, determined the range over which the appearance of long-term afterimages obey Bloch's law. He finds that for lights of up to 2 sec duration, the appearance of long-term afterimages (excluding the first 15 sec after stimulation) is dependent only upon the total energy of the light. Furthermore, afterimages appear nearly the same for lights up to 5 sec duration.

Brindley argues that such long integration times imply that appearance of afterimages, excluding the first 15 sec, is totally dependent upon photochemical effects; in particular, he suggests that their appearance is solely a function of the amount of photopigment in the bleached state. Indeed, photopigment regenerates slowly (as discussed in Section I); therefore the amount of bleached photopigment will be a function of the total energy of the stimulus up to rather long durations. Brindley's hypothesis is also consistent with Barlow's "dark light" hypothesis that was discussed in Section II, in that he assumes that the afterimages arise from bleached photopigment.
Are the short-term afterimages observed in the present experiment photochemical in origin? This is possible, but they are probably of a somewhat different nature than the long-term afterimages. If, as Rushton (1964) says, the expected time for a molecule of visual pigment to finish the bleaching sequence is around 1 sec, then the short-term afterimages come and go before most of the final bleached products (the ones supposedly responsible for long-term afterimages) have formed. The short-term afterimages may of course, originate from some earlier stages of the bleaching sequence. Unfortunately, matters are complicated by the fact that afterimages are stabilized in the visual system, and like stabilized real light images, one might expect them to fade within a few seconds. Thus, the fading of the short-term afterimages may be due to the effects of stabilization.

D. **Intensity Discrimination after Preadaptation to a Fixed Level**

As long as afterimages are prevented from mediating detection, increment thresholds in the unadapted eye do not at all obey Weber's law. Is this also true if the eye is light adapted to a fixed level instead of dark adapted?

**Experiment 4.** This question was answered by obtaining increment threshold functions exactly as before, but instead of a 10 sec dark interval between stimulus presentations, the interval was filled with an adapting background whose intensity was fixed throughout the experiment.

**Method.** The stimulus configuration and method of obtaining thresholds were the same as in Experiments 2 and 3. The stimulus presentation sequence is shown in the inset of Figure 15. The only difference between this experiment and Experiment 3 was that an adapting field of fixed intensity was turned on 1/2 sec after offset of the background field, and it was turned off 1/2 sec before the background field was turned back on, 10
seconds later. The adapting field was of the same size (5° visual angle), and in the same position as the background field.

Subjects first dark adapted for 10 min., and then adapted to the fixed intensity adapting field for several minutes before increment thresholds were measured. Increment threshold functions were obtained with and without a 3.3 log td. adapting field for background durations of 50 and 500 msec.

Results. The data for subject W. G. are shown in Figure 15 (data for subject P. D. are in Table 3 of the Appendix). The open triangles and circles are the dark adapted increment thresholds for the 500 and 50 msec backgrounds, respectively. The solid circles and triangles are the thresholds obtained with a fixed level of preadaptation.

The increment threshold functions for the fixed level of adaptation have approximately the same shape as those obtained in the dark adapted eye — they are continuously accelerating when detection is based upon initial appearances, and they obey Weber's law when detection is based upon afterimages. However, now the functions are slid up and to the right approximately alone a 45° line. The sliding seems, however, to be a bit more to the right than up, for the 50 msec background condition, in that afterimage thresholds are a little lower in the preadapted case. Perfect 45° sliding would leave the afterimage thresholds unchanged (as is the case with the 500 msec background).

Discussion. There are two important implications of this experiment. First, the results lead to the conclusion that intensity discrimination, on the basis of initial appearances, does not obey Weber's law when the eye is either dark adapted or light adapted to any fixed level; it is only when the eye is adapted to each background before threshold is measured, as in the classical increment threshold experiment, that Weber's law is found.
Figure 15
Second, preadapting to a fixed level shifts the dark adapted increment threshold function up and to the right approximately along a 45° line. This is exactly what is expected if the effect of adapting to a fixed level is to reduce visual response to all lights as if multiplying their intensities by a factor between 0 and 1. To see this, note that an increment threshold function plotted in log-log coordinates is of the form of equation (15). If preadapting to a fixed level in effect multiplies all lights by a factor $\mu$ ($0 < \mu < 1$), then the visual system will respond as if it were presented with lights of intensities $\mu \cdot \Delta I$, and $\mu \cdot I$. Thus, after light adapting, thresholds should be given by,

$$\log \mu \cdot \Delta I = f(\log \mu \cdot I)$$

or,

$$\log \Delta I + \log \mu = f(\log I + \log \mu).$$

Since $\log \mu$ is less than zero this increment threshold function is simply eq. (15) plotted in the coordinate system translated up and to the right - log $\mu$ units.

The results of Craik and Onley & Boynton, that were discussed earlier, showed that the effect of light adapting to a fixed level was to reduce the brightness of all lights as if multiplying their intensities by a factor between 0 and 1. The results of the present experiment suggest that this may also be approximately true for increment thresholds.

E. **Intensity Discrimination After Partial Light Adaptation**

The experiments in this section have shown how the subtle intervention of afterimages have, in the past, masked the dramatic deviations from
Weber's law that now seem to be the rule rather than the exception. However, this is not the first time deviations from Weber's law have been observed.

First of all, the paradigm used here to mask the afterimages is just a special case of one first used by Crawford (1947) to study the time course of light adaptation. He determined thresholds for detecting increment flashes that were presented at various times before, during, and after onset of a 524 msec background. One of his conditions was the case in which the onset of the increment field was simultaneous with that of the background. Unfortunately, since Crawford was mainly interested in the temporal aspects of adaptation, he only measured thresholds for a few background intensities falling within one a log unit range (2.5 - 3.5 log td.). However, his data do show that increment threshold at the onset of the background is increasing somewhat faster than expected from Weber's law (see the 2.5 - 3.5 log td. range in Figs. 10-12).

Recently, Alpern, Rushton, and Torii (1970) have found deviations from Weber's law at high intensities on pulsed backgrounds. However, their function is not like those shown in Experiments 3 and 4 -- it closely follows Weber's law up to very high background intensities, and then begins to positively accelerate. Furthermore, their function does not show kinks or any other sign of the afterimage process.

The main procedural differences between the Alpern et al. experiment, and all the others presented (or cited) here are, (1) the increment field (of 20 msec duration) was presented 40 msec after onset of the 100 msec background (i.e., it was centered halfway through presentation of the background), and (2) the subject initiated each stimulus presentation, and thus the level of light adaptation was not well specified.

By delaying presentation of the increment field, Alpern et al. presumably
have measured one of the increment threshold functions that fall between the continuously accelerating function at one endpoint of adaptation, and the generalized Weber's law at the other endpoint. In other words, the eye has time to partially adapt to each background intensity before threshold is measured. Thus, perhaps it is the adaptation that has gone on during the first 40 to 60 msec that has produced the differences in shape. Experiment 5 shows that apparently this is the case.

**Experiment 5**

**Method.** The stimulus configuration and general procedure are the same as in the previous experiments. Increment threshold functions were measured on a 200 msec background for the three conditions shown in the inset of Figure 16. The onset of the increment flash was either simultaneous with the onset of the background, delayed 80 msec, or delayed 160 msec. As usual, there was 10 sec between stimulus presentations, and the subject dark adapted for 10 min. before any thresholds were measured.

**Results.** The three increment threshold functions that were obtained are shown in Figure 16. The open circles show the increment threshold function obtained for simultaneous onset of the increment and background fields, and it agrees closely with those shown in Figures 11 and 12. The triangles are increment thresholds obtained for an 80 msec delay of the increment field, and the squares for a 160 msec delay. The shapes of these increment threshold functions agree much more closely with the one obtained by Alpern et al. They show that the longer the increment field is delayed, the higher the background intensity before deviations from Weber's law are observed. However, the Alpern et al. function does not show any afterimage thresholds (dotted lines in Figure 16).

**Discussion.** There are two possible reasons why the Alpern et al. function
does not display afterimage segments. First is that the self-paced presentation of the stimuli probably resulted in far less than 10 sec between presentations, and thus the resultant greater level of adaptation may have pushed afterimage intervention to even greater background intensity levels. Second, in their experiment a thin cross hair was stretched across the increment field, and subjects were required to adjust the intensity of the increment until the cross hair was just detectable. The cross hair may be relatively less visible in the afterimages, and this could have prevented the afterimages from mediating detection.

In our opinion, the Alpern, et al. condition is complex from a theoretical standpoint, because like increment thresholds measured on continuous backgrounds, the level of adaptation is different at each background intensity. In other words, as background intensity is increased a greater and greater amount of light immediately precedes the increment flash.

An interesting aspect of the Alpern et al. function, and those in Figure 16, is their similarity in shape to those obtained for rod increment thresholds on continuous adapted backgrounds (Aquilar & Stiles, 1954). Perhaps, use of the procedure of Exp. 3 will show that rod increment thresholds in the relatively dark adapted eye also follow a continuously accelerating function.

In any event, the experiments presented here show that all the differently shaped increment threshold functions that have been obtained, fit within one consistent picture -- the one given by Figures 11 (or 12) plus 15.

This section set out to determine the discriminability of lights at the endpoints of the light/dark adaptation continuum, by measuring increment thresholds on background lights pulsed in the dark adapted eye, and by measuring increment thresholds on continuous background lights to which
the eye has become adapted. The first experiment, in conjunction with
previous results, led to the conclusion that Weber's law describes intensity
discrimination at both endpoints of adaptation. However, this apparently
straightforward result was drawn into question because subjects reported
that short-term afterimages of the background and increment fields appeared
in the pulsed condition, at high background intensities. In order to mask
the afterimages, subsequent experiments used the simple procedure of
extending the duration of the background field beyond offset of the incre-
ment field. The results of these experiments lead to the following con-
clusions:

(1) There are two fundamentally different processes underlying
intensity discrimination if background lights are not on continuously. At
low background intensities discrimination is based upon initial appearances,
at high intensity levels it is based upon afterimages.

(2) The experimental procedure of extending the duration of the
background field clearly separates the increment threshold functions for
the two processes so now they presumably can be studied independently.

(3) Intensity discrimination on the basis of initial appearances
does not obey Weber's law if the eye is in any fixed state of light adap-
tation, rather it is described by a continuously accelerating function
whose slope exceeds 2 at high background intensities. Weber's law holds
(for intensity discrimination on the basis of initial appearances) only
when the eye is allowed to adapt, at least partially, to each background
intensity level before threshold is measured.

(4) Intensity discriminations made on the basis of afterimages are
approximately described by Weber's law, although the slope of the incre-
ment threshold function is slightly less than 1.0.
(5) The process responsible for producing the short-term afterimages apparently integrates the energy of lights (obeys Bloch's law) for durations up to 1/4 sec to 1/2 sec.

(6) As is the case for brightness matching and dark adaptation thresholds, the depletion effect can account for only a small fraction of the effects of adaptation on intensity discrimination. However, at high steady state intensities the depletion of photopigment becomes a significant factor, and may be responsible for the fact that cone increment thresholds are described by Weber's law on arbitrarily intense continuous backgrounds. On the other hand, "dark light" signals apparently play a negligible role.

(7) The other adaptation processes that are responsible for most of the changes in increment threshold, seem to behave in approximately the same simple fashion observed for the brightness results -- adaptation reduces neural response to the background and increment lights as if multiplying their intensities by a factor between 0 and 1.

(8) Intensity discrimination at the endpoints of the light/dark adaptation continuum is not described by two generalized Weber functions, but by a continuously accelerating function at one end, and the generalized Weber law at the other. These two functions and Craik's function form a basic set of results that adequate theories of adaptation should be able to explain.

F. Some Temporal Aspects of Light Adaptation Thresholds

The remainder of this section is concerned with some temporal aspects of light adaptation thresholds. In particular, an experiment is described that tests the hypothesis, proposed by Sperling (1965), that the decreases in threshold observed immediately after onset of a background field are due to decision factors. Sperling's hypothesis is rejected, and in the
process a curious sensitization effect is observed at the offset of the background field.

As described earlier, Crawford (1947) measured threshold for detecting increment flashes that were presented at various times before, during, and after onset of a 524 msec background field. Crawford found that threshold is maximum when the background and increment fields onset simultaneously, and that threshold decreases quickly, and then more slowly, as the increment field comes on further and further after onset of the background field. The decrease in threshold at the onset of the background field is often referred to as the "on-effect" or the "on-response effect" (Boynton and Kandel, 1957).

The relationship of the Crawford experiment to Exp. 3 should be obvious -- for a given background intensity, the Crawford experiment measures the transition over time from the increment threshold given by the continuously accelerating function, to the increment threshold given by the generalized Weber function (see Figure 10). The continuously accelerating function measures the maximum of the on-effect as a function of background intensity.

A common explanation of the on-effect (e.g., Boynton & Kandel, 1957) is based upon the large body of electrophysiological data showing that neural responses, recorded at almost any level in the visual system, are at a maximum when a light is first turned on, and decline quickly thereafter.

Although the theory presented later in Section VII takes the view that these neural (or photochemical) adaptation processes are responsible for on-effects, it is important to realize that the mere existence of transient adaptation effects in the visual system does not imply that increment thresholds should display on-effects. The reason is that even
though at the onset of the background the visual system is responding more vigorously to the background field, it is also responding more vigorously to the background plus increment fields. At a later time, response to the background is reduced, but so is response to the background plus increment. Therefore, without more knowledge about the mechanisms underlying these transient neural responses, it is impossible to say whether they predict that increment threshold should be raised, lowered, or left unchanged. (As will be seen in Section V., the same logic applies to the effects of inducing fields on increment thresholds.) The point here, is that reasonable hypotheses for the on-effect need not be based either implicitly or explicitly on anything like the transient neural responding that has been observed electrophysiologically.

Sperling (1965) suggested that decision factors are responsible for thresholds being maximum at the onset of the background. (However, Sperling may no longer consider his 1965 hypothesis reasonable, in light of his recent and more elaborate models of light adaptation - Sperling and Sondhi, 1968; Sperling, 1970). In particular, he proposes that detection of the increment may arise either in the temporal, the spatial, or in both dimensions. If detection is purely spatial, then it is mediated by simultaneous differences in neural response from different retinal locations (e.g., the background plus increment area, and the surrounding background area). On the other hand, in purely temporal detection, threshold is mediated by changes in neural response from one retinal location over time. Sperling argues that only spatial information is available when the onset of the increment is simultaneous with that of the background; however, as presentation of the increment field is increasingly delayed, temporal information becomes available and threshold decreases.
It is not difficult to see how this argument would apply if the background and increment fields were of the same size, since then the only way to detect the increment is to compare appearance of the background plus increment with that of the background which precedes and follows it. However, Sperling never states explicitly why or how the temporal information adds to the spatial information that is always available when the increment has a smaller diameter. Nevertheless, Sperling's hypothesis has been taken seriously enough (Kahnemann, 1968; Boynton, 1972) that it was decided to test it directly. The experiment also allows us to eliminate certain other hypotheses. For example, on-effects may be observed simply because the onset of the background constitutes a dramatic change in stimulation; in other words, thresholds might be raised as if a hammer was hooked up to hit the subject's chin whenever the increment was presented.

**Experiment 6.** The test of Sperling's hypothesis is simply to force all detections to be made in the spatial dimension regardless of when the increment field is flashed relative to the onset of the background. This was accomplished by always incrementing the intensity of the background field by a fixed amount (i.e., adding a fixed pedestal) just during the time when the increment field was flashed. Since the briefly flashed increment field must be detected on top of an equal duration (and visible) pedestal, only spatial information (in Sperling's sense) is available. Furthermore, because the pedestal intensity is fixed, all observed changes in threshold must be due to effects produced by the background field. Therefore, if the background still produces the on-effect then Sperling's hypothesis is incorrect.

**Method.** The stimulus configuration, shown in the top half of Figure 17, was the same as was used in the previous experiments, except that the background (and pedestal) was 3° in visual angle rather than 5°. (Note,
this is a 3-dimensional drawing -- the vertical axis is intensity.) Again, the entire display was presented in maxwellian view to the right eye, and subjects fixated the center of the imaginary cross formed by the fixation lights.

After dark adapting for 10 min. at the beginning of the session, subjects were presented with one of the two types of stimulus conditions shown in the bottom half of Figure 17. The lower condition is a typical Crawford paradigm. The background field is pulsed for 500 msec once every second, and the increment field is flashed for 8 msec at some time either before, during, or after onset of the background field. Two intensities of the background were used, 2.5 and 3.5 log td. Thresholds were obtained by the method of adjustment.

In this experiment the increment field was flashed only on every other presentation of the background field. This procedure was used because, chronologically, this experiment was the first carried out, and all subjects (including the author) were inexperienced in making psychophysical judgments. Everyone was more confident in their settings if, for comparison purposes, they could frequently see the stimulus without the increment. (However, after practice it was found that the comparison stimulus was unnecessary, and in later experiments it was excluded.)

The pedestal conditions (upper condition shown in Figure 17) were the same as the standard Crawford paradigm, except that during the 8 msec that the increment was flashed, the entire 3° background was also incremented in intensity by a fixed amount. Pedestal intensities were picked so that the pedestal was clearly visible if flashed while the background was on.

Results. The data for subject G. G. are shown in Figure 18. Three other subjects participated in this experiment, and all produced data very
similar to those shown in Figure 18. (Data for all subjects are given in Table 4 of the Appendix.)

Only the data for the 3.5 log td. background are shown here. The lower most curve (solid circles) are the data obtained in the standard Crawford paradigm. The vertical axis gives the log intensity of the increment field needed for threshold. The horizontal axis gives ΔT, the time of onset of the background minus the time of onset of the increment. At ΔT = 0 the background and increment fields onset simultaneously, and threshold is at a maximum. Threshold then decreases as ΔT increases; in other words, threshold decreases as the increment flash comes on further after onset of the background field. This is Crawford's on-effect. Each of the upper curves in Figure 18 gives the thresholds obtained for the same background intensity, but with the added pedestal whose log intensity is given at the right.

Discussion. The first thing to note is that the results of the pedestal conditions, especially those for the 4.4 and 4.9 log td. (i.e., 2.3 and 2.8 log td. sec) pedestals, contradict Sperling's hypothesis. Since the pedestal produces a visible increase in brightness of the background, temporal information (in Sperling's sense) was never available, and thus the on-effect should have disappeared. On the contrary, the on-effect is of equal magnitude for the 4.4 log td. pedestal, and only slightly smaller for the 4.9 log td. pedestal.

Although obtaining the on-effect for any of the pedestal conditions is sufficient to reject Sperling's hypothesis, it is, however, true that the on-effect is diminished as pedestal intensity is increased. This is probably due to the fact that afterimages were mediating detection on the high energy pedestals. Curiously, at the time this experiment was run we didn't know what to make of subjects reports that the increment was
not seen when the pedestal was flashed, but was seen afterwards against
the background field. Subjectively, afterimages were clearly visible
with the 5.4 log td. (3.3 log td. sec) pedestal, and perhaps to some
extent with the 4.9 log td. pedestal. Since afterimages tend to persist
for some time (see Figure 9), transient neural responses produced by onset
of the background field may only temporarily interfere with perception of
the afterimage, leaving threshold for the most part unaffected.

One other interesting aspect of the data obtained with the 4.4 log td.
pedestal is that there is a dip in threshold at the offset of the back-
ground field. The other three subjects in the experiment show the same
effect. Increases in threshold, the "off-response" effect, have been
reported before, but never a sensitization effect.

Perhaps, this dip in threshold reflects the recovery of whatever
adaptation process is producing the on-effect. In particular, the background
field does produce adaptation effects that lower increment threshold. At
the offset of background, neural response to the background light itself
may die away quickly, but leave adaptation effects that still lower
increment threshold on the pedestal. However, some of the adaptation
effects may also recover fairly quickly (perhaps about as fast as they
develop), and thus increment threshold on the pedestal climbs back up.

In conclusion, it appears that decision factors are not responsible
for threshold being maximum at the onset of a background field; rather,
the decreases in threshold observed after onset of the background field
are probably due to some neural adaptation mechanism. Experiment 4 presented
some evidence that this mechanism has the property of reducing neural res-
response to lights as if multiplying their intensities by some factor between
0 and 1. As shown in Figure 15, a mechanism with this property predicts
that adaptation to a 3.3 log td. background field lowers increment threshold on backgrounds of equal or greater intensity; therefore, it also predicts that on-effects would be observed in the present experiment. However, this is only because the dark adapted increment threshold function has slope greater than one at all but the lowest background intensities. If the increment threshold function in the dark adapted eye obeyed Weber's law (like the afterimage thresholds), then multiplying by a factor between 0 and 1 would not have any effect on threshold.
Footnotes

8 In these studies, the increment flash duration was shorter than in the present experiment. With durations less than 50 to 100 msec (the maximum range over which Bloch's law holds (Graham and Kemp, 1938)), it is inappropriate to compare thresholds for continuous and pulsed backgrounds on the basis of the luminance of the background field. This is because Bloch's law insures that with the continuous background, threshold will depend on more than just the energy of the background field that is presented during presentation of the increment field. Thus, for example, in Cornsweet and Pinsker's experiment, that used 5 msec increment fields, appropriate comparison of the pulsed and continuous conditions requires that the continuous increment threshold function be shifted 1 to 1 1/2 log units to the right. This corrects for the fact that Bloch's law holds for up to 50 to 100 msec.

9 This prediction only holds when the increment field is pulsed. If the eye were allowed to adapt to the background plus increment field, then the proportion of pigment bleached would increase above that produced by the background alone, and this leads to the prediction that the increment threshold function be continuously accelerating at high background intensities.
V. Lateral Effects on Brightness and Incremental Threshold

Earlier sections have examined some of the powerful effects that the previous history of lights falling on a region of the retina can have on absolute threshold, brightness, and intensity discrimination of subsequent lights falling on the same region. This section briefly examines some of the important effects that lights falling on neighboring regions exert on each other. However, due to space limitations, discussion will be restricted to lateral effects involving continuously presented lights to which the eye has become adapted.

A. Simultaneous Brightness Contrast

Lateral effects on brightness, in particular simultaneous brightness contrast, is often measured with a binocular matching technique much like the one used by Craik to measure adaptation effects on brightness. A typical stimulus configuration is shown at the top of Figure 19. The stimulus presented to the right eye is comprised of a center field, and an annular nonoverlapping surround field. The left eye views a matching (or comparison) field of the same diameter as the center field in the right eye. In one version of this experiment (Diamond, 1953; Heinemann, 1955), the center and surround fields are set to various intensities, and the intensity of the matching field is adjusted by the subject until it has the same apparent brightness as the center field. Another procedure (Leibowitz, Mote, and Thurlow, 1953; Heinemann, 1961) is to set the surround and matching fields to various intensities and have the subject adjust the center field intensity until it has the same brightness as the matching field. (Obviously, both of these procedures should yield sets of data that are consistent with each other.)
Heinemann (1955) carried out a simultaneous brightness contrast experiment with a surround field outer diameter of 55', and with center and matching field diameters of 28'. His results are shown in Figure 20. Each curve gives the log intensity of the matching field that has the same apparent brightness as the center field (whose log intensity is given at the end of the curve) as a function of the log intensity of the surround. (In Heinemann's figure inducing luminance means the same thing as surround luminance. "Inducing field" is the general name given to the field whose contrast effects are being measured, "test field" is the name given to the field being affected.) What each of the curves in Figure 19 show is that as the intensity of surrounding annular field is increased, the brightness of the center area remains constant (or increases slightly) until the surround intensity approaches that of the center field. Center brightness then decreases sharply to the point where it appears blacker than an unilluminated center without a surround; that is, dimmer than the matching field can be adjusted.

Heinemann's conditions tend to optimize simultaneous brightness contrast effects. If the inducing field does not completely enclose the test field (Diamond, 1953), has smaller area (Heinemann, 1972), or is separated from the test field (Leibowitz, Mote, and Thurlow, 1953), contrast effects are diminished. However, under all the different conditions that have been examined the same pattern arises -- brightness of the test field is relatively unaffected until the intensity of the inducing field approaches that of the test, then test field brightness begins to decrease. The rate at which brightness decreases as a function of inducing field intensity is the primary aspect of the data affected by changes in the stimulus configuration.
Figure 20
Other contrast effects, such as Mach bands (see Ratliff, 1965), are observed in non-uniform fields. Although space limitations prohibit discussion of these effects, they are probably produced by the same mechanisms responsible for the contrast effects observed in paradigms like that of Figure 19.

B. Effects of Steady State Inducing Fields on Increment Threshold

Aside from producing effects on brightness, inducing fields also affect the sensitivity of the eye to changes in test field intensity. The most well known experimental method of investigating these effects is to measure incremental thresholds on continuous center fields, with and without surrounds (Heinemann, 1961; Cornsweet and Teller, 1965; Alpern and Rushton, 1967; Guth, 1973). A typical experiment of this type is illustrated in the bottom half of Figure 19. In the without-surround condition the surround is turned off, and increment thresholds are measured in the continuous center field, as a function of center intensity. This, of course, is simply the classical increment threshold experiment in which the background and the increment fields are of the same diameter. In the with-surround conditions, the surround is set to some fixed intensity and the increment threshold function is measured again.

In order to uncover relationships that might exist between the brightness matching results and the increment threshold results, it is preferable to carry out both experiments on the same subjects, and under as nearly identical conditions as possible. (The two conditions shown in Figure 19 would be reasonable in this respect.) Unfortunately, no real efforts have been made to keep the two conditions comparable; although an experiment reported by Heinemann (1961) comes closest.

In Heinemann's experiment, the stimuli were like those in Figure 19, with the outer diameter of the surrounds being 1° 36', and with the
diameter of the center and matching fields being 30'. However, unlike the stimulus configuration in Figure 19, the increment field was a 10' spot. It pulsed on and off for 200 msec once every 15 seconds. Thresholds were measured with a forced choice technique.

The without-surrond increment threshold function is given by the open circles (the curve labeled \(-\infty\)) in Figure 21a. These data are accurately described by a generalized Weber function. The solid circles are the increment threshold function obtained with a 3 log ml surround. It is seen that when the center is much less intense than the surround, threshold is elevated relative above the no-surrond case; however, this relationship reverses as the intensity of the center approaches and exceeds that of the surround (that is, the effect of the surround is now to lower threshold.)

Similar results have been found by Guth (1973) using a stimulus configuration like that in Figure 19 (i.e., the center and increment fields were of the same diameter). However, there appear to be conditions under which the surround never produces decreases in threshold (Cornsweet and Teller, 1965; Alpern and Rushton, 1967).

An often studied special case is when the surround and center are of equal intensity. In Figure 21a this condition is met when center intensity is 3 log ml. As in Figure 21a, these studies typically find that the effect of the surround is to lower threshold in the center (Ratoosh and Graham, 1951; Westheimer, 1967).

Figure 21b shows the brightness matching results that Heinemann obtained with approximately the same surround intensity as that used to obtain the increment threshold function (solid circles) in Figure 21a. (The construction lines will be explained in Section VI.) Figure 21b shows the log intensity of the matching field needed to have the same apparent
Figure 21
brightness as the center field, whose log intensity is given along the horizontal axis. (This is simply another way of plotting brightness matching data. The results obtained in this experiment are actually very similar to those shown in Figure 20.)

In the without-surround (or control) condition, the data would fall along the diagonal line of slope one shown in the figure, because without being differentially affected, the center and matching fields would always be set to the same intensity. The solid circles show the results obtained with a 2.93 log mL surround. The difference between the diagonal line of slope one and the solid circles is a measure of the change in brightness produced by the surround. Again, these data show that when the center is more intense than the surround, brightness of the center is unaffected; however as center intensity approaches and then falls beneath that of the surround, center brightness decreases very quickly.

Comparing the brightness matching and increment threshold data shows that center brightness is decreasing quickly over the range of center intensities for which increment thresholds are reduced. Over the range where increment thresholds are elevated, center brightnesses are too low to be measured with the matching technique.

A complete set of increment threshold functions obtained with various surround intensities are shown in Figure 22a. (These data are also from Heinemann's experiment.) They all show the same pattern of elevated thresholds when the center is dim relative to the surround, and reduced thresholds when the surround is dim relative to the center. Figure 23a shows a complete set of brightness matching data obtained for the same subject. These data are plotted differently than those in Figures 20 and 21b in order to show a different aspect of the data, but again they agree well with those Heinemann obtained in 1955, that are shown in Figure 20.
Figure 22
Figure 23
Each of the curves in Figure 23a shows the log intensity of the center needed to have the same apparent brightness as the matching field (whose intensity is given on the left) as a function of log intensity of the surround. Thus, each curve is an "equal brightness contour." The two curves farthest from the left were obtained with a 4 log mL surround around the matching field.

C. The Relationship of Lateral Effects on Brightness to Those on Threshold

What produces the lateral effects on brightness and increment threshold shown in Figures 22a and 23a? There is much physiological evidence that lateral inhibitory mechanisms exist in the visual system, and they have often been called upon to account for the changes in brightness produced by surrounds (Brown and Mueller, 1965; Ratliff, 1965; Cornsweet, 1970). However, there has been much less consensus concerning the importance of lateral inhibitory mechanisms in threshold studies. A number of investigators have concluded that the only effect of the surround is to scatter light onto the center area (Cornsweet and Teller, 1965; Rushton and Gubish, 1966; Alpern and Rushton, 1967). This conclusion cannot be generally valid because scattered light cannot account for the sensitization effects (i.e., decreases in threshold) so often observed when the surround intensity is less than or equal to that of the center (e.g., Figure 22a).

Apparently, a great deal of confusion in this area has been generated by the belief that the large changes in center brightness, produced by surrounds, should be associated with equally large changes in increment threshold; and because they are not (see Figure 21) neural response to the threshold flash must somehow have escaped the inhibitory effects of the surround. Guth (1973) has pointed out that the reason for this confusion is that thresholds are not a simple uncontaminated measure of inhibitory effects. The difficulty is that if the surround does inhibit
neural activity in the center region, then it most likely inhibits the neural activity produced by the center (i.e., background) and the center plus increment. Thus, depending on the nature of the inhibitory interaction, changes in threshold may or may not be expected. For example, if the surround causes inhibitory reductions in neural response over the range where Weber's law holds (that is, over the range where \( \frac{\Delta I}{I} \) is constant), and if the effect the surround is equivalent to reducing \( I \) and \( I + \Delta I \) by the same factor, then absolutely no change in threshold is expected, even though apparent brightness of the center has decreased markedly.

This point is made even stronger by Geisler and Guth (1975). They show that a number of very simple and well known models of lateral inhibition can account for many of the important effects that continuous surrounds exert on center brightnesses and incremental thresholds. Predictions of three of these models, for Heinemann's data, are shown in Figures 22b - d and in Figures 23b - d. The specific assumptions used in making these predictions will be summarized in Section VII. The important point for now is that these models show that it is perfectly reasonable to expect large changes in brightness to be associated with small changes in threshold, even though the neural response produced by all lights falling in the center area are reduced by the same simple lateral inhibitory mechanism.

However, this is not to say that the effects of stray light are unimportant. On the contrary they no doubt become very significant when center intensities are low relative to that of the surround, and the models take this into account.
D. A Fundamental Difference Between Lateral and Adaptation Effects on Brightness

What can be said about the relationship of the adaptation effects examined in previous sections and the lateral effects discussed in this section? To begin with, an important difference between lateral and adaptation effects on brightness is seen by comparing Figures 6 and 21b. If lateral processes behaved like light adaptation and reduced neural responses to all lights in the center area as if multiplying their intensities by a factor between 0 and 1, then the solid circles in Figure 21b would fall along a diagonal line of slope one that is shifted to the right of the diagonal line already drawn in the figure. This is clearly not the case, as it is approximately in Figure 6. Apparently very different mechanisms are responsible for adaptation effects on brightness than those responsible for lateral effects on brightness. This, of course, does not rule out the likely possibility that to some extent, the adaptation effects and the lateral effects observed in these experiments are due to both types of mechanisms, working together.

E. Effects of Photopigment Depletion on Lateral Interactions

Analysis of the role of the depletion effect in simultaneous brightness contrast leads to a fascinating but almost paradoxical conclusion. (Note, that according to the analysis presented in Section II, the effects of "dark light" signals are again likely to be negligible since with continuous test and inducing fields, the "dark light" intensity is always less than 3% of the "real light" intensity.) Recall first, that at photochemical equilibrium a steady light of intensity $I$ will bleach all but proportion $\alpha/(\alpha + I)$ of the available photopigment, and therefore this steady light is equivalent, in terms of quantum absorptions per second, to a light of intensity $I' = \frac{I \cdot \alpha}{\alpha + I}$, presented to an eye with
a full complement of unbleached photopigment. Multiplying the top and bottom of the right hand side of this equation, by \( \frac{1}{I} \) shows that \( I' \) asymptotically approaches \( \alpha \) as \( I \) increases. It was argued in Section III that this is probably the reason that the brightnesses of steady lights reach an asymptotic value at high intensities. For the very same reason one would expect that the lateral effects produced by a surround should reach an asymptotic level at high surround intensities. For example, if a 3 log td. surround is increased by one log unit, then the quantum absorptions per second increase almost a full log unit. But, if a 5 log td. surround is increased by a log unit the quantum absorptions per second only increase by .06 log units. Therefore, the inhibitory effect produced by a 6 log td. surround should not be much greater than that produced by a 5 log td. surround. This is not at all what Heinemann's data show; increasing the surround from 1/2 log td. below, to 1/2 log td. above center intensity, has as much (or more) effect on center brightness when center intensities are low as when they are high. In fact, a quick calculation shows that at high intensities, increasing the quantum absorptions per second in the surround by a few hundredths of a log unit is enough to take an almost equally intense center from its without-surround brightness all the way down to being blacker than an unilluminated comparison field.

If this analysis is correct it implies that lateral inhibitory effects get tremendously powerful at high intensities. No current models of lateral inhibition can predict such huge effects; and this includes the model described in Section VII.

However, there are two possible reasons why this analysis may not be completely correct. First, it is possible that with the small fields that Heinemann used, difficulty in maintaining fixation might have reduced
the amount of bleaching in the surround and increased the amount of bleaching in the center, or vice versa depending on which field is more intense. To take an extreme case, if it is assumed that, due to eye movements, the amount of bleached pigment in the center and surround is always the same, then a log unit difference between surround and center intensity would always result in a log unit difference in quantum absorptions per second. If this is the case, then the depletion effect would have very little effect on brightness contrast; since, as Figure 20 shows, it is the difference in intensity of the center and surround that determines the magnitude of the contrast effects.

The second possibility is that brightness contrast effects are not actually as powerful as Heinemann's data suggest. In a pilot study, using stimulus conditions very similar to Heinemann's, we obtained much smaller brightness contrast effects. In particular, comparing our data to those in Figure 20, we find (when the surround is more intense than the center) that the slopes of the brightness matching functions are on the order of -2 to -3, rather than on the order of -10, as in Figure 20. Buehler (1971) also reports slopes on the order of -2 to -3, under stimulus conditions like those in Heinemann's study. On the other hand, even though the brightness contrast effects observed in our pilot study and in Buehler's study are less powerful than those shown in Figure 20, the overall shapes of the functions are quite similar.
VI. The Relationship Between Brightness and Threshold

This section provides a simple theoretical framework within which to analyze the relationship between brightness matching and threshold results. The analysis is based upon some of the general assumptions usually associated with the Theory of Signal Detectability (TSD), however very little use is made of the power of TSD analysis, since all the data of interest here were obtained by the method of adjustment -- there are no psychometric functions, no ROC curves, and no estimates of hit and false alarm rates. (For more detailed discussion of TSD see Green & Swets (1966) or Luce (1963).)

There are several important reasons for including this section. First, some reasonable picture of the relationship between brightness matching and threshold results must be developed. Second, the framework allows us to state explicitly the simplifying assumptions that are made in the quantitative model described in the next section, and as a result it makes clearer the relationship of the model to other models of visual processing. And finally, stating the model within a TSD type framework also makes clear how the model can be generalized, or modified, to deal with a wider range of psychophysical data.

A. A TSD Framework for Brightness Matching and Increment Threshold

In general, it is reasonable to assume that the internal effect of a stimulus can be represented by a continuous real valued k-dimensional vector (Luce, 1963). In order to keep the present analysis simple, it will be assumed that the various internal states produced by changing a light's intensity are represented by a single continuous dimension, which for expository purposes, will be referred to as the "achromatic response"
dimension. (This term is used since we are here primarily concerned with perception of achromatic light.)

The achromatic response produced from trial to trial, under the same stimulus conditions, is assumed to be described by a continuous random variable whose distribution function is characterized completely by its mean and standard deviation. In other words, for any given intensity, level of preadaptation, and level of surrounding illumination, the achromatic response to a light is described by a random variable with some mean, $\mathbf{R}$, and standard deviation, $\sigma$.

Typically, the mean achromatic response is thought of as being a monotonically increasing function of intensity. On the other hand, increasing lateral stimulation or the level of preadaptation is viewed as producing decreases in the mean.

There are a number of sources that might contribute to the variability of the achromatic response. One source of variability is due simply to the random character of light; the number of quanta absorbed by receptor photopigment molecules, in a given time period, is a Poisson distributed random variable (see Nachmias, 1972). Other possible sources of variability are, (1) fluctuations in the transmission of neural signals through various levels in the visual system, or (2) random spontaneous neural activity that is added to the signals.

The second set of assumptions in this analysis, that must be specified are the decision rules used to generate appropriate responses in the various tasks to which the theory will be applied.

The situation for brightness matching tasks is illustrated in Figure 24a. This figure depicts the distributions associated with two lights of different intensity that produce the same mean achromatic response. One light is presented to an eye in state $A$, and the other light to an eye
a) BRIGHTNESS MATCHING

STATE A

$R_0(I')$ ACHROMATIC RESPONSE

STATE B

$R(I)$

b) INCREMENT THRESHOLD

STATE A

$R_s(I)$ $R_s(I + \Delta I)$

STATE B

$R(I)$ $R(I + \Delta I)$

Figure 24
in state B. State A would correspond, for example, to the dark adapted eye, and state B to an eye light adapted to a fixed level. In general, the variability (i.e., the standard deviation) of the achromatic response to the two stimuli need not be equal.

In the matching experiment, it is assumed that the subject attempts to adjust the intensity of the light he has control over, so that the achromatic responses produced by the two stimuli are equal. For example, in Craik's experiment, described in Section III, the subject is assumed to be adjusting the intensity, I', of the light presented to the unadapted eye until it produces the same achromatic response as the light of intensity I presented to the adapted eye. Presumably, the subject calculates for each look at the stimuli, something like the difference in achromatic response, \( X_0(I') - X(I) \) (\( X_0 \) and \( X \) denote the random variables associated with the distributions whose means are \( R_0 \) and \( R \).) If this difference is less than zero, he changes \( I' \) so that \( R_0(I') \) gets larger; if it is greater than zero, he changes \( I' \) so that \( R_0(I') \) gets smaller. This procedure is repeated until a setting is found such that the differences in achromatic responses that are greater than zero occur about as often as those that are less than zero.

Naturally, the subject does not produce the same value of \( I' \) every time. Some of the variability is, of course, due to the variability of the achromatic responses. However, some is probably also produced by criterion variability, such as variability in calculating the difference in achromatic response. In any event, by averaging enough settings one obtains, for any light of intensity I, presented to an eye in state B, the intensity, \( I' \), of a light presented to an eye in state A, that produces the same mean achromatic response. In other words, the value of \( I' \) is found such that
\[ R_0(I') = R(I) \]  \hfill (17)

The function obtained by carrying out brightness matches for all values of \( I \), with the states \( A \) and \( B \) fixed, will be referred to as a "brightness matching function." Naturally, a different function is obtained for each pair of states \( A \) and \( B \). The curves shown in Figures 6 and 21b are examples of brightness matching functions. (As mentioned earlier, data from any parametric matching experiment can be plotted in this fashion.) Finally, note that a brightness matching function is of the following form:

\[ \log I' = f(\log I) \]  \hfill (18)

For each intensity \( I \), equation (18) gives the value of \( I' \) such that equation (17) is satisfied.

Next, consider the decision rule that applies for increment threshold experiments. Each pair of curves in Figure 24b represents the achromatic response distributions for the background and the background plus increment, when the increment field is at threshold. The upper distributions represent threshold on a background of intensity \( I \), presented to an eye in state \( A \) (e.g., dark adapted), and the lower distributions represent threshold on the same background, presented to an eye in state \( B \) (e.g., light adapted to some level).

The figure demonstrates that in general, both the mean and the standard deviation of the achromatic response may change if, say, the state of light adaptation is changed. However, for present purposes, it will be assumed that, as a function of intensity, the mean achromatic response changes fast relative to the standard deviation; therefore, at
threshold, the standard deviation of response to the background plus increment is approximately the same as that to the background alone. In other words, it is assumed that

$$\sigma_0(I + \Delta I) = \sigma_0(I) \quad \text{and} \quad \sigma(I + \Delta I') = \sigma(I).$$

With this simplification, $d'$, the difference in the means of the normalized distributions, is given by,

$$d' = \frac{R_0(I + \Delta I) - R_0(I)}{\sigma_0(I)} \quad (19)$$

when the eye is in state $A$, and by

$$d' = \frac{R(I + \Delta I') - R(I)}{\sigma(I)} \quad (20)$$

when the eye is in state $B$.

It will be assumed that for thresholds obtained by the method of adjustment, subjects, on the average, set the intensity of the increment so that $d'$ equals some constant $\delta$. This assumption is the same used in the familiar TSD analyses that are applied to thresholds obtained by other methods, such as forced choice, and Yes-No procedures.

From equation (19) (or (20)), it is seen that thresholds can change, under different conditions, either because of changes in the variability of the achromatic response (the denominator), changes in the rate at which the means of the achromatic response distributions separate (the numerator), or both. In terms of this distinction, most theoretical analyses of visual
thresholds fall into one of two categories. In one type of analysis, changes in threshold are assumed to depend only upon changes in the variability of visual responding. These include, for example, those models in which the primary source of variability is assumed to be the quantum fluctuation of the stimuli themselves (DeVries, 1943; Barlow, 1957). The other typical type of analysis assumes that variability is approximately constant, and that observed changes in threshold are the result solely of changes in the rate at which the means of the response distributions, for the background and background plus increment, separate. This is the sort of model that Fechner used to derive his well known logarithmic brightness scale (see Luce, 1963).

B. The Predicted Relationship Between Brightness Matching and Increment Threshold

An important aspect of the framework presented here is that the predicted relationship between brightness matching and increment threshold data is very simple. In particular, if a brightness matching function (eq. 18) and increment threshold functions have been obtained for the eye in states A and B, then the following relationship must hold,

\[ m \cdot \frac{\sigma_0(I')}{\sigma(I)} = \frac{\log K' + 1}{\log K'' + 1} \]

(21)

where,

\[ m = \text{the slope of the brightness matching function at log } I \]

\[ K' = \text{the Weber fraction } \Delta I'/I' \text{ obtained when the eye is in state A} \]

\[ K'' = \text{the Weber fraction } \Delta I''/I \text{ obtained when the eye is in state B.} \]
Proof of Eq. (21). It is convenient to define the following functions,

\[ g_0(\log X) = R_0(X) \]  \hspace{1cm} (22)

\[ g(\log X) = R(X) \]

Now, from the assumption that threshold is achieved when \( d' = \delta \), the following equations must hold,

\[ \sigma_0(I') \cdot \delta = R_0(I' + \Delta I') - R_0(I') \]

\[ \sigma(I) \cdot \delta = R(I + \Delta I'') - R(I) \]

or using eq. (22),

\[ \sigma_0(I') \cdot \delta = g_0(\log I' + \Delta I') - g_0(\log I') \]

and

\[ \sigma(I) \cdot \delta = g(\log I + \Delta I'') - g(\log I). \]

But, assuming \( R_0 \) and \( R \) are differentiable, it follows, to close approximation, that

\[ g_0(\log I' + \Delta I') - g_0(\log I') = \frac{d}{d \log I'} g_0(\log I') \cdot (\log I' + \Delta I' - \log I') \]

and, \( g(\log I + \Delta I'') - g(\log I) = \frac{d}{d \log I} g(\log I) \cdot (\log I + \Delta I'' - \log I). \)

Therefore,
\[
\log I' + \Delta I' - \log I' = \sigma_0(I') \cdot \delta \frac{dg_0(\log I')}{d \log I'}
\]

and

\[
\log I + \Delta I'' - \log I = \sigma(I) \cdot \delta \frac{dg(\log I)}{d \log I}
\]

But, from the definitions of \(K'\) and \(K''\) it is also true that,

\[
\log I' + \Delta I' - \log I' = \log K' + 1
\]

and

\[
\log I + \Delta I'' - \log I = \log K'' + 1.
\]

From these two equations and equations (23),

\[
\frac{\log K' + 1}{\log K'' + 1} = \frac{\sigma_0(I')}{\sigma(I)} \cdot \frac{dg(\log I)}{d \log I} \cdot \frac{dg_0(\log I')}{d \log I'}.
\]

Therefore, eq. (21) is proved if it is shown that,

\[
m = \frac{dg(\log I)}{d \log I} \cdot \frac{dg_0(\log I')}{d \log I'}.
\]

To do this, note that from equations (22) and the definition of the brightness matching function (eq. (18)), it follows that,

\[
g_0(\log I') = g(\log I).
\]

Taking the derivative of both sides with respect to \(\log I\) gives,

\[
\frac{d}{d \log I'} \frac{g_0(\log I')}{d \log I'} \cdot \frac{d \log I'}{d \log I} = \frac{d}{d \log I} \frac{g(\log I)}{d \log I}.
\]
or,

\[
\frac{d \log I'}{d \log I} = \frac{d g(\log I)}{d \log I} \left/ \frac{d g_0(\log I')}{d \log I'} \right.
\]

The left hand side of this equation is the slope of the brightness matching function; therefore equation (21) is proved.

An important special case of eq. (21) is when \( \sigma(I) = \sigma_0(I') \).
Since \( I \) and \( I' \) necessarily produce the same mean achromatic response, this is equivalent to saying that the variability of the achromatic response is dependent only upon its mean. Obviously, this restriction includes the case in which the variance is the same under all conditions.

With this simplification, eq. (21) reduces to,

\[
m = \frac{\log K' + l}{\log K'' + l}
\]

(24)

It is very easy to test eq. (24) since all the relevant quantities can be read directly from the brightness matching and increment threshold data.

Some predictions of eq. (24) are demonstrated in Figure 21. The dotted lines through the open circles in Figure 21b show the slopes of the brightness matching function predicted from the increment threshold functions in Figure 21a.

The predicted slopes were calculated as follows. For a center intensity of \( \log I \), the matching intensity, \( \log I' \), was read off from the brightness matching function, then \( \log \Delta I' \) and \( \log \Delta I'' \) were read off the increment threshold functions above. Using these numbers,
K' (i.e., ΔI'/I') and K'' (i.e., ΔI''/I) were calculated, and then substituted into eq. (24) to give the predicted slope, m, at center intensity log I.

If the predictions of eq. (24) are correct, then the solid circles should fall along the envelope, concave to the right, formed by the dotted lines. The predictions are seen to be quite reasonable, but it should be emphasized that Heinemann's increment threshold and brightness matching data were not obtained under exactly the same conditions, and therefore application of eq. (24) is not completely appropriate. Experiments can be carried out that are better suited to explore the relationship between brightness matching and increment threshold.

The analysis presented here suggests that brightness matching and increment threshold data should be plotted as in Figure 21. In fact, by plotting data in this way, it often turns out that a rough picture of how brightness and threshold are related can be obtained without carrying out any calculations. For example, in Figure 21a the without-surround increment threshold function obeys Weber's law over the entire range of center intensities for which the brightness matching function is defined. This means that the Weber fraction at log I, call it K, is always the same as the Weber fraction at log I'. Therefore,

\[ m = \frac{\log (K+1)}{\log (K''+1)} \]  

(25)

But, K and K'' are just the Weber fractions for the center intensity of log I under the two states (with and without surround), and m is the slope of the brightness matching function at log I. Thus, eq. (25) says that a rough analysis of the relationship between brightness and threshold can be obtained simply by looking at Figure 21; if threshold is lower in
the with-surround condition then the slope of the brightness matching function should be steeper than 1, if threshold is higher in the with-surround condition the slope should be shallower than 1, and if the thresholds are the same the slope should equal 1.

An interesting consequence of eq. (25) (but not necessarily of eq. (24)) is the prediction that very steep slopes in the brightness matching function should be associated with small changes in threshold (see Figure 21). This makes testing eq. (25) convenient, since brightness matching data tend to be more variable than threshold data.

Another interesting example is when the brightness matching function has a slope of 1 over its whole range. (This is approximately what happens for light adapting to a fixed level - see Figure 6.) Under these conditions eq. (24) predicts that $K' = K''$, and it is not difficult to show that this is equivalent to predicting that the increment threshold function for state $B$ should be exactly the increment threshold function obtained for state $A$, but translated along a 45° line (in a log-log plot).

Returning to the more general relationship, eq. (21), note that unless the ratio of the standard deviations, $\sigma_0(I') / \sigma(I)$, can be estimated from some other data, or unless some theoretical assumptions are made, eq. (21) cannot be directly applied like eq. (24). However, if the assumptions of the TSD framework are accepted, then estimates of the ratios of the standard deviations can be obtained from the brightness matching and increment threshold data.

Heinemann (1961) has also looked at the relationship of increment threshold data to brightness matching data; however he uses a rather complex and error prone method of adding "jnd's" (Luce & Edwards, 1958). The procedure suggested here is very simple, and it makes clear the relationship of the data to the underlying theoretical framework.
Perhaps the main limitation of the present analysis is the assumption that the internal dimension used in making brightness matches is the same dimension along which discriminations are made. Undoubtedly there are situations for which this assumption is incorrect, however the important question is not whether there always exists a simple relationship between brightness and threshold, but rather, under what conditions does a simple relationship exist.
VII. A Theoretical Framework and a Model

Previous sections have presented some of the basic results on photopigment kinetics, dark adaptation, light adaptation, and lateral effects. Furthermore, an effort was made to uncover relationships that might exist between the various results. For example, we have considered the relationship of brightness matching and increment thresholds results for both lateral and adaptation effects. This analysis is extended in this section, with the description of one possible theoretical framework that proposes how photopigment kinetics, adaptation, and lateral effects interrelate. Then, as a concrete example, some predictions are shown for a simple quantitative model derived within this framework.

A. The General Framework.

The general framework is pictured in Figure 25. At the outset, it should be made clear that some of the particular processes and stages shown here are similar to those in other theoretical treatments; they are brought together here in order to deal with the range of results presented in previous sections.

Figure 25 depicts the processing of inputs to two neighboring regions of the retina. One region is illuminated with a light of intensity $I$ and the other with a light of intensity $J$. Processing of inputs to the two regions remains independent up to the lateral inhibition stage, so consider, say, just the upper limb.

When light hits the retina, some of it is absorbed by photopigment molecules in the receptors. This absorption produces a photochemical reaction which in turn sets off a long chain of dark or thermal reactions, the end product of which is the molecule labeled $X$ (opsin). This end product then recombines with another molecule (11-cis retinal) so that it
Figure 25
returns to its original state, and is again ready to absorb light. Much is known about this chain of reactions (see Dartnall, 1972), but for present purposes it will not be considered in detail. Rather, it will be assumed that the densitometry results described in Section I are relatively accurate, and therefore that eq. (2) in Section I describes this bleaching and regeneration process. With eq. (2) the proportion, \( p \), of unbleached photopigment, \( A \), can be calculated at any time. Furthermore, since the chain of thermal reactions occur quickly relative to the rate of regeneration, \( q = 1 - p \) gives the proportion of photoproduct, \( X \), due to bleaching.

One of the reactions early in the sequence is the trigger for the primary visual response of the receptor (Wald, 1971). The signal arising from this reaction will be called the absorption signal, \( S_A \).

This is also the first point in the system at which adaptation occurs, since it is here that the depletion effect operates. As photopigment becomes used up, less and less is available to respond to incoming light; therefore the absorption signal is attenuated. Since the depletion of all but proportion \( p \) of the maximum available pigment is equivalent to reducing a light of intensity \( I \) to \( p \cdot I \), the absorption signal can be thought of as a function of \( p \cdot I \).

The final photoproduct \( X \) is also assumed to have effects on responses of the visual system, so it is assigned a signal, \( S_X \). Using Rushton's (1965b) terminology this will be called the bleaching signal. Furthermore, it will be assumed that the bleaching signal effects the visual system exactly in the same way as the absorption signal. In other words, it is assumed that Barlow's (1964) "dark light" hypothesis (see Section II) is correct.
Rushton (1965a) has proposed a somewhat different model in order to account for certain dark adaptation results that were discrepant with Barlow's hypothesis. In his model, the bleaching signal behaves like the absorption signal in many ways, but in other ways does not. As mentioned earlier, there is still some debate over the implication of the discrepant findings. For now it will be assumed that the simpler version (Barlow's) is correct, although in the near future it may have to be altered.

According to the "dark light" hypothesis, the bleaching signal is responsible for long-term afterimages, and is responsible for the elevations in absolute threshold (above and beyond those produced by the depletion effect) observed during dark adaptation, but excluding the first several seconds after a bleaching light is turned off. Presumably, during the first several seconds there are also some residual neural adaptation effects (due to the effect of prior absorption signals), in addition to the effects of bleaching.

Since the bleaching signal affects the visual system just like presenting a steady background light, the combined absorption and bleaching signals can be written as a function of the actual light presented, $p \cdot I$ (corrected for the depletion effect), plus an equivalent background, $I_X$, due to the bleaching signal. However, remember that unlike real light backgrounds (under normal viewing conditions), "dark light" backgrounds are stabilized in the visual system, and somehow this stabilization results in fading of the "dark light" background so that only faint afterimages are seen in the dark.

At present, it is an open question as to how and where this fading process operates. One possibility, is that it occurs relatively peripherally in the visual system; perhaps as a result of the neural adaptation
process described below. On the other hand, it could just as well arise central to all the processes in Figure 25 (excluding perhaps the decision processes). The problem of explaining the fading process is avoided in the model presented later, by restricting predictions to conditions in which "dark light" intensity is negligible compared to that of the "real light" (with one exception that will be explained later). This insures that the "dark light" has negligible effects on predictions.

The dotted line in Figure 25 indicates the possibility that photo-products arising at other stages in the bleaching sequence may produce signals that have important effects on visual processing. For example, the short-term afterimages described in Section IV may arise from some intermediate stage in the bleaching sequence.

Next, the combined absorption and bleaching signals are sent to the following stage of the system labeled "neural adaptation." Neural adaptation is a way that the system tunes down its own responses. When a light is turned on in the dark adapted eye, there is initially no neural adaptation, and signals pass through freely. As the stimulus remains on, the response to it will become more and more attenuated. Furthermore, if the eye has already been adapted to a continuous light, then any new signals will immediately be attenuated by this mechanism. This sort of attenuation process is necessary in order to deal with the large effects of adaptation on apparent brightness and on increment threshold as described in sections III and IV. This is because the depletion effect and the effects of the bleaching signal (dark light) are apparently not adequate to account for more than but a small proportion of these adaptation effects.

In general, the amount of attenuation due to the neural adaptation process is determined by previous light history. However, neural adaptation develops and recovers much faster than the photochemical bleaching and
regeneration process.

Also, the experimental results described in sections III and IV suggest that the neural adaptation process has the simple property of approximately reducing neural responses to lights as if multiplying their intensities by some factor between 0 and 1.

The use of the label "neural adaptation" is not meant necessarily to imply that this adaptation process is some type of neural circuit such as, say, one neuron feeding back on another; it is quite possible that neural adaptation processes may also arise within the receptor itself. In fact, single cell recordings of receptor responses typically show that when a light is turned on, response is initially at a maximum and becomes attenuated thereafter (see, for example, Fuortes, 1972).

After passing through the neural adaptation mechanism, the attenuated signals are then sent to the third stage in the system labeled "lateral inhibition." At the lateral inhibition stage, signals leaving the neural adaptation process, inhibit and are inhibited by signals arising from neighboring regions. Thus, in Figure 25, the final outputs, $R_1$ and $R_2$, are functions of the signals arising from both regions.

This lateral inhibitory mechanism is needed in order to deal with the lateral effects discussed in Section V. Furthermore, as shown in that section, the effects, on apparent brightness, of a fixed level of preadaptation and a fixed level of surround illumination are very different, and this supports the assumption that two different mechanisms are involved.

In summary, there are three points at which signals may be attenuated; at the photochemical level because of the depletion effect, at the neural adaptation level, and finally at the lateral inhibition stage.

In terms of the TSD framework of the previous section, the outputs of the lateral inhibition stage, $R_1$ and $R_2$, are the mean achromatic
responses for the two regions. In general, the variability of the achromatic response may also be a function of intensity, the current state of bleaching, the level of neural adaptation, and the amount of lateral inhibition.

The outputs of the lateral inhibition process are fed into higher level processes, some of which are the decision rules that are applied to these outputs in order to make appropriate responses. Two such decision rules, one for brightness matching and one for increment threshold, were described in the previous section.

One important fact that was not mentioned earlier in the discussion of data, is that for the most part, the adaptation and lateral effects described in this paper are monocular in origin; for example, light adapting one eye has little effect on either brightness or threshold in the other eye (Boynton, 1961). This means that these effects arise early in the visual system.

This completes the outline of the general framework. Obviously, the framework is fairly broad and can incorporate many models that deal with lateral and adaptation effects. As an example, the remainder of this section is devoted to the development and testing of one simple quantitative model that attempts to deal with the brightness matching and increment threshold data discussed in Sections III, IV and V.

B. A Quantitative Model

In order to construct a quantitative model, specific choices need to be made for the photochemical processes, the neural adaptation mechanism, the lateral inhibitory stage, and the decision rules. Although these processes are actually random stochastic processes, the equations that follow describe only the mean outputs. Variability is handled in the simplest fashion by assuming that the final output has some fixed standard
deviation independent of conditions.

The photochemical processes, and the effects of the current state of bleaching, have already been specified. At any moment, the state of bleaching will be such that, in effect, only a proportion \( p \) of an input intensity \( I \) is absorbed and results in an absorption signal. Furthermore, bleached photopigment generates a signal that has the effect of adding a continuous stabilized background light, of intensity \( I_x(p) \). Thus, if proportion \( p \) of the photopigment is in the unbleached state, then a light of intensity \( I \) has the same effect as a light of intensity

\[
I_E = p \cdot I + I_x(p),
\]

presented to an eye in which all the photopigment is in the regenerated state. This quantity, \( I_E \), will be called the "effective intensity." The effective intensity can be calculated at any point in time with equations (26) and (27), given below. These equations are simply eq. (2) and eq. (11) rewritten in terms of the proportion of unbleached photopigment. Also included are the appropriate constants for cone bleaching:

\[
\frac{-dp}{dt} = \frac{I \cdot p}{Q_e} - \frac{(1 - p)}{t_0}, \tag{26}
\]

where \( Q_e = 2.4 \times 10^6 \) td. sec, and \( t_0 = 120 \) sec.

\[
I_x(p) = I_0 \cdot p \cdot e^{\gamma \cdot (1 - p)} - I_0 \tag{27}
\]

where \( I_0 = 12 \) td. and \( \gamma = \frac{f}{d} \).

How is the effective intensity converted into the neural signals that are transmitted through the visual system? There are obviously many
possibilities, but we choose a very simple formulation that has a number of reasonable and desirable properties. In particular, it is supposed that the transduction of effective intensity into neural signals is described by,

\[
\frac{dT}{dt} = (T_{\text{max}} - T) \cdot I_{\varepsilon} \cdot \varepsilon_h - \rho_h \cdot T.
\] (28)

Equation (28) describes two subprocesses, an excitatory process and a recovery process. Obviously, all neural systems must have both processes, since without an excitatory process no signals are transmitted, and without a recovery process output would simply build up to a maximum and remain there forever.

The excitatory process is described by the term \((T_{\text{max}} - T) \cdot I_{\varepsilon} \cdot \varepsilon_h\). It says that there is a maximum possible output, \(T_{\text{max}}\), and that in any given small time period, the output \(T\) increases in proportion to the effective intensity, and to the additional amount of output that may still be attained. The excitatory rate parameter is \(\varepsilon_h\); the greater \(\varepsilon_h\), the faster the output \(T\) increases.

The recovery process goes on simultaneously with the excitatory process and is described by the term \(-\rho_h \cdot T\). This says that in any given small time period the output \(T\) decreases in proportion to its current level. The recovery time constant is \(\rho_h\); the larger \(\rho_h\), the faster is decay of the output produced by the excitatory process.

Equation (28) describes the processing of neural signals up through the neural adaptation stage. In particular, neural adaptation operates by changing the excitatory or recovery parameters, \(\varepsilon_h\) and \(\rho_h\). (The subscript \(h\) simply indicates that either or both parameters may depend on previous light history.)
Next, note that eq. (28) is exactly the same sort of equation as eq. (26), that describes the bleaching and regeneration of photopigments; except, that now because it describes neural response, the excitatory (bleaching) and recovery (regeneration) rate constants are very much larger. In fact, it will be assumed that for all practical purposes neural response reaches equilibrium instantaneously; except for the slower changes in neural response (i.e., neural adaptation) due to changes in the excitatory and recovery parameters. With this assumption, the left hand side of eq. (28) is always, within a very short time, very nearly equal to 0, and therefore the solution to eq. (28) is given approximately by,

$$T = \frac{I_E \cdot T_{max}}{I_E + \mu_h},$$

(29)

where $\mu_h = \frac{\rho_h}{\epsilon_h}$.11

The output $T$ is seen to be dependent on the effective intensity, and on the ratio of the excitatory and recovery parameters; the greater is $I_E$ the greater the output, and the greater is $\mu_h$, the smaller the output.

It is clear from eq. (29) that the way that neural adaptation affects output is by changing the ratio of the excitatory and recovery parameters. In particular, the output is reduced if either the recovery process is speeded up ($\rho_h$ increased) or the excitatory process is slowed down ($\epsilon_h$ decreased). In any event, to derive predictions, it is only necessary to describe how $\mu_h$ changes under various conditions. A natural assumption is that when a light is first turned on in the dark adapted eye, $\mu_h$ is at its minimum, while the light remains on $\mu_h$ increases toward some
asymptotic value, and when the light is turned off, $\nu_h$ drifts back to its minimum. (Note, because the amount of neural adaptation is dependent only upon the ratio of the excitatory and recovery parameters, they can be chosen to vary over a range of values that are high enough to insure that eq. (29) is an approximate solution to eq. (28).)

There are several desirable properties of eq. (29). First, multiplying the numerator and denominator by $1/\nu_h$ shows that with the constraint that $\nu_h$ be greater than one, the effect of neural adaptation is to reduce the effective intensity as if multiplying it by a factor between 0 and 1. This is approximately how adaptation seems to work in the brightness matching and increment threshold data. Second, in the electrophysiological literature, eq. (29) has been used to describe the response characteristics of visual receptors and other cells in the retina (e.g., see Gouras, 1972). Third, a series of transduction stages like eq. (28) would behave in a fashion similar to having just one stage. This can be seen by substituting an equation of the same form as eq. (29), for $I_E$ in eq. (29).

In this paper, the primary concern is with deriving predictions for steady state conditions. In particular, $\nu_h$ must be specified when the eye is dark adapted, and after the eye has viewed a steady light until neural adaptation is complete. It is assumed that in the dark adapted eye,

\[
\nu_h = K_1
\]

(30)

where $K_1$ is a constant, and under steady state conditions after neural adaptation is complete,

\[
\nu_h = K_1 + K_2 \cdot I_E^\eta
\]

(31)
where $K_1$, $K_2$, and $\eta$ are constants. Equation (31) was literally derived from Craik's curve (Figures 4 and 5) at low intensities -- a power function (as in eq. (31)) is necessary in order to predict linear functions on a log-log plot.

Next, the lateral inhibitory process must be specified. Geisler and Guth (1975) considered two types of lateral inhibition; subtractive recurrent and subtractive nonrecurrent. Nonrecurrent inhibition means that it is feed-forward, in that the amount of inhibition arising from an input region depends only upon the output of the neural adaptation process, and not upon the magnitude of the achromatic response. On the other hand, an inhibitory process is called recurrent (or feedback) if the amount of inhibition arising from an input region depends only upon the level of its achromatic response. (For more discussion of recurrent and nonrecurrent inhibition see Ratliff (1965)).

Geisler and Guth show that either type of inhibition process can account for at least some of the important lateral effects observed in brightness matching and increment threshold data. However, their models are not concerned with adaptation effects. In particular, it is assumed that all processing prior to the lateral inhibition stage is described simply by either a power transform of the input intensity ($T = (I + \omega)^{\eta}$), or a log transform of the input intensity ($T = \log(I + \omega) + \eta$). The predictions in Figures 22 and 23 were made with the following models: 22b and 23b - power transform and nonrecurrent inhibition, 22c and 23c - log transform and recurrent inhibition, and 22d and 23d - power transform and recurrent inhibition.

In the present model, the inhibition process is assumed to be subtractive and recurrent. In other words, the mean achromatic responses, $R_1$ and $R_2$, are given by the solution to the following pair of equations:
\[ R_1 = T(I^*_E) - \beta R_2 \]
\[ R_2 = T(J^*_E) - \phi R_1, \]

where \( 0 < \beta < 1 \) and \( 0 < \phi < 1 \), and with the constraint that negative achromatic responses are excluded.

Equation (32) says, that the achromatic response from a region is equal to the output of its neural adaptation stage minus some proportion of the achromatic response from the other region. Furthermore, in the case that the two regions are a center and a surround, as shown in Figure 19, it is reasonable to require that the surround to center inhibition parameter be greater than the center to surround inhibition parameter.

In order to make predictions for lateral effects, two theoretical considerations remain. First, some assumption is needed in order to account for the fact that in simultaneous brightness contrast experiments, the center often appears "blacker" than an unilluminated comparison field (when the center is dim relative to the surround). A presumably related electrophysiological observation is that in the absence of stimulation, there is spontaneous neural activity even in the dark adapted eye (Kuffler, Fitzburgh, and Barlow, 1957). It is not unlikely that this spontaneous activity is responsible for the non-zero level of brightness (observed in the dark), and that this spontaneous activity can be suppressed by lateral inhibitory mechanisms, thereby producing center areas that appear "blacker" than unilluminated comparison fields. In the model, this spontaneous neural activity is represented by a positive constant \( \omega \) added to the output of the neural adaptation stage. (Another possibility, is to treat spontaneous neural activity as an added constant intensity (Barlow, 1957).)
The second theoretical consideration concerns stray light. Due to scattering of light within the eye itself, images falling on the retina are somewhat blurred, even under optimal conditions. In particular, some of the light intended for a surround will fall on its center area, and vice versa. The distribution of stray light is most concentrated at the border separating the center and surround (Westheimer and Campbell, 1962); however, predictions in the present model are made under the simplifying assumption that 5% of the surround intensity falls uniformly on the center area, and because of the relatively smaller center, a negligible percent of the center intensity falls on the surround. (Allowing these values to vary a couple percent does not greatly effect predictions.)

The final consideration is to choose appropriate decision rules for brightness matching and threshold tasks. These are exactly the same ones described in Section VI:

1. Two regions match in brightness if their mean achromatic responses are the same;

\[ R_0 = R . \] (33)

2. An increment on a background is just detectible when,

\[ d' = \delta = \text{const.} , \]

where \( d' \) is the difference in the means of the normalized achromatic response distributions. However, since the standard deviation, \( \sigma \), is assumed here to be constant under all conditions, this is equivalent to saying that a constant difference in mean achromatic response is needed
for threshold;

\[ R(I + \Delta I) - R(I) = d, \quad (34) \]

where \( d = d' \cdot \sigma \).

C. Predictions

The model can now be fit to a variety of brightness matching and threshold data. There are a total of 7 parameters that need to be estimated. All of the adaptation predictions depend only upon the 4 parameters \( K_1, K_2, \eta, \) and \( d \). Their estimated values are as follows: \( K_1 = 80, \)
\( K_2 = 160, \eta = .3, \) \( d = .0026 \). In order to make predictions for lateral effects, the two inhibition parameters, \( \beta \) and \( \phi \), and the neural noise parameter, \( \omega \), must also be estimated; their estimated values are:
\( \beta = .65, \phi = .55, \omega = .6. \) The value of \( T_{\text{max}} \) in eq. (29) has no effect on predictions for either brightness matching or increment threshold, and therefore may be arbitrarily set equal to 1.0. Similarly, the "dark light," \( I_X \), plays almost no role in the predictions, since for the experiments considered below it is almost always negligible compared to the "real light," even after correction for the depletion effect.\(^{13}\)

The seven parameters above, were estimated from various aspects of the data, but they remain fixed across all predictions presented here.

Before describing the actual predictions, it should be emphasized that the model is viewed mostly as a demonstration of the type of models that can be constructed within the framework shown in Figure 25. The model roughly predicts the form of much of the data, but it does not make accurate quantitative predictions (at least when the parameters are kept the same across all experiments).
To begin with, consider predictions for the effects of adaptation on brightness. These predictions depend only upon the three parameters in eq. (31); in particular, predictions depend upon the ratio of \( K_2 \) to \( K_1 \), and upon \( \eta \). Predictions for Craik's experiment are shown in Figure 26. The lowermost curve gives the predicted intensity of a light flashed in the dark adapted eye that has the same apparent brightness as the continuously presented light whose intensity is given along the abscissa. The upper curve gives the predictions when the matching field is presented to an eye that is light adapted to a fixed level. Comparing these predictions to Figures 4 and 5 in Section III shows that the model does predict the main aspects of the data. The model predicts that the curves become flat at high intensities because of the depletion effect. The roughly linear part of the curves (with slope less than 1) is due to neural adaptation; the slope is determined by \( \eta \), and the intercept by the ratio \( K_2/K_1 \). The curves are shifted apart by a constant amount because, in the model, light adapting to a fixed level has the effect of multiplying all intensities by some factor between 0 and 1.

The predictions for Onley and Boynton's (1961) experiment are given in Figure 27. Each curve gives the predicted intensities of lights flashed in an eye adapted to 1 log td., that have the same brightneses as lights flashed to an eye that is adapted to the intensity level given at the base of the curve. The predicted curves are similar in shape to those in Figure 6. The predicted curves are spaced equally at low intensities due to the assumption that neural adaptation increases as a power function of adapted light intensity. They are spaced out more at high levels, because of the added depletion effect. Finally the predicted curves are parallel because adaptation has the effect of multiplying intensities by some factor between 0 and 1.
In order to make some of the predictions shown in Figure 27 some assumption had to be made about how "dark light" signals add to the brightness of real light signals. Since "dark light" is stabilized in the visual system it is known to contribute far less to brightness than its equivalent (in terms of threshold) unstabilized background. Therefore, it was simply assumed that the "dark light" makes a negligible addition to the brightness of lights flashed in the adapted eye (for the conditions in Onley & Boynton's experiment). Assuming that the "dark light" contributes the same brightness as its unstabilized equivalent background, gives the right-hand-most curves in Figure 27 a slope of less than one at low test field intensities. Also, we mention again that in all of the other predictions presented here, no special assumptions about how stabilized images fade are necessary, since in these cases, even if the "dark light" is assumed not to fade at all, predictions are not significantly affected.

Next consider predictions for the effects of adaptation on increment threshold. As shown in Figure 13, a continuously accelerating curve must be predicted for increment threshold in the dark adapted eye, and the generalized Weber law must be predicted when the eye is light adapted to each background intensity before threshold is measured. Predictions of the model are shown in Figure 28. The model does predict that increment thresholds in the dark adapted eye follow a continuously accelerating function, and this prediction is due to the non-linear function, eq. (29), that describes the output of the neural adaptation process. The model also predicts that when the eye is adapted to each background before threshold is measured, thresholds approximately obey a generalized Weber function. At low intensities this prediction is primarily due to neural
adaptation. At high intensities the depletion effect becomes important and prevents the increment threshold function from positively accelerating.

The predicted increment threshold functions overlap at lower intensities, but the data show no such tendency. Within the framework there is one obvious reason why the model might fail. Namely, the variability of the achromatic response may not be independent of the state of adaptation. If it is assumed that adapting to a background field not only reduces its mean achromatic response but also its variability, then predictions can be improved.

Figure 29 shows predicted increment threshold functions for the dark adapted eye, and for an eye light adapted to a fixed level. As can be seen, the model predicts that light adapting to a fixed level results in an increment threshold function that is simply the dark adapted function shifted up and to the right along a 45° line. Again, this prediction follows since adapting to a fixed level has the effect of multiplying all intensities by some factor between 0 and 1 (see Figure 14).

At the end of Section IV, experiments were described in which thresholds were measured for detecting an increment flash that was presented before, simultaneous with, or after onset of a background field. These experiments typically show that threshold is at a maximum when the background and increment fields onset simultaneously, and that threshold declines quickly and then more slowly, the more delayed is onset of the increment field. This is known as the on-effect. Although our primary concern in this paper is not with the temporal aspects of adaptation, it is perhaps worth while to demonstrate that straight forward generalizations of the model will allow it to predict on-effects.

In order to make predictions, something must be said about how neural adaptation develops over time. It will be assumed that when a light is
presented to the dark adapted eye, \( \mu_h \) approaches its asymptotic steady state value given by eq. (31). In particular, comparing equations (31) and (32) shows that it is the term, \( K_2 \cdot I_E^n \), that develops over time. For present purposes it is assumed that when a light is turned on in the dark adapted eye, this term is initially 0 and then exponentially approaches the asymptotic value.

Choosing an appropriate exponential time constant gives the predictions shown in Figure 30. The solid curves are the predictions for backgrounds of two different intensities. Clearly, the model can predict on-effects, and furthermore, it predicts that on-effects are smaller for dimmer backgrounds. This latter prediction is also consistent with the data (Crawford, 1947).

Section V described the effects that annular surrounds have on brightness and increment thresholds under steady state conditions. Now consider the predictions for these effects. Figure 31, shows the predicted increment threshold functions for a without-surrond condition, and for a 4 log mL surround condition. Comparing these predictions to the data in Figure 22a, shows that the model correctly predicts that the effect of the surround is to raise threshold when the center is dim relative to the surround and to lower threshold when the surround is dim relative to the center. Predicted sensitization effects (i.e., reductions in threshold) are due to the amplifying property of recurrent inhibition, and the predicted elevations in threshold at low center intensities are due to a combination of inhibition and stray light effects. (See Geisler & Guth (1975) for more details on how recurrent inhibition and stray light affect increment threshold.)

Finally, consider the predictions for simultaneous brightness contrast. Under most conditions, the model does about as well as the lateral inhibition
models whose predictions are shown in Figure 23. However, the model fails when the surround and center intensities are both high at the same time.

There are a couple of factors contributing to this problem, but by far the most serious is the one discussed at the end of Section V. In particular, it was shown, in Section V, that because of the depletion effect, the quantum absorptions per second for a continuous light (at photochemical equilibrium) approach an asymptotic value as intensity is increased. Therefore, we were led to expect that at high intensities, further increases in either center or surround intensity should produce essentially no further laterally induced changes in brightness. This is exactly what the present model predicts, since it incorporates the depletion effect. However, Heinemann's data indicate that at high intensities very large brightness changes are associated with very small changes in center and/or surround intensity.

Some possible solutions to this paradox were also described in Section V. First of all, if because of eye movements, the proportions of bleached photopigment in the center and surround are always nearly identical, then the depletion effect would have little affect on simultaneous brightness contrast. Secondly, replications of Heinemann's experiment, by Buehler (1971) and in a pilot study (in our laboratory), suggest that brightness contrast effects may be much smaller than Heinemann's data suggest. This could only help the model since the depletion effect leads to smaller predicted contrast effects.
Footnotes

10 Normally, $I_0$ should be estimated from an increment threshold function obtained under the same stimulus conditions that Rushton used when he obtained the dark adaptation thresholds (in Figure 2) upon which eq. (27) is based. However, Rushton did not report increment threshold functions, so the value of $I_0$ used here was estimated from the increment threshold functions (for continuous backgrounds) obtained in Experiment 3.

11 However, caution must be exercised in using eq. (29) as a solution to eq. (28). If $e_h$ and $\rho_h$ are controlled by feedback; for example, if they are a function of the output, $T$, then in some cases eq. (29) may not be an accurate approximation. Similarly, eq. (29) will not provide an approximate solution of eq. (28) if it is assumed that $\mu_h$ changes very quickly over time, since then either (or both) $\rho_h$ or $e_h$ must also be changing quickly. Therefore, $dT/dt$ will not remain near zero as $\rho_h$ and $e_h$ change.

In the present theoretical treatment, eq. (28) is only meant to serve as a rationalization for eq. (29). The theoretical development could just as well have begun by taking eq. (29) as given.

12 Although there are few models that make predictions for both lateral and adaptation effects on intensity discrimination and brightness, there are a number of models of adaptation that deal with a range of results involving temporal aspects of perception such as flicker detection and temporal summation, that will not be dealt with here (Matin, 1968; Sperling and Sondhi, 1968; Sperling, 1970). Judging from the complexity of these models it is unlikely that a single transduction stage, like eq. (29), can make adequate predictions. On the other hand, it is not unlikely that, if desired, the present model could be expanded to deal
with a wider range of results.

As discussed in footnote 7 on page 35, we are assuming throughout this paper that 1/2 sec gap in a continuous background is not long enough for the adaptation effects of the "real light" signals to decay to the point where the "dark light" signals make a significant contribution. However, it would not be difficult to alter the model appropriately if current experiments, in our laboratory, should disprove this assumption.
VIII. Summary

1) Using the results of Rushton's measurements of the bleaching and regeneration of cone pigments, the effects of photopigment depletion on dark adaptation thresholds were analyzed. Although the depletion effect makes large and significant contributions to the elevations in threshold observed after intense bleaches, the greater part of the adaptation effects are due to another process (see 2 below).

2) As Barlow (1964) has argued, bleached photopigment apparently generates a "dark light" signal whose effects on the visual system are equivalent to that produced by some continuous background light that is stabilized on the retina. A formula was derived that relates the intensity of this equivalent background to the proportion of bleached photopigment. It differs from the formula derived by Barlow since he did not take into account the depletion effect. This "dark light" induces the remaining dark adaptation effects not accounted for by the depletion effect.

Changes in the absolute sensitivity of the eye are only one aspect of adaptation. Adaptation effects on brightness and intensity discrimination are equally important. Two key experiments mapped out the range of adaptation effects on brightness and intensity discrimination, by measuring the brightness and discriminability of lights at the endpoints of the light/dark adaptation continuum.

3) The first key experiment was the replication of an experiment, carried out by Craik in 1940, that determined the intensity of lights pulsed in the dark adapted eye that have the same apparent brightness as steady lights to which the other eye has become completely adapted. The experiment confirmed Craik's finding that, as a function of intensity, the brightness of a steady light increases more slowly than the brightness
of a light pulsed in the dark adapted eye; and furthermore, that once a steady light's intensity exceeds around 3.5 to 4.0 log td., its brightness remains constant. Among other implications of these studies is that the constancy of brightness at high intensities is probably due to the depletion effect.

4) The second key experiment measured increment thresholds on backgrounds pulsed in the dark adapted eye, and on steady backgrounds to which the eye has become completely adapted. An initial experiment, together with previous results, indicated that Weber's law describes intensity discrimination under both conditions. However, it was shown that this is only because thresholds on pulsed backgrounds are mediated by initial appearances (i.e. a percept occurring while the stimulus is physically present) at low background intensities, and by short-term, positive, homochromatic afterimages at high background intensities.

5) Intensity discrimination on the basis of initial appearances does not obey Weber's law if the eye is in any fixed state of adaptation, rather it is described by a continuously accelerating function. On the basis of initial appearances, Weber's law holds only when the eye is allowed to adapt, at least partially, to each background intensity before threshold is measured.

6) Intensity discriminations made on the basis of afterimages are approximately described by Weber's law, although the slope of the increment threshold function is slightly less than 1.0.

7) The process responsible for producing the short-term afterimages apparently integrates the energy of lights (obey's Bloch's law) for durations up to 1/4 to 1/2 second.
8) It was shown that the depletion effect is probably responsible for brightness remaining constant above 4.0 log td., and for cone increment thresholds obeying Weber's law on arbitrarily intense continuous backgrounds. Other adaptation effects on brightness and intensity discrimination are due to some other adaptation processes, but are probably not due to "dark light," at least in the present experiments.

9) These other adaptation processes are shown to have the property that adaptation to a fixed level approximately reduces neural responses to all lights as if multiplying their intensities by some factor between 0 and 1.

10) The hypothesis that short-term adaptation effects on increment threshold are due in part to decision factors (Sperling, 1965) was tested experimentally and rejected.

11) On the basis of theoretical analyses, it was concluded that simple inhibitory mechanisms can simultaneously account for the lateral effects that continuous inducing fields exert both on the brightness and on the discriminability of adjacent test fields.

12) Unlike the effects of preadaptation to a fixed level, a fixed level of surround illumination does not reduce neural activity in center regions as if multiplying all center intensities by some factor between 0 and 1. When the center is more intense than the surround, center brightness is almost unaffected, but when the center is only slightly less intense than the surround, its brightness is greatly reduced. Therefore, lateral effects appear to be produced by different mechanisms than those responsible for adaptation effects.

13) The relationship between brightness matching and increment threshold was examined within a simple framework, based upon some of
the assumptions of the Theory of Signal Detectability (TSD). In particular, the relationship between brightness matching and increment threshold was derived under the assumptions: (a) that the various internal states that a light produces, as a function of intensity, level of preadaptation, and level of surround illumination, are represented by a single dimension, (b) that two lights match in brightness if their \textit{average} values along this dimension are the same, and (c) that threshold is defined by some constant value of $d'$ (that is, by a constant difference in the means of the normalized background and background plus increment distributions). The predicted relationship between brightness matching and increment threshold was shown to obey a simple and easily tested law, a law which roughly held true in the one instance we examined.

14) A general theoretical framework was described, based upon the points 1 through 13 above, that interrelates photopigment kinetics, adaptation effects, and lateral effects. A simple model, derived within the general framework can account qualitatively for many of the important adaptation and lateral effects on brightness and intensity discrimination.
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Appendix

Table 1

Log Pulsed Field Intensity (trolands) — Experiment 1

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**These data are shown in Figure 10.**

Table 2
The data for this condition are from Experiment 3 (both experiments were run within a few days of each other).

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Table 3
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<th>Log Background</th>
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Table 4
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Table 4 (continued)
VITA

Name: Wilson S. Geisler III

Age: 27

Marital Status: Married

Educational Background:

West Valley College
A.S. Degree
1967-1969

Stanford University
A.B. Degree in Psychology
1969-1971

Indiana University
Ph.D. Degree in Psychology
1971-1975