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Basic Concepts in the Interpretation of Visual Phenomena

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Basic Concepts in the Interpretation of Visual Phenomena

THEODORE LOUIS JAHN

During the past decade several attempts have been made to formulate equations which would explain certain visual phenomena, namely flicker fusion frequency, brightness discrimination, visual acuity, and instantaneous thresholds as functions of intensity, and light and dark adaptation as functions of time. These various equations are based on several fundamental concepts regarding the mechanism by which the visual sensation is determined. Each concept has been explained by the original author at the time the theory was proposed, but no comparison of these basic ideas has yet appeared in the literature. The purpose of the present paper is to make such a comparison available.

The visual phenomena which these equations and theories are designed to explain are briefly described below:

1. **Flicker fusion frequency.** The flicker fusion frequency is the frequency at which a flickering light appears to be continuous. This frequency varies with the intensity of the light as shown in the

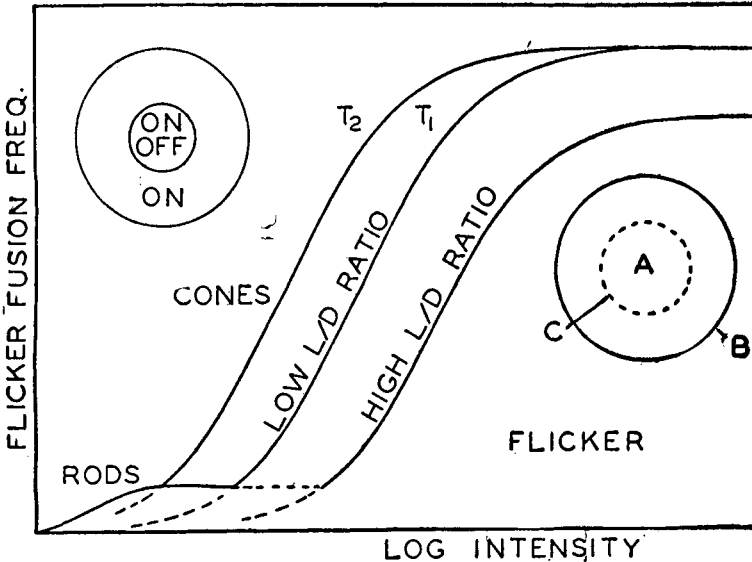


Fig. 1—Diagram showing the shape of rod and cone curves for flicker fusion frequency plotted against log of intensity, and the changes produced in the cone curve by changes in temperature (T_2 is higher than T_1) and by changes in the ratio of the light to dark (L/D) periods, during a flicker cycle. Similar changes which occur in the rod curve are not shown. For explanation of the inserts see text.

curves of fig. 1. In experiments on man the subject is usually confronted with a uniformly illuminated field, and in the center of this field is an area which flickers as shown in the upper left insert of fig. 1. The lower right insert shows the arrangement used for animals. The animal is placed at A, C is a rotating glass cylinder with longitudinal opaque black stripes, and B is a circular source of light. The animal is free to look along any radius, and as the cylinder rotates the black stripes give the appearance of a flicker. Many animals (turtles, frogs, fish, isopods, insects) react to the light as long as it appears to flicker and cease to react as soon as it appears to be continuous. If the light to dark ratio of the flicker cycle is altered the curve is shifted as shown. If the temperature of a cold blooded animal is raised (e.g., from T_1 to T_2) the curve is shifted to the left.

2. **Brightness discrimination.** By brightness discrimination we mean the ability to detect a change in brightness. The observer is confronted with uniformly illuminated field of intensity I . Then an

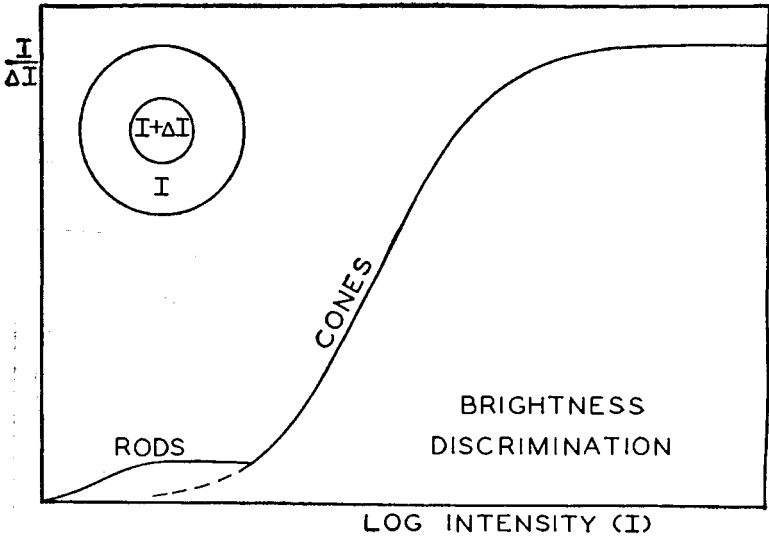


Fig. 2—Diagram showing shape of curve for brightness discrimination as a function of log of intensity. For explanation of insert see text.

additional intensity (ΔI) is briefly superimposed on part of this field, and the observer determines the value of ΔI which can just barely be detected. A plot of $I/\Delta I$ against $\log I$ is shown in the curve of fig. 2, and one form of the experimental field of view is shown in the insert.

3. **Visual acuity.** By visual acuity we mean the ability to see small objects. One simple form of experiment is shown in the insert of fig. 3. The observer is confronted with a field of intensity I and

a black line of variable width, and he is allowed to determine the width of the line which can just barely be seen at various intensities. Results of a typical experiment are shown in the curve of fig. 3 where the reciprocal of the width is plotted against intensity.

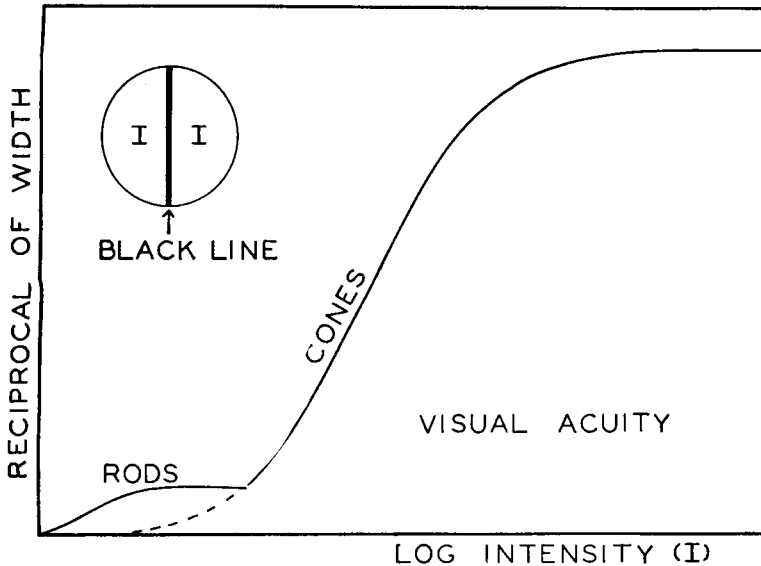


Fig. 3—Diagram showing shape of curve for visual acuity as a function of log of intensity. For explanation of insert see text.

Because of diffraction the image on the retina for the narrowest line that can be seen is not in black and white, but in gray and white. Therefore, this experiment is really one in brightness discrimination, and any explanation for brightness discrimination should also explain visual acuity.

4. **Dark adaptation.** By dark adaptation we mean the increase in sensitivity (or the lowering of the threshold, the sensitivity being the reciprocal of the threshold) which occurs when a subject exposed to light is placed in darkness. Results of typical experiments are shown in fig. 4. If the adapting light is of low intensity and duration the change in the threshold is rapid as shown by the curve for slight light adaptation (L.A.). If the adapting light is very bright and of long duration the recovery curve is of the type shown for intense light adaptation. In the latter case the threshold may fall 5 to 6 log units during forty minutes in the dark. That means that the sensitivity of the eye has been increased as much as 1,000,000 times.

Fig. 5 shows similar data plotted in terms of sensitivity instead of threshold. The numbers on the curve represent the intensity of the adapting light in photons. The ordinate is units of sensitivity and the abscissa is in minutes.

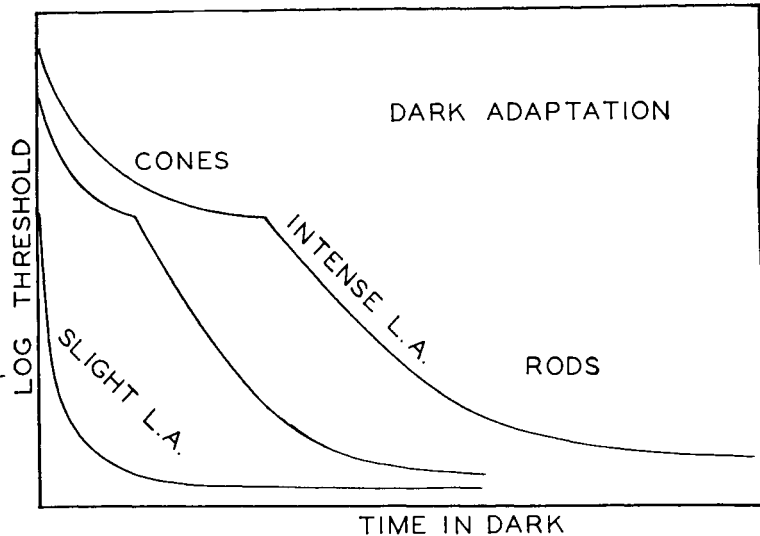


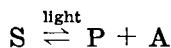
Fig. 4—Diagram showing the lowering of the visual threshold during the course of dark adaptation. The total time scale is about 40 minutes.

5. **Light adaptation and instantaneous thresholds.** If a person is subjected to an adapting light which is then turned off and the threshold is determined immediately the measurement is known as that of an instantaneous threshold. By this method it is possible to determine the threshold as a function of time during the course of light adaptation or to determine the threshold as a function of the intensity of the adapting light if the time of adaptation is long enough to allow a state of equilibrium to occur for each intensity.

The purpose of the present paper is to examine the similarities and differences of the basic concepts used in deriving equations which are supposed to fit data of the types listed above. At present, in the literature there are six sets of equations representing the theories outlined below.

1. *Photochemical Theory of Hecht* (1918, 1934, 1937).

The photochemical cycle as postulated by Hecht on the basis of sensory kinetics and later demonstrated by chemical investigation (particularly by Wald, 1935, 1938; review, Hecht, 1942) has been the basis for several variations (3, 4, and 6, below) of the original photochemical theory. According to the original theory of Hecht a photosensitive substance S is converted by light into its precursor P and an accessory substance A. P and A, by means of a thermal reaction, are converted back into S, i.e.,



In the original formulation an intermediate stage between S and P

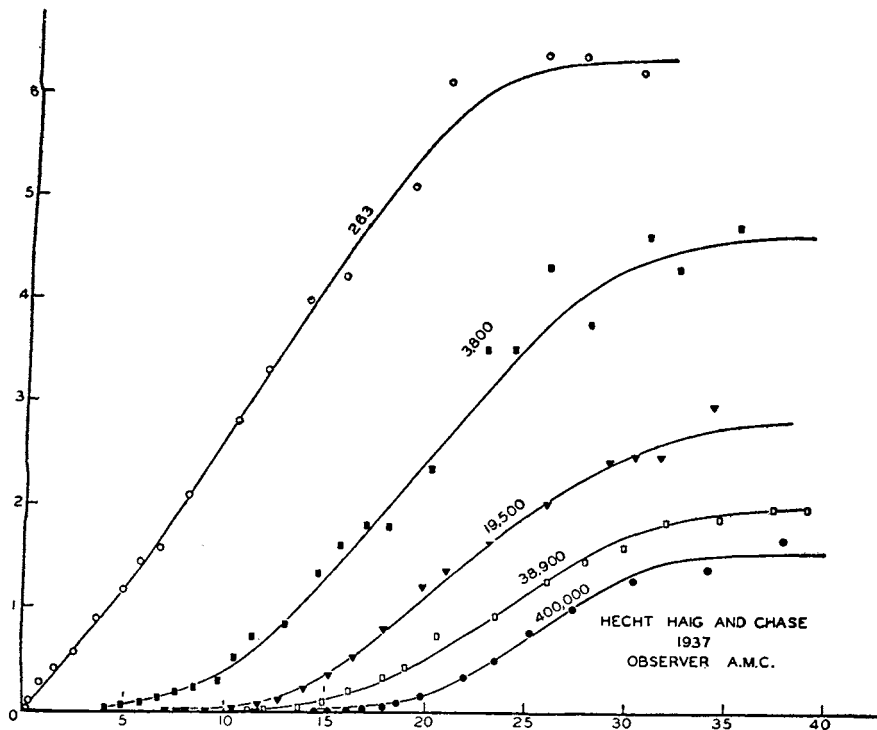


Fig. 5—Data from Hecht, Haig and Chase (1937) recalculated to show the increasing sensitivity of the eye, plotted on the ordinate, as a function of time in the dark, plotted in minutes on the abscissa. Numbers on the curves denote the intensity of the adapting light in photons. (From Jahn, 1946b).

+ A was denoted as “new” P + A, a short-lived substance which was supposed to catalyze a secondary reaction ($L \rightarrow T$) which resulted in stimulation of the nerve. In the later papers of Hecht and his associates, particularly those on flicker fusion frequencies (Hecht, Shlaer, and Smith, 1935), brightness discrimination (Hecht, 1935) and visual acuity (Hecht and Mintz, 1939) the concept of “new” and “old” P + A has been largely ignored, and a correlation has been pointed out between the equilibrium concentration of photoproduct (“old” P and A) and the above visual phenomena as functions of intensity.

The data on flicker fusion, brightness discrimination, visual acuity, and instantaneous thresholds as functions of intensity can be described by various forms of the equation which describes the equilibrium between S and P + A as a function of intensity. This equation is

$$k \cdot I / k_2 = x^n (a - x)^m$$

where x represents the concentration of P + A, (a - x) the concen-

tration of S, k_1 and k_2 , and m and n are the velocity constants and the orders of the reactions $S \rightarrow P + A$ and $P + A \rightarrow S$, respectively, and I is intensity.

The form of this equation used for flicker is

$$F = (k_1 I)^{1/n} (F_{\max} - F)^{m/n} / k_2 p$$

where F is the flicker fusion frequency and $1/p$ the fraction of the flicker cycle during which the light is on. It is assumed that F varies directly as x , i.e., as $P + A$.

Brightness discrimination and visual acuity are described by the equation

$$\Delta I / I = \alpha = C [1 + 1 / (k_1 I / k_2)]^{1/2}$$

where ΔI is the superimposed brightness just barely perceptible, α is the angle subtended by a barely perceptible object, and C is a constant which is different for the two types of data. The sensitivity, as measured by $\Delta I / I$ or by α is assumed to vary directly as x .

No complete equation was ever published for the process of dark adaptation, but it was assumed that the sensitivity varied as the concentration of S, i.e., as $(a - x)$.

For instantaneous thresholds it was assumed that the equilibrium equation was applicable and that the sensitivity varied as the concentration of S.

The various applications of the theory of Hecht are not entirely consistent. In explaining the data on dark adaptation as a function of time and on instantaneous thresholds as a function of intensity, the sensitivity of the eye is assumed to vary as the concentration of S, i.e., as $(a - x)$. However, in the explanation of the data on flicker fusion, on brightness discrimination, and on visual acuity as functions of intensity, the sensitivity is assumed to vary as the concentration of photoproduct, $P + A$, i.e., as x . The assumption that sensitivity varies with S is in agreement with the original theory and with all of the modifications of this theory described below.

Difficulties have developed in applying the equations of Hecht to visual phenomena, especially to data on flicker fusion. In flicker experiments the prediction of the equation in regard to change of temperature and change of ratio of the light to dark periods is incorrect, data for certain animals can not be fitted, and it is necessary to assume that the photochemical reaction is usually bimolecular. Furthermore it is implied in the equations that the "old" $P + A$ catalyzes the $L \rightarrow T$ reaction. This implied assumption is apparently responsible for the erroneous prediction regarding change of temperature and change of the ratio of the light to dark period (Jahn, 1946).

2. *Statistical Theory of Crozier (1936, 1936a), and Crozier, Wolf and Zerrahn-Wolf (1937, 1938).*

According to the theory of Crozier, Wolf, and Zerrahn-Wolf (summarized by Morgan, 1943) the sigmoid curves for flicker fusion, brightness discrimination, and visual acuity as functions of intensity are probability integrals (i.e., ogive curves) in log I. The fundamental assumption is that the controlling mechanism in these phenomena is the statistical distribution of thresholds (in log I). At low intensities only the most sensitive elements (rods or cones and associated neurones) respond; at high intensities all of them respond. This theory can explain all of the data which can be explained by the Hecht theory and furthermore does not make the erroneous predictions regarding temperature and light-dark ratios. Dark adaptation curves as a function of time are explained as the progressive increase of sensitivity of individual units and may be fitted if the sensitivity is treated as a probability integral in log of time in the dark.

On the basis of this theory the assumed distribution of thresholds covers at least four and sometimes as many as eight log units. The thresholds are supposed to vary from element to element and from moment to moment. If one is willing to accept these postulates, all of the data can be explained.

This theory, of course, is a source of frustration to investigators who wish to reveal the mechanism of either the sense cells or associated neuronal networks by means of measurements of sensory phenomena. It is generally agreed that the photochemical cycle is responsible for sensation in that it is the mechanism by which the sense cell is activated. However, Crozier's theory holds that in explaining the shape of the curves for various visual phenomena, only the statistical distribution of thresholds need be considered.

3. *Photochemical Theory of Byram (1944).*

According to this theory emphasis is placed on the rate at which energy is made available for stimulation of the nerve by the sense cell. Visual acuity, for instance, is determined by the energy rate discrimination in the mechanism of the sense cell. This energy is supposedly released by the conversion of the intermediate active photoproduct ("new" P or A of Hecht) into the inactive form ("old" P + a). It is assumed that rate of release of energy by this reaction is approximately equal to the rate of the photochemical reaction and that this, in turn, is dependent upon the intensity and the concentration of photosensitive material. The theory differs from that of Hecht in that visual sensation is assumed to vary with the rate at which energy is made available rather than with the equilibrium concentration of the photoproducts P and A. So far this theory has been applied by Byram only to visual acuity, but it seems possible to develop the same idea for other phenomena.

4. *Photochemical Theory of Moon and Spencer (1945).*

The theory of Moon and Spencer is fundamentally similar to that of Byram in that the rate of the photochemical reaction is assumed to be in the controlling mechanism in sensation. In the Moon-Spencer theory this is supposed to be effected through a linear relationship between rate of energy release and the visual sensation. In the last analysis both theories should lead to identical conclusions.

The outstanding characteristic of the Moon-Spencer equations is that factors have been included to permit predictions concerning change of pupil diameter, and area of the stimulus. This makes it possible to cover a wide variety of experimental data with a single equation, complex though it may be. In many respects these equations are admittedly quite arbitrary and are presented as empirical equations rather than as a theory. So far Moon and Spencer have published equations only for light and dark adaptation, and instantaneous threshold, but their fundamental postulates, like those of Byram, have possibilities in explaining other types of data.

5. *Neuronal Theory of Householder and Landahl (1945).*

In this theory the responsibility of determining the shape of curves for visual phenomena is entirely removed from the sense cell and is placed in the central nervous system (or possibly in the neurone layers of the retina). On the basis of assumed dynamics of synaptic transmission Householder and Landahl have derived equations which describe the relationship between critical flicker, light to dark ratio and intensity, between relative brightness, light to dark ratio and frequency, and also between brightness discrimination and intensity. Provision is made in the equations for the excitatory and inhibitory processes at the synapses, and it is implied that different intensities of light cause excitation of completely different sets of neurones. As far as they go the derived equations offer a reasonably good fit for the experimental data.

6. *Photochemical Theory of Jahn (1946, 1946a, 1946b).*

This theory is essentially a mathematical formulation of a slight modification of the Hecht theory (as distinct from the Hechtian equations) treated in Section 1 above. The fundamental assumption is that of the threshold (or any other given level) of sensitivity is equivalent to some fixed value for the rate of the $L \rightarrow T$ reaction, i.e., for dT/dt . The factors which affect this rate are the concentration of the substrate L , the concentration of the enzyme E (an intermediate product in the $S \rightarrow P + A$ reaction which becomes $S \rightarrow E \rightarrow P + A$, the "new" $P + A$ of Hecht, and presumably transient orange in the rods), and a velocity constant which varies with temperature. In the case of flicker it is assumed that the value of the maximum critical frequency is determined not by the photochemical cycle but by some other process which is unaffected by temperature.

On this basis the phenomena of flicker fusion, brightness discrimination, and visual acuity may be described as functions of intensity, and none of the objections listed above to the Hecht equations are applicable to this formulation. The same assumptions have also been applied to dark adaptation, and when combined with equations for the kinetics of regeneration of visual purple, offer a satisfactory explanation of all of the existing data on dark adaptation.

The equation for flicker fusion frequency is

$$F = [k_1 I (a - x)]^q (F_{\max} - F)^r k_2 p / C'$$

where k_1 is the velocity constant of the $L \rightarrow T$ reaction, q pertains to the mechanism whereby the photoproduct E is utilized by the sense cells, and r denotes a mathematical function of F (Jahn, 1946).

The equation for brightness discrimination and visual acuity is

$$\Delta I / I = \alpha = \frac{C_1 (C / k_1)^{1/q}}{k_3 x^2 t} - \frac{1}{k_2 t}$$

where l denotes the concentration of L , k_1 the velocity constant for $E \rightarrow P + A$ reaction, k_2 the velocity constant of the $P + A \rightarrow S$ reaction, and t the duration of the flash of light (Jahn, 1946a).

The equation for dark adaptation is based on the dual regeneration of S from $P + A$ along two paths. For the human rods S is visual purple and $P + A$ are retinene and a protein. Retinene and the protein (known collectively as visual yellow) may be converted directly into visual purple or first into vitamin A and a protein (known collectively as visual white) and then into visual purple. It can be shown (Jahn, 1946b) that the equation for the increase of the concentration of visual purple (z) with time in the dark (t) is

$$z = 1 - \frac{1}{t + a} - \frac{t + a}{t + a + 1 + Ke^t}$$

where a denotes the reciprocal of the initial concentration of visual yellow at the beginning of dark adaptation. Since the concentration of visual purple determines the sensitivity directly, this equation can be fitted to all of the data on dark adaptation.

Discussion

Before examining the relative merits of the above theories it seems advisable to mention the various factors which are known to control the sensitivity of the eye. The following list of such factors, together with the direction of the effect they have on sensitivity, has been compiled from numerous sources.

| Factor | Sensitivity |
|------------------|-----------------|
| 1. Area of pupil | varies directly |

- | | | |
|-----|-------------------------------------------------------------------------------------------------------------------|-----------------------|
| 2. | Retinal location; concentration of rods | |
| | Darke adapted eye: | |
| | Fovea (no rods) | |
| | 10°-20° peripherally(most numerous rods) | lowest highest |
| | Light adapted eye: | |
| | Fovea (all cones) | highest |
| | 10°-20° peripherally (fewer cones) | lower |
| 3. | Area (a) of retina stimulated | f (A) |
| 4. | Absorption by lens, cornea, humors, etc. increased by cataract, clouded cornea, etc. | decreases |
| 5. | Imperfect focussing because of defect of cornea, lens, or shape of eyeball | decreases |
| 6. | Color of light | |
| | Dark adapted eye (rod function) | highest at 510 mμ |
| | Light adapted eye (cone function) | highest at 557 mμ |
| 7. | Amount of visual purple in rods, determined by State of adaptation, in dark several hours | highest |
| | State of adaptation, just after exposure to bright light | lowest |
| | Vitamin A feeding or injection, if deficient | increases |
| | Vitamin A removal by blood and liver during prolonged light adaptation | decreases |
| | Reduced V.P. regeneration because of low temperature (cold blooded animals only) | decreases |
| 8. | Amount of iodopsin in cones. Factors and effects on sensitivity apparently similar to above but no so well known. | |
| 9. | Neurone thresholds (retinal and/or central), determined by factors which control nerve metabolism | |
| | Blood supply to eye, decreased | decreases |
| | Partial anoxia (lack of O ₂) | decreases |
| | Partial anoxia, plus glucose feeding | partial counteraction |
| | Glucose feeding alone (increased blood sugar) | no effect |
| | Insulin hypoglycemia (low blood sugar) | decreases |
| | Rapid forced breathing, alkalosis | increases |
| | Increased atmospheric CO ₂ , acidosis | decreases |
| | Tobacco Smoke (carbon monoxide) | decreases |
| 10. | Central facilitation | |
| | Attention of the observer | increases |
| 11. | Unknown or slightly known mechanisms | |
| | Ultra violet during light adaptation (fluorescent lights or bright sunlight) | decreases |
| | Alcohol, large quantities | decreases |
| | Age | decreases |

Whenever one performs any series of careful observations on the sensitivity of the eye it is necessary to maintain constant most of the above factors so that one or more of them can be varied experimentally. During the conduct of most of the published experiments on flicker fusion, brightness discrimination, visual acuity, and dark adaptation, all items in the list have been carefully maintained constant except 7 and 8, and these have been varied either purposely or inadvertently during the course of the experiment. It is for this reason that it seems plausible to examine in detail the possibility that the photochemical cycle may determine the results of the experiments. It seems probable that if an adequate photochemical theory had been proposed many years ago there might never have been any serious doubt cast upon its validity. However, the early photochemical theories, although seemingly adequate at the time they were proposed, were subsequently shown to be inadequate for the rapidly accumulating mass of data. Consequently, rival theories were proposed. Fortunately one of these rival theories (Crozier, Wolf, and Zerrahn-Wolf) has served as a stimulus for investigators to obtain an enormous amount of very precise data. A vast quantity of data has also been recorded for other reasons. Recently it has been proposed to explain all of the available data on the basis of a new photochemical theory (Jahn, 1946, 1946a, 1946b).

Let us now examine the basic concepts of the six theories outlined above. These basic concepts fall into three groups: (1) Photochemical (Hecht, Byram, Moon and Spencer, and Jahn); (2) Statistical distribution of thresholds (Crozier, Wolf, and Zerrahn-Wolf); (3) Interrelationships of neurones in the central nervous system (Householder and Landahl).

Some of these theories are not as mutually exclusive as they at first seem. The existence of a statistical distribution of thresholds was proposed by Hecht as early as 1924 (Hecht, 1924, 1926, 1928) and by Forbes and Gregg in 1915-16 and Lasareff in 1923. At that time it was pointed out that the data on visual acuity and intensity discrimination could be explained on a statistical basis and also that the distribution of thresholds may be considered a *necessary consequence of the photochemical system*. In later discussions the relationship between photochemical cycle and threshold distributions has been more or less ignored, but it has always been assumed to be present. These principles may be related logically in several ways. Hecht (1924, 1928) assumed that different amounts of P and A were necessary to excite the various rods or cones and that the thresholds were evenly distributed in regard to the concentration of P and A necessary. The total number functional at any one time is then directly proportional to the concentration of P and A, and the equations for the photochemical equilibrium describe the sensitivity of the eye as a function of intensity. Several variations of this assumed relationship between threshold and photoproducts are possible, but on the basis of any of them the statistical distribution of thresholds is a necessary consequence of the photochemical system

and the photochemical equations may, therefore, be used for describing the visual phenomena.

How, then, does the theory of Crozier, Wolf, and Zerrahn-Wolf differ from that of Hecht? Only in that the photochemical system is not assumed to be the controlling factor in producing the statistical distribution of thresholds. The evidence against such a relationship consists of erroneous predictions of the Hecht equations in regard to changing temperature and light to dark ratios, in the fact that the equilibrium equations do not fit the data from certain animals, and in the fact that the photochemical reaction is monomolecular.

The assumption of Crozier, Wolf, and Zerrahn-Wolf is that the controlling factor which produces this distribution may be located any place along the optic pathway (retina, nerve, or brain), but if the location should be in the sense cell it is not determined directly by the photochemical equations. In general, they seem to prefer to think of the location as being beyond the sense cell.

If the net photochemical effect in the sense cell is assumed to vary as $\log I$ rather than as I (Hecht, 1935; see below) then this distribution of thresholds in $\log I$ could be among the sense cells and still not necessarily be in conflict with the photochemical theory. However, in all experiments in which the data obey the reciprocity law ($It = c$) the net photochemical effect varies as I rather than as $\log I$. The frequency of impulses in a single nerve fiber (within limits) varies as $\log I$ (Hartline and Graham, 1932), and it may seem plausible to assume on this basis that the thresholds of the fibers are distributed normally in $\log I$. This argument is defective in that the data concern stimulation well above threshold. Furthermore, the impulse is initiated by secondary activity in the sense cell (and not directly by light), and, therefore, a linear relationship with $\log I$ can be predicted on a photochemical basis. For conditions under which the reciprocity law could be considered applicable to the threshold distribution of the fibers, the threshold might very well be distributed in I ; these conditions have not been investigated.

However, if one accepts the distribution of fiber thresholds in $\log I$, then on exactly the same basis the location of the distribution may be placed within the central nervous system, and the theory thereby becomes directly applicable to all types of sensory data, i.e., auditory, tactile, etc., as well as visual. In the case of flicker, Crozier, Wolf, and Zerrahn-Wolf have demonstrated that for any given value of the critical frequency the probable error is distributed in $\log I$. The mechanism is the only point of argument.

The photochemical theory of Jahn was proposed in order to overcome the deficiencies of that of Hecht. Actually, the principal change is in the equations, not in the fundamental theory. The only new assumption is that at threshold the rate of the $L \rightarrow T$ reaction, which is directly related to the initiation of nerve impulses, must reach some given value. It is also assumed that the flash of light is brief and that the cyclic nature of the reactions is negligible *during the*

flash. On these assumptions the derived equations have none of the defects of the original Hecht equations. For longer flashes the equations could be modified. On the basis of this theory one may continue to assume as Hecht does that there is a wide range of thresholds and that the abilities of the sense cells to achieve excitation with any given stimulus is dependent on the photochemical system. The photochemical system, therefore, is the controlling factor, and the statistical distribution, if present, need not be considered.

However, one need not assume that the thresholds of the sensory elements have a wide statistical distribution. One alternative is to consider that each rod or cone functions over a wide intensity range and that the frequency of the impulses produced in the nerve is a measure of the effectiveness of the stimulus. The threshold for the sense cell (the amount of light which will produce a single impulse or a given volley of impulses with a barely perceptible effect, i.e., a just noticeable difference in sensations) will depend upon the amount of photosensitive material, and this amount will vary according to the photochemical equations for equilibrium.

The threshold is considered to be the minimum stimulus which will produce a certain rate of the $L \rightarrow T$ reaction just sufficient to cause a sensation of change. This value of the rate, dT/dt , is assumed to be constant for any one type of experiment (e.g., flicker, visual acuity, etc.), and it might very well be the same for all types. It is assumed to be equal to $k_1 [L] [E]$, i.e., to the velocity constant times the concentrations of L and E. The phenomena studied (flicker, brightness discrimination, and visual acuity and instantaneous thresholds as functions of intensity, and light and dark adaptation as functions of time) may be considered as different types of threshold determinations, and all of the data seem to be explicable on this basis. The existence of a statistical distribution of thresholds is not denied, but consideration of such a distribution in the equations appears to be quite unnecessary.

However, there seems to be another cause of apparent variation in the threshold which is really a variation in the effectiveness of the stimulus. Hecht, Schlaer, and Pirenne (1941) and Hecht (1942a) have demonstrated that only one molecule of transient orange is necessary to excite a human rod. During a threshold flash of light a small number of quanta strike the sense cell, and the chance that one molecule of transient orange will or will not be formed puts the matter on a statistical basis. The effective value of the stimulus reaching any given rod is subject to a random distribution even though the intensity striking the cornea is relatively constant. Supposedly this is true not only at the absolute threshold but at all relative thresholds. In accordance with the Poisson equation as the stimulus is increased above threshold, the statistical distribution due to this cause is greatly decreased. When the amount of S is reduced through light adaptation the average effectiveness of the stimulus (that is, the chance that any given quantum will be ab-

sorbed by S) becomes less, and the threshold as measured at the cornea becomes greater. This concept gives us an entirely new mechanism by which the apparent threshold of the sense cell might seem to vary.

In regard to the relationship between the intensity and the response of the sense cell, Hecht (1924) considered three possibilities: 1) Each cell can respond to all intensities, but with a frequency determined by the equilibrium condition of the photochemical system, 2) Each cell responds in an all or none manner whenever the intensity is above the particular threshold for that cell, 3) A combination of the above in which each cell responds over a limited range with an increase in frequency of discharge and maximally at all higher intensities, the range being different in different cells. Hecht discarded the first possibility as probably being too simple. However, if interpreted in terms of the Jahn theory, it does explain all of the facts. According to this theory the frequency of impulses would be determined not directly by the intensity but by all of the factors which determine dT/dt . On this basis possibilities 2 and 3 seem quite unnecessary.

The outstanding characteristic of the theory of Byram (1944) is that the rate of energy release produced by the transformation of "new" to "old" $P + A$ is the controlling factor in excitation. This is an idea apparently first expressed by Hecht (1924). Moon and Spencer (1945) assume the identical effect through the mechanism of the nerve impulse frequency varying with the amount of transformation (see below). These two theories assume that a molecule of the catalytic material ("new" $P + A$, E, transient orange, etc.) is used only once in bringing about the $L \rightarrow T$ reaction, and that the molecule thereby becomes inactive ("old" $P + A$, visual yellow). The photochemical cycle is regarded as an energy transformation system in which a molecule becomes activated by absorbing radiant energy and then becomes inactive by transferring this energy to another molecule. Stimulation of the nerve is assumed to depend upon this transfer of energy from the activated molecule, and no provision is made for the loss of activation without the production of stimulation.

This is in contrast to the theory of Jahn in which it is implied that a molecule of E may be used over and over again, or if no substrate happens to be locally available it may become inactive without taking part in the $L \rightarrow T$ reaction. The performance of catalysis is not dependent upon the molecule being converted into "old" P or A, and it is assumed that the energy removed from the catalyst during catalysis is replaced by a secondary reaction.

If we accept Hecht's (1942) demonstration that stimulation of a sense cell can be caused by a single molecule of active photoproduct (E) then we must assume either that the molecule is used over and over again or else that only one molecule of L must be converted into T in order to cause stimulation of the nerve. It seems preferable to assume that any given chemical reaction involves

more than one molecule unless we have evidence to the contrary. In this case the $L \rightarrow T$ reaction is assumed to initiate a nerve impulse and presumably must involve numerous molecules. The one molecule of E must serve as the release of some sort of "trigger" reaction, and at present the $L \rightarrow T$ reaction seems to be the most logical place for the "trigger" mechanism. Therefore, we may consider that the $L \rightarrow T$ reaction involves catalysis of many molecules of L by only one molecule of E , the exact number catalyzed by a given quantity of E being under the influence of a velocity constant (k_1) which is in turn affected by temperature. This interpretation favors the Jahn concept as opposed to those of Byram and Moon and Spencer.

The Byram and Moon-Spencer concepts strongly remind one of reactions in atomic physics, while the Jahn concept is more in the style of biochemistry. Neither concept seems impossible. In the case of photosynthesis, where there must be some mechanism whereby energy is added to the molecule, some assumption similar to that of Byram and Moon and Spencer seems to be necessary. However, in visual processes, where any necessary energy is readily available through cell oxidation, there seems to be no reason for preferring the energy concept to that of a typical enzymatic reaction.

The assumptions of Byram, of Moon and Spencer and of Jahn that the physiological effect varies directly with the amount of photochemical transformation has certain limitations which should be recognized. For brief flashes of light of a given duration and for a given total quantity of photosensitive pigment the direct photochemical effect, e.g., the conversion of visual purple to transient orange, is proportional to the intensity. This is in agreement with the Einstein law of photochemical equivalence and with data on the bleaching of visual purple solution (Hecht, 1920) and is implied in all equations for the visual photochemical process.

However, the physiological effect as measured by frequency of nerve impulses, by latent period, by voltage of the electroretinogram, by apparent brightness, or by any other non-threshold criterion seems to vary within limits as the logarithm of the intensity. This apparent violation of the equivalence law is a natural result of the cyclic nature of the photochemical process and is to be expected whenever the intensity (or the duration) of the stimulus is great enough. It was pointed out by Hecht (1934) that the complex equation for the net course of the photochemical process is approximated by that for a monomolecular reaction if the maximum effect is assumed to be that of photostationary state and the velocity constant is assumed to be proportional to $\log I$. The physiological effect seems to be dependent upon such a course.

A similar apparent violation of the equivalence law is found in all violations of the reciprocity law (where $I_t = C + Dt$ instead of $I_t = C$) and for exactly the same reason. Whenever no allowance is made for the cyclic nature of the reaction it should be remembered

that application of the conclusions reached is limited to those conditions under which the reciprocity law holds, not necessarily for the overall physiological effect but certainly for the net photochemical process involved. Under conditions in which the reciprocity law is invalid for the net photochemical reaction, the physiological effect, if it is in direct proportion to the net photochemical effect, should vary approximately as $\log I$.

Although the detection of flicker may be treated as a threshold phenomenon the reciprocity law is not applicable to data on the critical frequency. In any consideration of whether or not $I = C$ where the data are obtained in terms other than the direct photochemical change it must be assumed that the intermediate mechanism by which the photoproduct produces a measurable visual effect is also constant. At the critical flicker frequency the concentration of L is assumed to undergo periodic fluctuations which modify the sensitivity of the total mechanism to light. For this reason $I = C$ would not be true of the critical flicker frequency even if it were known that $I = C$ for the net increase in active photoproducts. In experimental data (eg., Crozier, Wolf, and Zerrahn-Folf, 1938) the variation of I with t for any given frequency is the opposite direction from that predicted by the reciprocity law.

A related flicker phenomenon, quite distinct from that of flicker fusion, is that of brightness enhancement under conditions of low frequency flicker. It is generally recognized that during the flicker cycle the amount of S and therefore the sensitivity of the eye does not remain constant. However, it has not been recognized until recently that under conditions of low frequency flicker (far below that for fusion, namely ten cycles per second in man under conditions where the fusion frequency would be much higher) the sensitivity may be greater than that of the eye adapted with the same light viewed continuously. This increased sensitivity during low frequency stimulation can be explained on a photochemical basis (Jahn, 1941), and some form of enhancement at low flicker frequencies seems to be inherent in all photochemical cycles, even in photosynthesis.

Evaluation of the Householder and Landahl interpretation in terms of other theories or of known facts is very difficult, principally because the equations have been derived on the basis of a few assumptions concerning synaptic transmission within the central nervous system, without reference to photochemistry or to statistical distribution of thresholds. The equations are applicable to all types of sensory discrimination, and at present there seems to be no way of proving or disproving them or even of estimating their potential value. Eventually it may be possible to link this concept with that of Crozier, Wolf, and Zerrahn-Wolf, especially if the site of the statistical distribution of thresholds is placed in the central nervous system, but the path in that direction is not yet clear.

The process of vision is a very complex series of events and involves a photochemical reaction ($S \rightarrow E$), at least one enzymatic reaction ($L \rightarrow T$), the production of an electromotive force in the

sense cell, the initiation of a nerve impulse which may pass two synapses on the retina, thence along the optic nerve, and thence through many more synapses in the brain before we have the sensation of seeing even a tiny spot of light on a dark field. We may call these events the series A to Z. If the stimulus is a large spot of light or a geometrically complex light source, then there are many parallel series of such events and a number of Z processes in the brain. As such, the Z's are subject to statistical variation. This would also be true if a single chain (A to Z) were repeated time after time; the sensation (event Z) would not always, at least under experimental conditions, involve exactly the same neurones in exactly the same way. This would be especially true near the threshold intensity.

It is in analyzing the relationship between event Z and the stimulus that we have arrived at the divergence of theories outlined above. The six theories have already been grouped into three types (photochemical, statistical and neuronal). The new photochemical theory is not purely photochemical because it involves the use of $L \rightarrow T$ reaction. We may consider the photochemical reaction to be event A, the $L \rightarrow T$ reaction event B, and the electromotive force event C, D, or E, depending upon the detail of our analysis. The neuronal theory may be considered to offer an analysis in terms of events W to Z. A broader term which would include both the new photochemical and the neuronal theories would be "dynamical" by which we mean the study of the series of causes and effects which lead to Z.

We then have two general types of interpretations: "Dynamical" and "Statistical." The statistical theory is quite satisfactory for working out rules between variations in the stimulus and variations in Z, but it offers no possibility of exploring the events A to Z. The dynamical theories permit this exploration, and one of the principle differences between them is that they focus attention on opposite ends of the chain.

These two methods of approach, i.e., dynamical versus statistical, are not peculiar to visual phenomena but are found elsewhere in physics and biology (Schrodinger, 1945). The two types of explanation are not mutually exclusive, but the usual question concerns the relative importance of each. "How many dynamical laws should we consider before we apply statistics?" Or, in the particular matter under consideration, "May we omit statistics entirely?"

At present no interpretation of all of the visual phenomena listed above has been proven to be correct. The original equations of Hecht which remained unchallenged before 1936 certainly need modification. The modifications suggested by Jahn seem to eliminate the deficiencies of the original in regard to flicker and to offer a logical basis for dark adaptation. Whether or not this theory is also subject to serious deficiencies is yet to be seen. The Byram and Moon-Spencer modifications have not been applied to flicker, the phase of the original theory which is most susceptible to criticism. The Crozier, Wolf, and Zerrahn-Wolf and the Householder and Landahl theories

seem to explain all of the data, including those on flicker. Ultimately we should be able to decide whether the shape of the experimental curves is determined in the sense cell or in the central nervous system, but the discussion concerning this decision is apt to continue for some time. We do not seem to have a scarcity of theories which will explain all of the facts but rather a scarcity of adequate criteria for choosing between them.

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