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PSYCHOLOGICAL REVIEW

CHANGES IN THE APPEARANCE OF STIMULI OF VERY HIGH LUMINANCE [1]

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When quanta of light strike the retina, some of them are absorbed by the pigment molecules contained in the visual receptor cells, and this absorption ultimately results in the activation of the visual nervous system. Recent developments in the biochemistry of the visual pigments has given us a fairly clear picture of the microstructure of quantal absorption. A theoretical analysis of this first stage in the visual process will be presented and this analysis will be shown to furnish a possible explanation of certain striking changes in hue and brightness that occur when a stimulus of very high luminance is steadily viewed.

THEORY OF VISUAL PHOTOCHEMISTRY

There is fairly good agreement that light triggers neural events by processes of the following general type. Quanta of light, after passing through the other media of the eye, arrive at the retina where they may or may not hit receptor cells. Those quanta that finally arrive in the region of the visual pigment of the receptor cells may or may not be captured by the molecules of pigment. If a quantum is in the close vicinity of a particular pigment molecule, the probability that it will actually be captured by the molecule depends upon the relationship between the wave length, or energy, of the quantum and the physical structure of the molecule and its surroundings. If all these probabilities are satisfied, the quantum is absorbed by a visual pigment molecule. When, before absorption of the quantum, the pigment molecule was in a state that will hereafter be called the "regenerated" state, the absorption will cause the molecule to change its state (to what will be called an "unregenerated" state). For example, Kropf and Hubbard (1958) suggest that the change in state is a cis-trans isomerization. The changing of state of a regenerated pigment molecule sets up a process in the receptor which eventually results in the discharge of a packet of some chemical mediator at a synapse farther along in the retina. When the concentration of chemical mediator at the synapse is great enough, a nerve impulse is triggered, and either that impulse or another

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resulting from it, travels up the optic nerve. At the synapse, there is also a substance that destroys the chemical mediator and this, combined with diffusion effects, give the mediator a short "half life." Therefore the probability of triggering a nerve impulse depends upon the *rate* of discharge of packets. Above threshold, the frequency of nerve impulses will be greater, the greater is the rate at which packets of mediator are being discharged. Since each discharged packet is the ultimate result of the absorption of a quantum by a regenerated molecule, the frequency of nerve impulses will depend upon the rate at which quanta are absorbed by regenerated molecules.

The changes that occur in retinal photopigment when light is absorbed are reversible, and, if the eye remains in darkness long enough, virtually all of the pigment will have regenerated to its initial, ready-to-trigger, state. Some of the more recent evidence on cone pigments *in vivo* indicates that at least the main part of this regeneration process goes on at the same rate whether the eye is in darkness or in light, the rate depending only upon the concentration of unregenerated pigment present (Rushton, 1958).

If the above general conceptions are correct, then, when a subject is steadily fixating a field of fixed luminance, retinal pigment is both being broken down and regenerated, and the frequency at which nerve impulses are being fired in any one optic nerve fiber depends upon the rate at which regenerated molecules are being broken down. Hereafter, the term "output" will be used to denote the instantaneous concentration of chemical mediator at the receptor terminus. This receptor output is thus directly related to the rate at which quanta are absorbed by regenerated molecules,

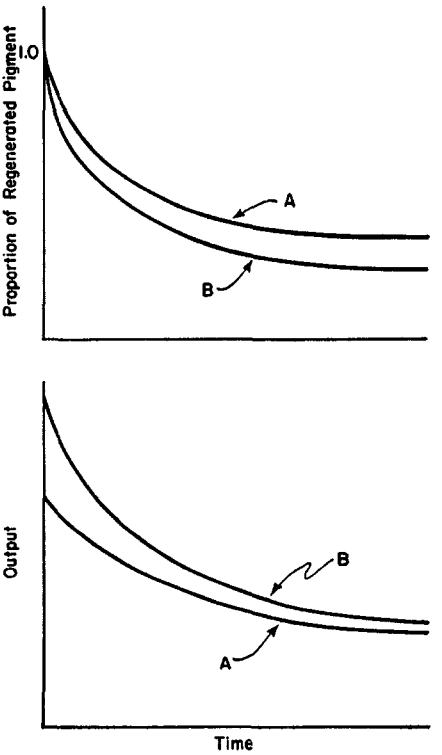

FIG. 1. Proportion of regenerated pigment as a function of the time after onset of the stimulus, for two different illuminances (B greater than A); and output as a function of the time after onset of the stimulus for the same two illuminances.

and it is similarly related to the frequency of triggering of nerve impulses somewhere farther along the retinal activity chain.

The upper curve, labeled A, in the upper part of Figure 1 is a generalized representation of the changes in pigment concentration that would occur during stimulation of a single receptor if the preceding considerations are correct. The receptor is completely dark adapted before the onset of the stimulus, so that the proportion of regenerated to total pigment is 1.0. At the time represented at the origin, a steady light is turned on. The pigment concentration will drop rap-

idly at first and then level off as it approaches some asymptotic level, the level at which the rates of breakdown and regeneration are equal. The lower curve, labeled B, represents the same events for an identical receptor under a more intense stimulus.

The curves in the lower part of Figure 1 are a generalized representation of the outputs (rates of pigment breakdown) of the same two receptors under the conditions of the upper part of Figure 1. Since the receptors are taken to be identical, and since at time 0 both concentrations are 1.0, the initial output of B will be greater than the initial output of A. Further, since the time constants of regeneration for A and B are taken to be equal, the output of B must approach a final level that is higher than the asymptote of A. This is true even though the equilibrium concentration of regenerated pigment is lower for B than for A.

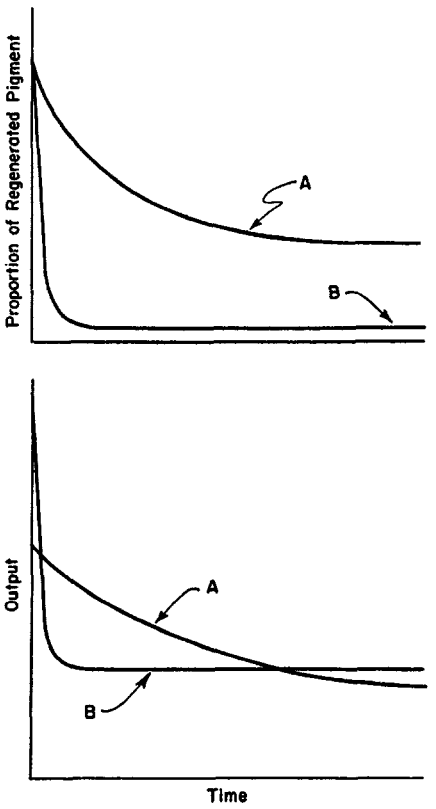

FIG. 2. Proportion of regenerated pigment as a function of time after onset of the stimulus, for two different illuminances (A at moderate illuminance and B approaching an infinite illuminance); and output as a function of time after onset of the stimulus for the same two illuminances.

The upper part of Figure 2 represents the regenerated pigment concentration curves for the same two receptors when the illuminance on B has been raised almost to infinity, but the illuminance on A is the same as in the preceding figure. In the first short interval after the light is turned on, virtually all of the pigment molecules in B will be broken down. From that time on, each molecule that flips back to the regenerated state will immediately be broken down again. In other words, when the illuminance approaches infinity, the concentration approaches equilibrium extremely rapidly, and the equilibrium level depends only upon the time constant of regeneration of the pigment. The lower part of Figure 2 shows the output curves for these receptors, again when the illuminance on B approaches infinity. It will again be true that, when the stimuli are first turned on, B will have the higher output. Further, at equilibrium, B must still have the higher output, even though its regenerated pigment concentration is very much lower. In general, the equilibrium rate of breakdown of regenerated pigment (output) is greatest when the illuminance is infinity, since that rate equals the rate of regeneration and since the rate of regeneration will be greatest when the concentration of *unregenerated* pigment is greatest. But, since

Receptor B will reach its equilibrium level almost instantaneously, its output curve must cross the output of A twice, as in the lower part of Figure 2. (This is necessarily true as long as the illuminance on A is great enough that its initial output level is greater than the equilibrium level for B.) Obviously the illuminance on one of a pair of receptors need not be nearly infinite in order that the pair exhibit a reversal of output relations. There will be a large set of pairs of illuminances for which reversal should occur.

A More Specific Set of Assumptions and Their Consequences

Now let us substitute, for each of the general conditions described above, a corresponding specific assumption about the operation of the visual system. From these assumptions, certain quantitative aspects of the visual phenomena to be discussed may be derived, and the derivations examined in comparison with the data themselves.

If the absorption of a quantum by a particular molecule is independent of the state of the other molecules in the receptor, then it follows from statistical considerations that the rate of absorption by regenerated molecules is:

$$\left(\frac{dN}{dt}\right)_{-} = AQN \qquad [1]$$

where N is the number of regenerated molecules, A is the probability that a quantum incident on a region containing a regenerated molecule will bleach that molecule (the photosensitivity of each regenerated molecule at the wavelength of the incident quantum), and Q is the number of quanta incident during the Time dt.

Recent studies of the bleaching of cone pigments in the living human eye support the notion that, at least to a good approximation, the regeneration of cone pigments is a first order chemical reaction (Rushton, 1958). We will assume, accordingly, that the probability that any particular unregenerated molecule will be regenerated in a unit of time will be independent of the states of the surrounding pigment molecules. It follows then that the rate of regeneration of unregenerated molecules is:

$$\left(\frac{dN}{dt}\right)_{+} = K(M - N) \qquad [2]$$

where M is the total number of molecules, regenerated or not, in the receptor, N is, again, the number of regenerated molecules, and K is the probability that an unregenerated molecule will be regenerated in Time dt.

The net rate of change of regenerated molecules is:

$$\frac{dN}{dt} = K(M - N) - AQN \qquad [3]$$

We will now define the quantity X, the proportion of regenerated pigment in a receptor:

$$X = N/M \qquad [4]$$

Substituting Equation 4 into Equation 3 and dividing through by M:

$$\frac{dX}{dt} = K(1 - X) - AQX \qquad [5]$$

The solution to this differential equation yields:

$$X = \frac{K}{K+AQ} + \frac{AQ}{K+AQ} \cdot e^{-t(K+AQ)} \qquad [6]$$

when the initial condition is $X = 1$, that is, complete dark adaptation.

In the preceding section, the output of a given receptor was defined as the rate at which quanta are absorbed by

regenerated molecules. Therefore:

$$\Omega \equiv \left(\frac{dN}{dt}\right)_{-} = AQN = AQMX$$

$$\Omega = AQM\left[\frac{K}{K+AQ} + \frac{AQ}{K+AQ}\cdot e^{-t(K+AQ)}\right] \quad [7]$$

This is an equation that relates the output of any given receptor to the irradiance and duration of a steady light falling upon it.[2] The lower parts of Figures 1 and 2 are actually plots of Equation 7 for various values of Q.

CONSEQUENCES FOR BRIGHTNESS

It seems to be a reasonable assumption that the brightness of a lighted area will increase as the frequency of nerve impulses originating from the retinal region corresponding to that area increases. If this assumption and those concerning the conversion of quanta to impulses are correct, then the falling of the curves in the lower parts of Figures 1 and 2 represent the fact that the brightness of a stimulus of fixed luminance decreases as the eye light adapts to it.

The considerations illustrated in the lower part of Figure 2 also lead to the following prediction. If the eye is first dark adapted, then one area of the retina is illuminated (say with white light), and another area is simultaneously illuminated much more intensely, the more intensely illuminated area will look first brighter than the other, then darker, and finally somewhat brighter again. That is, there should be a period of time during which the less intensely illuminated region should look brighter than the more intensely illuminated one. This paradoxical prediction has been tested and it is correct. The predicted brightness reversal does indeed occur, and is very easy to demonstrate.

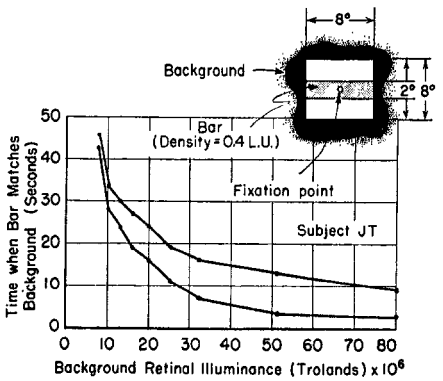

FIG. 3. Times of brightness reversals as a function of retinal illuminance for the stimulus configuration shown in the upper right corner. (The surround was dark, the background illuminated, and the horizontal bar consisted of a strip of 0.4 log unit neutral density filter. Each point is a mean of four judgments.)

The data in Figure 3 were taken under the following conditions. The subject fixated a small bright point in the center of the field shown in the upper right corner of the figure. The field was shown in Maxwellian view, through a simple optical system whose effective aperture was 3.5. The source was a 32-candle power automobile taillight bulb, run from a regulated DC supply. The filament image at the pupil was 1 millimeter in diameter, centered on the natural pupil. The luminance of the field was varied with neutral density filters. Heat glass was used to filter out the infrared.

[2] None of the steps in this derivation is original. Pieces of it can be found in the writings of Troland (1930), Hecht (1935), Rushton (1958), for example. And, although the writer has not found the complete derivation all in one place in the literature, it may well be there somewhere.

When the field is first turned on, it looks like a dark bar on a bright field. But after a time that depends upon the luminance relations, the field abruptly reverses, so that the bar looks considerably brighter than the background. Then the brightnesses gradually converge and reverse again, until finally the background looks just slightly brighter than the bar.

To collect the data in Figure 3, the following procedure was used on each trial. The subject's viewing eye was dark adapted for 5 minutes. Then the stimulus figure was turned on and two clocks started. The subject looked steadily at the fixation point, and at the first instant when the bar and its background were equally bright (changing from normal to reversed brightnesses) he pressed a key, stopping one of the clocks. When the brightnesses were again equal (changing from reversed to normal) he pressed a second key, stopping the second clock. The two times were recorded, and each point on the curves in Figure 3 is a mean of four such times. The area between the two curves in Figure 3 represents the times when the brightnesses are reversed. At least 45 minutes elapsed between successive trials, and the order of illuminances was balanced.

The second equality point is much harder to judge than the first one, and the judgments are less reliable. Part of the reduction in reliability is due to the fact that the changes are occurring very gradually, but, in addition, strong hue differences between the bar and ground appear after the first 20 seconds or so; the background turns reddish and the bar less red. (There is not much point in trying to interpret these color differences physiologically, because the wave length composition of the stimuli in this set of experiments

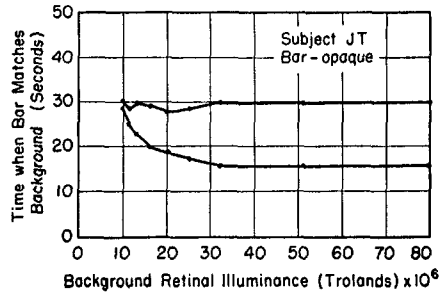

FIG. 4. Times of brightness reversals as a function of retinal illuminance. (For these data, the bar, as shown in Figure 3, was replaced by an opaque strip. Each point is the mean of four judgments.)

was very complex, due to absorption by the heat glass, etc.)

The brightness reversal occurs equally strongly whether the fixation point is in the bar or the background. It cannot be explained by inhomogeneities in the retinal structure.

The data in Figure 3 were taken when the bar was .4 log units less intense than the background. (The bar was simply a strip of .4 density neutral gelatin filter pasted across the larger square aperture that formed the background.) But brightness reversal also occurs when the bar transmits no light to the retina. The data for Figure 4 were taken after the strip of .4 density filter was replaced by an opaque strip. In this case, the time relations are less strongly dependent upon the illuminances (and the hue differences more extreme), but the effect is still very strong. The fact that the strip is opaque does not mean that the actual retinal illuminance in the region of the image of the bar is zero. There is extensive evidence in the literature to indicate that the stray light in this sort of stimulus situation is appreciable (see DeMott & Boynton, 1958, for an extreme example). Furthermore, there is a good possibility that the illuminances at

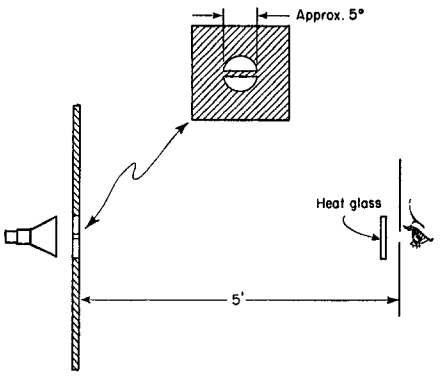

FIG. 5. Apparatus for a demonstration of brightness reversal. (The inset figure shows the subject's view.)

the edges of the figure (where stray light is greatest) are the critical ones. (This possibility is currently being tested.) Thus, the retinal condition in which an opaque bar is used in the apparatus is on a continuum with any in which a filter of transmittance greater than zero is used.

It is easy to set up a demonstration of this brightness reversal, as illustrated in Figure 5. A strip of cardboard is placed across a round hole in a larger board. This hole is just a little smaller than the face of the sort of photoflood lamp that has a frosted face and a built-in reflector (e.g., GE #PH/RFL2). A small hole in the middle of the strip will serve as a fixation point (it is essential to fixate very steadily for this demonstration). The face of the photoflood lamp should be viewed through the hole and strip, and through heat absorbing glass, from about 4 or 5 feet away.

AN EXTENSION OF THE THEORY TO CHANGES IN HUE

When a subject steadily fixates a field of extremely high luminance in the long wave length region of the spectrum, the hue of the field undergoes very striking changes. Some of these changes have been mentioned independently by Auerbach and Wald (1955) and by Noddack and Jarzyk (1955), in the course of studies of other color phenomena. Cornsweet, Fowler, Rabedeau, Whalen, and Williams (1958) briefly reported a study of the color changes themselves. According to all of those articles, the nature of the color changes is as follows. The subject looks steadily at a field that is illuminated with light from the long wave length end of the spectrum. When the luminance is low or moderate, the field will look red or orange. However, if the luminance is extremely high, it will look orange at first, but then rapidly shift in hue through yellow to a vivid green. This pattern of changes is reported to occur for stimuli of several different wave lengths in the "red" end of the spectrum, and for monochromatic as well as broad band stimuli. Stimuli with wave lengths in the green region of the spectrum are reported to produce extreme desaturation, but no clear hue changes are reported. Auerbach and Wald (1955) also report that bright blues will change to red, but such a change was not observed in either of the other two studies cited. A review article by Cohen (1946) provides a number of references to other studies of the effects of high luminance stimulation.

The theoretical considerations discussed in the preceding sections suggest an explanation for some of these changes in hue. The explanation is based upon the retinal mechanisms already mentioned, along with some simple and widely held assumptions about the physiological bases for color vision.

First, we will assume that there are at least two sorts of cones that differ in the pigments they contain, the two pigments having different but overlapping absorption spectra. The absorption spectra for such a pair of

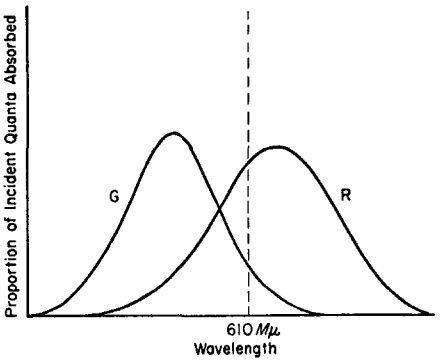

FIG. 6. Generalized spectral absorption curves for two hypothetical retinal pigments. (The wave length 610 mu, indicated on the abcissa, will be specifically referred to later in the text.)

cone types are shown in Figure 6.[3] The two cone systems will be labeled R and G, as in Figure 6. Now consider the situation in which a subject is shown a stimulus and is forced to call it either red or green, no other alternative being permitted. Let us assume that the probability of his giving a "red" judgment depends upon the ratio of the outputs of the R and G systems. In the simplest case, when the R output is greater, he will be more likely to call the stimulus red, when the G output is greater, he will call it green, and when they are equal, he will judge it green half the time and red the other half. There is no theoretical necessity that the output ratio be 1.0 for 50% "red" judgments, but that particular condition will be assumed for much of the remainder of this paper, merely to make the discussion easier to phrase.

Figure 7 shows the results obtained when a subject is forced to judge a flash of monochromatic light as either red or green, as the wave length in the region between red and green was varied by the method of constant stimuli. It should be noted that the slope of this curve is very steep, so that a change of just one or two millimu on either side of the 50% wave length will elicit reliable judgments of red or of green. Now if a subject is given a stimulus with a wave length right at the 50% point and asked what its hue *really* is, he says it is pure yellow. It follows from these observations that the last assumption discussed above is equivalent to assuming the following: when the R output exceeds the G output, the subject will see red, when the G output is greater, he will see green, and when the two are equal, he will see yellow. (This is of course true only for the spectral region between red and green. There may be other spectral regions in which the R and G outputs are also equal, but where the hue is given some other name, e.g., blue. The question of whether

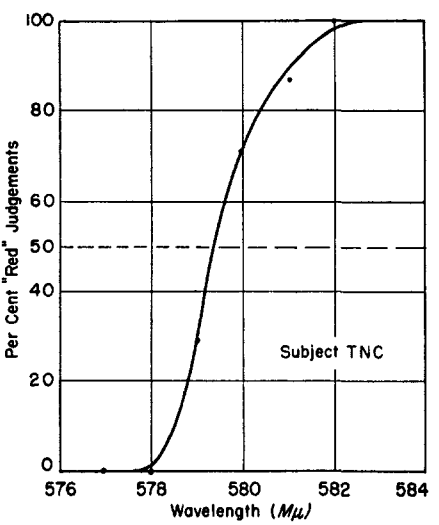

FIG. 7. Distribution of judgments for constant stimulus method. (On each 1/4-second flash, the subject was given a forced choice between responses "red" and "green.")

[3] The theory discussed in this paper requires that there be *at least* two cone systems, but does not approach the question of how many there may be altogether.

the yellow sensation is produced by a mixture of the R and G outputs or represents an excess of yellow over blue output with the red and green outputs cancelling each other, is not relevant to any of the present discussion.)

The explanation of some of the hue changes that occur to stimuli of high luminance follows directly from these assumptions. Monochromatic light in the long wave region of the spectrum, for example at 610 millimu, will be absorbed by both the R and the G cone pigments, but since the absorption coefficient for the R pigment is higher than the G at 610 millimu (see Figure 6), the R cones will absorb a greater percentage of the incident quanta. This is exactly equivalent to putting a greater illuminance on the R than the G cones. Therefore, if the R and G cones differ only in their absorption spectra, and a stimulus of very high luminance at 610 millimu is given, their output versus time curves will look like those in the lower part of Figure 2, Curve A representing the G and B the R system. The stimulus should look red at first, then change through yellow (when the curves cross) to green, and finally slowly change back through yellow to orange.

It has been reported in previous papers (Cornsweet et al., 1958) that a high-luminance red stimulus will appear to change from red through yellow to green. "No further color changes were observed, even though fixation was maintained for as long as three minutes" (p. 898). The present more extensive data at a variety of wave lengths, and at luminances greater than those used in the earlier study, clearly show that further changes do occur. In fact, the hue of the stimulus eventually changes back from green through yellow to orange as is predicted by the theoretical argument above. This later set of changes happens to take appreciably longer than 3 minutes at the relatively low luminances and at the particular wave lengths used in the earlier study (Cornsweet et al., 1958). But at other wave lengths and luminances, all of the changes appear to be over within a minute or two (see the data in succeeding sections).

GENERAL ASPECTS OF HUE CHANGES

The general course of the hue changes that occur when viewing a high-luminance stimulus at 620 millimicrons is illustrated in Figure 8. This figure is drawn from a set of crude binocular matchings, in which the high-luminance stimulus was presented to one eye and a matching stimulus of much lower luminance, whose wave length could be varied, was presented to the other. The curve in this figure should not be taken as anything more than a qualitative indication of the phenomenon under discussion. Quantitative data of a more reliable and useful sort will be presented later.

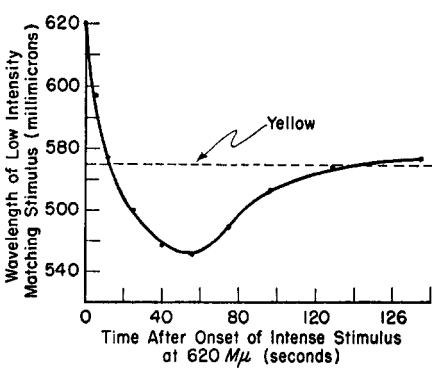

FIG. 8. Wave length of a low luminance stimulus flashed to the left eye that matches the hue of a high luminance stimulus, at 620 mu, steadily fixated by the right eye, as a function of the time of viewing the high-luminance stimulus.

At this writing, the limits of the range of wave lengths for which hue changes occur have not been well established. However, the following general statements are true. High-luminance stimuli with wave lengths in the "green-yellow" region of the spectrum (from about 560 to 580 millimu) look green at first, turn a much deeper green, then back through yellow to orange, and finally back to yellow or greenish yellow. Any wave length between 580 and 655 mu will look orange at first, change through yellow to a good, saturated green, and finally back to an orangish yellow. It is probable that light of wave lengths longer than 655 mu also appears to turn green if its luminance is high enough, but 655 mu is the limit with the present apparatus.

Stimuli below 560 mu have not been studied systematically, but in general they seem simply to desaturate to a white at the luminances available in the present apparatus.

For stimuli in the region of about 620 down to 560 mu or less, when the luminances are well above those necessary to produce the change to green, another change seems to be superimposed upon the first 15 or 20 seconds of viewing. The field begins its normal course of hue change, but then abruptly turns to a desaturated pink or violet. It retains that appearance for as long as 20 seconds, then changes back to orange, yellow, or green, and the normal sequence is resumed. This change to pink or violet has not yet been studied quantitatively.

All of the changes in appearance that have been observed depend in character and timing upon the luminance, and, of course, the wave length of the stimulus. These dependencies will be analyzed below.

QUANTITATIVE ANALYSIS OF HUE CHANGES

The photochemical theory outlined above requires that the time course of changes in hue be systematically related to the luminances and wave lengths of the stimuli. In order to evaluate the theory quantatively, data have been collected on the time course of hue changes as a function of retinal illuminance for a number of wave lengths. Those data and their relationship with the theory will be presented below.

PROCEDURE

Judgments Used for the Collection of Quantitative Data

The data presented here were collected by using two different sorts of procedures. The data for Figure 8 (and the data for the brightness reversals discussed earlier) are based upon a matching technique. Pairs of stimuli are found which differ physically but are judged the same along some perceptual dimension (hue in Figure 8, hue and brightness for the brightness reversal data). The other procedure used here is a sort of hue naming or identification. For example, most of the data in this report result from recording the times at which a subject judges the hue of the stimulus to be pure yellow, that is, neither reddish yellow nor greenish yellow.

In situations where a choice may be made between matching and hue naming techniques, it is usually far preferable to employ matching (Brindley, 1960). Hue naming was used principally here for two reasons. First, for the particular phenomenon studied, the problems introduced by matching are considerably worse than those of hue naming. For example, to determine the time at which a stimulus of high luminance produces a hue match with a standard hue (e.g., yellow) the matching field must be at a low enough luminance that its hue is not changing very much. Therefore, the luminance of the matching field should be at least 2 log units lower than of the test field. However, the stray light from the test field then approaches and perhaps even exceeds the direct illuminance of the matching field. If the matching field is presented to one eye and the test field to the other, the

effects of the stray light are not eliminated, but just rendered less estimable. The collection of the data represented in Figure 8 took advantage of the fact that, even when the two fields are projected on to noncorresponding parts of the two retinas, rivalry occurs. That is, if the stimulus of high luminance is presented continuously and the matching field is occasionally flashed to the other eye, the only thing visible during the flash seems to be the matching field. It is then possible to find a test flash wave length that is the same hue as the high-luminance field at a given time after the onset of the high-luminance field. However, this procedure clearly involves so many factors of unknown effect (stray light, rivalry, transients from the flash, etc.) that it is at best useful only to give a rough idea of the sorts of hue changes that do occur.

A different sort of matching technique might have been used in this study. Instead of determining the time at which the intense field matches one of a fixed hue, the subject might have been presented with two patches having different wave lengths and high but different luminances. Then as the patches both changed in hue (and brightness), the time when they match could have been determined. While not all pairs of stimuli would reach a match, there must be sets of them that would do so. This kind of matching procedure would not be so severely affected by stray light, and in many ways is preferable to the color naming procedure. Brindley (1960) has clearly pointed out that this type of matching procedure (or at least one almost identical with it) enables one to draw physiological conclusions from psychophysical data, without requiring what he calls "psychophysical linking hypotheses." However, it is also true that, when such a procedure is used, psychophysical linking hypotheses *cannot* be tested, and one of the aims of this paper is to examine just such a question, namely, what are the physiological correlates of the condition under which a subject reports the hue as red half the time and green the other half. The matching technique however does have many advantages over color naming as long as psychophysical linking hypotheses are not in question, and studies using strict matching procedures are now in progress.

On the other hand, the procedure that consists of recording the instants in time when the subject calls the stimulus neither reddish nor greenish yields very reproducible results, and results which may be interpreted in a relatively straightforward way.

Apparatus

The apparatus used to collect all of the color data in the present study is shown schematically in Figure 9. The source, S, was a tungsten-coil-filament lamp (GE PH/18A/T10P), run from a constant voltage transformer at 6 volts, 18 amperes. Lens L_1 formed an image of the filament on the entrance slit, En, of a Bausch and Lomb grating monochromator of 500 millimeter focal length, with a 600 lines per millimeter grating, blazed in the visible. The optics of the monochromator imaged the entrance slit (and the filament) on the exit slit, Ex, with an equivalent aperture ratio of 4.4. An airspaced, coated, achromatic lens, L_2, focal length 150 millimeters, f = 1.9, imaged the exit slit in the plane of the pupil of the subject's eye so that he saw a Maxwellian view of the back surface of the lens L_2. The entrance and exit slits of the monochromator were set to widths of 1.5 millimeters, resulting in stimuli with spectral band widths of 5 millimu. The

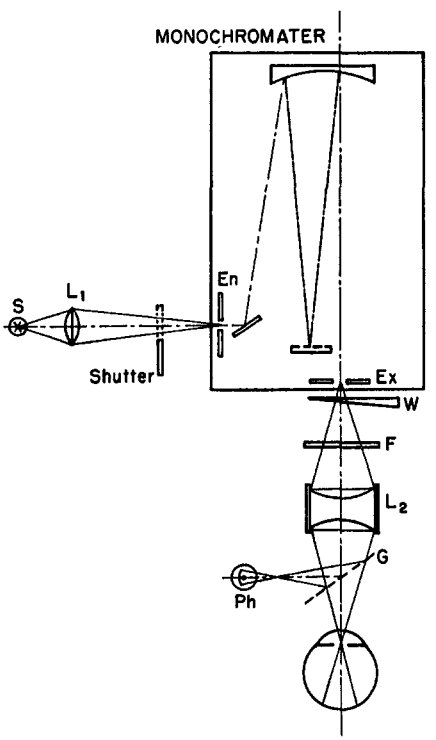

FIG. 9. Apparatus for delivering very intense monochromatic stimuli. (See text for description of specific elements.)

length of the exit slit was also set to 1.5 millimeters. Therefore, since Lens L_2 gave unit magnification, the image at the pupil was a square 1.5 millimeters on a side. This is small enough that as long as the exit slit is imaged at the center of the natural pupil, changes in the size of the natural pupil will not produce appreciable changes in retinal illuminance. A neutral-density wedge, W, and filters, F, were used to adjust the luminance of the stimuli. The wedge was close enough to the exit slit that no balancing wedge was needed. A clear piece of glass, G, reflected a small fraction of the stimulus light to a photomultiplier tube, PH, and the output of the phototube was used to monitor the luminance of the stimulus.[4]

A Hilger thermopile and mirror galvanometer were used to make the energy calibrations. The thermopile was placed at the pupil position during these measurements. The spectral purity of the stimulus lights was measured with a second monochromator set at a 5 millimu band width. When the stimulus was at any of the wave lengths studied, no other band had a luminance as great as 1% of the stimulus luminance, and the total light at other wave lengths was less than 5% of the stimulus luminance.

The subject's head was held in position by a dental-impression bar. At his hand was a control panel containing push buttons which operated timers, so that the timing of any changes in appearance could be recorded.

When the stimulus was on, the subject saw a circular field, uniformly illuminated, as illustrated in Figure 10. The dark circular line in this field was produced by cementing a circle of fine wire to the back surface of L_2. This circle helped the subject to make his judgments, in that he judged only the hue within the circle, ignoring the occasional edge effects that small eye movements produced at the outer margins of the field.[5]

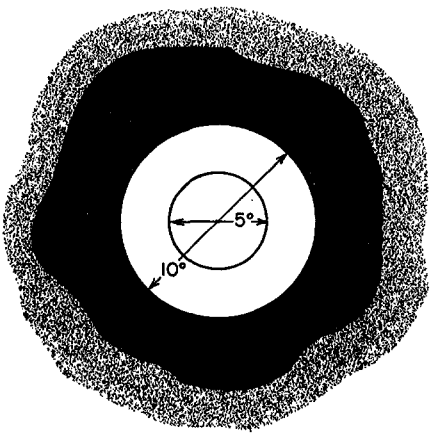

FIG. 10. Stimulus pattern as it appeared to the subject. (The entire 10-degree circular area was uniformly illuminated with monochromatic light. The subject was instructed to fixate the center of the pattern and judge the hue of the inner disk.)

RESULTS OF HUE CHANGE STUDY

The data plotted in Figure 11 show how the time taken to turn yellow varies as a function of the retinal irradiance of a monochromatic stimulus at 610 millimu. For example, at an irradiance of 3×10^{12} quanta per second per square millimeter of retina (uncorrected for ocular transmission losses), the patch looked red or orange at first. The subject pressed his key to indicate that it was yellow (neither reddish nor greenish) after 17 seconds of viewing. He pressed a second key to indicate the second occurrence of

[4] For the relatively short slit-length used here, the coil filament bulb delivered more energy through the system than did the ribbon filament bulb that is ordinarily supplied with the monochromater. However, using the coil filament, the energy at the exit slit varied somewhat from day to day in an unpredictable way. This variability was probably due to the fact that only a very small piece of the filament image was used, and, since the image is not uniformly intense, slight amounts of sagging of the coil or its supports could result in noticeable changes in output at the exit slit. For this reason, the monochromater output was continuously monitored, and the intensity settings were made from the photomultiplier output rather than from the wedge or filter calibrations.

[5] The particular choice of a 10-degree stimulus disc is not crucial. The hue changes occur with fields as small as 15 minutes of arc in diameter. (We have not tested still smaller sizes.) But the variance of the temporal aspects of the judgments is smallest when the field is large.

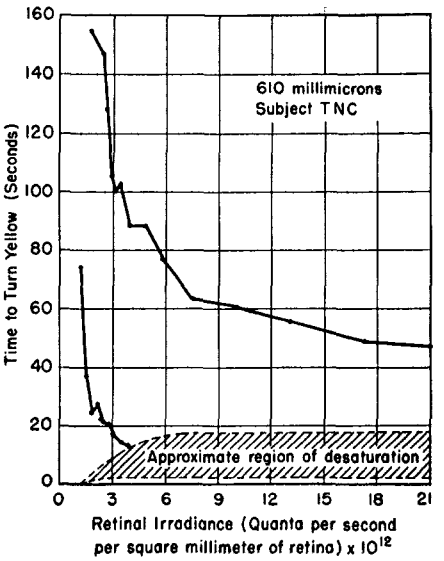

FIG. 11. Time to change hue as a function of the retinal irradiance of the stimulus, at 610 mu. (Each point is a mean of two readings.)

yellow 100 seconds after the stimulus had first been turned on. The area between the two curves represents the times during which the stimulus looked green.

The upper curve, for the second change to yellow, extends out to a retinal irradiance of 21×10^{12} quanta per second per square millimeter, the maximum irradiance available in the apparatus. The lower curve is not plotted beyond 3.9×10^{12} quanta/sec/mm^2 because the hue changes in that region were obscured by a change to desaturated pink or violet, as indicated roughly on Figure 11. For this wave length, the stimulus never appeared yellow at irradiances below 1.2×10^{12} quanta/sec/mm^2.

Figure 12 shows the same sort of data for light of three other wave lengths in the long wave end of the spectrum. The curves for 600 millimu are very similar to those for 610 millimu (Figure 11). As the wave length increases, the lower curves shift toward the higher irradiances, but retain the same general shape. The upper curve at 630 millimu shows evidence of a peak at the lower retinal irradiances. The upper curve at 640 millimu exhibits a very large amount of variability, and is not plotted beyond 9×10^{12} quanta/sec/mm^2 because the change back to yellow had not occurred during 210 seconds of continuous viewing. The variability in all cases increases very greatly as the time of viewing becomes extremely long. It will be shown that curves of this form may be expected from the theoretical considerations discussed previously.

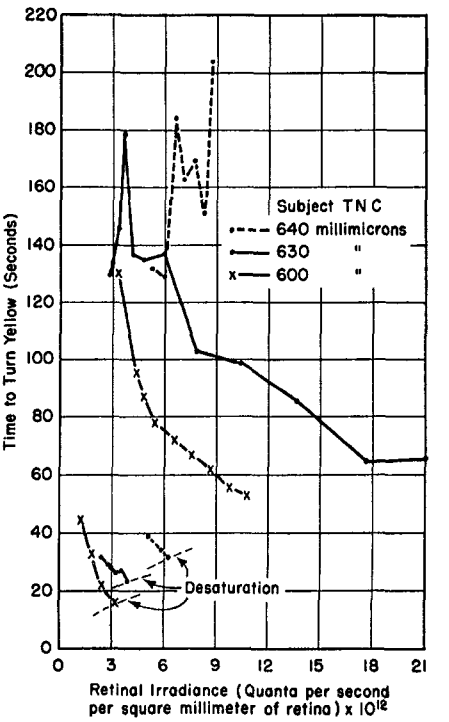

FIG. 12. Time to change hue as a function of retinal irradiance for three different wave lengths. (Each point is a single judgment.)

RELATIONSHIP BETWEEN THE DATA AND THE THEORY

The data in Figure 11 have been replotted as dots in Figure 13. They show how the time taken to turn yellow varies as a function of the irradiance of a monochromatic stimulus at 610 millimu. Every dot in this figure represents a time when the stimulus looked yellow. Therefore, according to the theoretical arguments outlined above, each of these points stands for a condition where the outputs of the R and the G systems are in some particular ratio. That is:

$$\Omega_r = C\Omega_g \qquad [8]$$

where C is the value of the ratio at which the hue is equally often called red and green in a forced choice. (In the preceding discussion C was assumed to be 1.0 for simplicity.)

Substituting the photochemical Equation 7 for output in Equation 8,

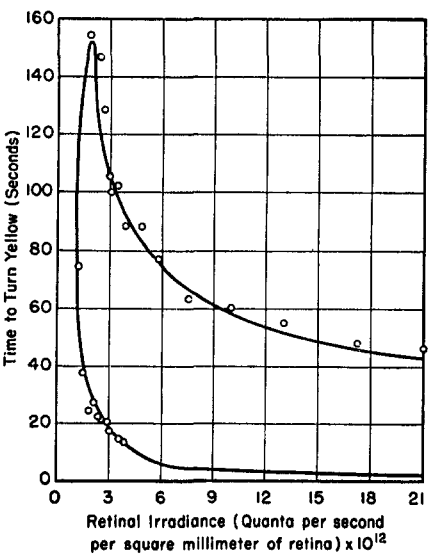

FIG. 13. Time to change hue as a function of retinal irradiance, for light at 610 mu. (Each point is a mean of two judgments. The smooth curve is a plot of the iterative solutions to the implicit Equation 10, using the parametric values listed in the text.)

and supplying the appropriate subscripts:

$$A_rQM_r\left[\frac{K_r}{K_r+A_rQ} + \frac{A_rQ}{K_r+A_rQ}\cdot e^{-t(K_r+A_rQ)}\right] = CA_gQM_g\left[\frac{K_g}{K_g+A_gQ} + \frac{A_gQ}{K_g+A_gQ}\cdot e^{-t(K_g+A_gQ)}\right] \qquad [9]$$

where t is the time of occurrence of yellow. This equation may be rewritten:

$$\frac{K_rA_r}{K_r+A_rQ} + \frac{A_r^2Q}{K_r+A_rQ}\cdot e^{-t(K_r+A_rQ)} = J\left[\frac{K_gA_g}{K_g+A_gQ} + \frac{A_g^2Q}{K_g+A_gQ}\cdot e^{-t(K_g+A_gQ)}\right] \qquad [10]$$

where $J = M_gC/M_r$.

A crude iterative procedure has been used to find the values for the five parameters of this equation that yield a good fit to the data. The two smooth curves drawn in Figure 13 are a plot of Equation 10, when the following values of the parameters are used:

time constant of regeneration of red system, $K_r = .010$ sec^{-1}

time constant of regeneration of green system, $K_g = .0083$ sec^{-1}

photosensitivity of red system at 610 mu, $A_r = 1.70 \times 10^{-15}$

photosensitivity of green system at 610 mu, $A_g = 1.32 \times 10^{-15}$

ratio of amount of green to red pigment multiplied by the output ratio for yellow judgment, $J = 1.18$.

These preliminary values may be compared with Rushton's (1958) esti-

mates:

$$K_r = .008 \text{ sec}^{-1}$$

$$K_g = .008 \text{ sec}^{-1}$$

$$A = .25 \times 10^{-15}$$

for the cone system as a whole, based upon measurements of the bleaching of cone pigments by white light, and corrected for an ocular transmission loss of 50%. Assuming that only an R and a G pigment are present, and correcting for 50% transmission losses, the estimate of A for the entire cone system on the basis of the present data is:

$$A_t = 1/.5A_{r,g} = 2[1-(1-A_r)(1-A_g)]$$

$$\approx 2(A_r+A_g)$$

$$A_t \approx 6 \times 10^{-15} \text{ cm}^2$$

The value of A_r determined from the color reversal data agrees much more closely with that quoted by Brindley (1960). From psychophysical data (quite different from those presented in the present paper), he estimates that $A_r = 1.61 \times 10^{-15}$ (p. 217). The writer has been unable to find estimates of the constant "J" in the literature. (This constant represents a psychophysical linking hypothesis, in Brindley's terminology.)

The agreement between these estimates is not perfect, nor is the fit in Figure 13. Its presentation is not intended to imply that the present formulation and these particular values are the "true" ones. The plot is meant to serve two purposes. First, it makes clear that the general formulation is consistent with the reported hue changes when put into at least this specific form. Second, it serves as a preliminary report on the extensive work now in progress attempting to evaluate, quantitatively, the specific theoretical arguments presented here. This work consists in making determinations of the best fit values of the parameters of Equation 10 under a number of independent conditions. For example, if this procedure is repeated at a number of different wave lengths in the red region of the spectrum, the best fit values of K_r, K_g, and J should be identical at each wave length, but the values of A_g and A_r should trace out the spectral sensitivity curves of the R and G systems.

The quantitative procedure used for finding parameters of the color phenomena may be applied to the achromatic brightness reversal phenomenon as well. However, the particular stimulus configuration used to gather the brightness reversal data presented in this paper do not lend themselves to straightforward analysis. For example, it is almost certain that the illuminances at the borders of a retinal region are more important in determining the apparent brightness of the region than are the illuminances in other regions; and, for a bar against a background, stray light and small eye movements have large and indeterminate effects on the effective illuminances at the borders. An experiment is currently in progress in which these factors are minimized, while the time course of brightness reversal is determined in much the same way as before. The results of this experiment should be directly analyzable in terms of the photochemical hypothesis presented above.

Observations on the rate at which the hue of the stimulus changes are qualitatively consistent with the theory, as plotted in the lower part of Figure 2. That is, the first change through yellow passes quickly, the stimulus actually appearing to be yellow for a very short time. The second change, where the theoretically determined output curves are running

more nearly parallel, occurs very slowly and gradually. This is borne out quantitatively by the fact that the variance of the judgments of the time of second yellow point is appreciably greater than the variance of the first yellow point. The brightnesses of the stimuli also agree qualitatively with the theory. Although brightness has not been measured for the monochromatic stimuli, it is always high at first, gradually dropping to a much lower equilibrium level.

From the theory as it has so far been stated, it might be expected that, just as a red light turns green, a green light should turn red, and a yellow one should not change in hue. This would indeed be the prediction if it happened to be true that (*a*) the rates of regeneration of the red and green systems were identical, and (*b*) the density of red and green pigment molecules were also identical. But if one regeneration rate were greater than the other, high-luminance stimuli near the yellow region would, at *equilibrium*, take on the hue of the system that regenerates faster. From the present findings, this hue seems to be red, but the data are not yet complete enough to draw firm conclusions about the relative rates of regeneration.

The fact that yellow and greenish yellow stimuli change toward purer greens before changing back through yellow would follow directly from the theory if there is more green than red pigment present in the stimulated region of the retina. Consider, for example, light of a wave length that looks yellow when it is first turned on. This means that it is initially isomerizing red and green pigment molecules at the same rate (again assuming that $C = 1$ for convenience). However, if there are actually fewer red molecules present per unit of area, the rate of isomerization of red molecules will immediately become smaller than the corresponding rate for the green system, and the stimulus should turn green. This sort of effect is superimposed upon the processes already discussed so that, at the proper irradiances, an initially green stimulus should first get greener, then change back through yellow to red, and finally again through yellow to green, as it does.

It was mentioned above that, when the wave length is not too long (in the "orange") and the irradiance is extremely high, the early stages of hue change seem to be obscured by a wave of desaturated pink or violet. This effect would be expected if short wave sensitive systems were present and did produce desaturation. In this case, during the early stages of adaptation, both the R and the G systems are so intensely bombarded, relative to the short wave sensitive systems, that the R and G outputs drop to values comparable with the short wave systems, and desaturation occurs.

Note: One should exercise caution when viewing stimuli of very high luminance. Fechner permanently damaged his retinae by staring at the sun, and ophthalmologists can count on an increased patient load after solar eclipses. Since there have been very few systematic studies of the pathological effects of intense lights (see Whiteside, 1960), there are no clear rules on what should be avoided. In general, the sun should not be used as a source unless it is very strongly filtered, and any source that contains a large amount of infrared radiation should be filtered by heat-absorbing glass. The writer and many others who have observed the phenomena discussed in this paper exercised these

precautions and experienced no discomfort except for afterimages that last for a few minutes.

SUMMARY

Evidence concerning the absorption of light quanta by visual pigment molecules is used to derive a theoretical relationship between the parameters of light incident on the retina and the output of the receptor cells. This relationship leads to the following prediction: when two retinal areas are illuminated, one very intensely and the other still more intensely, there will be a period of time during which the less intensely illuminated region will appear brighter than the more intensely illuminated one. Data verifying this prediction are presented.

When the theoretical treatment is expanded to include certain assumptions about retinal color mechanisms, it provides an explanation of some of the changes in hue that occur when a very intense colored stimulus is viewed steadily. Data on the temporal course of these hue changes are presented, and their relationship to the theory is discussed. This kind of analysis is shown to be a possible means for the quantitative evaluation of certain physiological properties of the visual system.

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