THE VISUAL DISCRIMINATION OF INTENSITY AND THE WEBER-FECHNER LAW.

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I.

Purpose of Work.

1. Differential Sensibility.—The power to distinguish differences in the brightness of objects is an outstanding property of the human eye, and is used constantly in judgments of distance and form. It is not possible, however, to estimate quantitatively the magnitudes of the corresponding differences in sensation. A light may be described as appearing slightly brighter or much brighter than another light, but no numerical values can be assigned to such judgments.

Direct estimation being impossible, it is customary to evaluate differential sensibility indirectly in terms of the minimum change in illumination which can be distinguished as a change in brightness. If I is the intensity to which the eye is adapted, and ΔI the increase in that intensity which is just perceptible, then the ratio $\dfrac{\Delta I}{I}$ may be considered a measure of the discriminating power of the eye.

The description of the relation between the discriminable threshold ΔI and the original intensity I has had an interesting evolution, culminating in what is currently known as the Weber-Fechner law. According to this law the ratio $\dfrac{\Delta I}{I}$ is constant within wide limits of intensity, not only for vision but also for other senses. A systematic survey of the literature on the Weber-Fechner law is beyond the scope of the present paper. However, the historical development

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of the Weber-Fechner concept is significant because it illustrates how an idea, on account of its apparent reasonableness, may be absorbed into the body of scientific knowledge and tenaciously held as a general truth, even though it expresses only an extremely circumscribed portion of reality.

2. Statement of Problem.—There exists a body of data which describes accurately and without any preconceived notions the behavior and magnitude of the discrimination ratio $\frac{\Delta I}{I}$ over a great range of illuminations. Clearly, these data represent manifestations of the mechanism in the retina which determines vision. The characteristics of the discrimination ratio, therefore, should find an explanation in terms of this mechanism; and conversely, the capacity of any system to serve as a mechanism of vision may be tested by its ability adequately to furnish the basis for intensity discrimination.

It is the aim of this paper to study the existing facts of intensity discrimination and to suggest an explanation of them in terms of our knowledge of the photochemistry of vision as derived from investigations on the clam, *Mya arenaria*, and on the human eye.

II.

Historical Development of the Weber-Fechner Law.

1. Original Evidence.—The idea embodied in the Weber-Fechner law was described several times independently. The first time seems to have been by Bouguer (1760) as the result of experiments " .... faites pour déterminer quelle force il faut qu'ait une lumière pour qu'elle en fasse disparaître une autre plus faible." Two candles are placed at different distances from a screen, one of them throwing a shadow which is obliterated by the other. Bouguer found that the ratio of the two intensities at this point was $\frac{1}{64}$. He noted cautiously that he had not observed a change in the ratio when the brightness (*vivacité*) of the lights was varied. In developing Bouguer's work, Arago (1858) added that no matter what the ratio $\frac{\Delta I}{I}$ happens to be, it can be reduced still further by keeping the shadow in motion. The

experiments were repeated with a new method by Masson (1845), who reported that though different people give different values of $\frac{\Delta I}{I}$ the ratio is constant for a given person regardless of intensity or color.

Independently of this development, Steinheil (1837) had found that the just perceptible difference in intensity measurable with his newly invented prism photometer was 1 part in 38.

About the same time as Steinheil, and also independently, Weber (1834) discovered for the sense of touch that one could discriminate between two weights if they differed by 1 or 2 parts in 30. Similarly one could just discriminate visually between two lines if they differed by 1 part in 100 regardless of the absolute magnitude of the lines.

Finally the relation was observed by Fechner, from whom it received the impetus which has carried it to the present day. Fechner (1858) had noticed that a slight difference in the shade of a cloud remained perceptible even after the brightness of the cloud was reduced by the interposition of smoked glass. Repetition of Bouguer's experiments with two candles and a shadow showed $\frac{\Delta I}{I}$ to be uniformly $\frac{1}{100}$.

Fechner investigated on this basis the relation between the magnitude of a star and its photometric intensity. Stars had been classified visually into six magnitudes, the brightest being a first, and the dimmest a sixth magnitude star. If each member of this sequence represents a constant fractional decrease in actual intensity, then the arithmetical series of star magnitudes should correspond to a decreasing geometrical series of photometric intensities. Using the then available astronomical data, Fechner described the relation between the magnitude, M, of a star and its intensity, I, by an equation of the form: $M = k \log I + C$.

Such a relation and a similar interpretation of it had already been found by Steinheil (1837) with the first series of measurements of star intensities made with his prism photometer.

Fechner developed the idea of a constant fractional relation between two intensities which produce a threshold difference in brightness. This constant fractional relation he called Weber's law. On the as-

sumption that the difference threshold represents a unit change in sensation, ΔS, he wrote Weber's law as

$$S = k\ \frac{\Delta I}{I}.$$ (1)

On integration this yields $S = k \log I + C$, a relation which Fechner called the psychophysical law, and used as a foundation for his speculations in psychology and philosophy (Fechner, 1860).

2. Criticism.—It was apparent even to Fechner that Weber's ratio is constant only within limits, but he set these limits at the two extremes of the intensity scale. According to Fechner, the upper limit is due to the dazzling effect of high intensities; the lower to the intrinsic light of the retina. To take the latter into account Fechner (1860) introduced its value I_0 into the equation for Weber's law, which then became

$$S = k\ \frac{\Delta I}{I_0 + I}.$$ (2)

It was on this matter of limits that Helmholtz (1866) made the first criticism of the Weber-Fechner law. Helmholtz had experimented with Masson's method, and, contrary to Masson, had found the ratio $\frac{\Delta I}{I}$ to vary at different intensities. Outside daylight gave a ratio of $\frac{1}{150}$ or even $\frac{1}{167}$, whereas interior daylight yielded a ratio of $\frac{1}{117}$. From this Helmholtz concluded significantly that the circumstances " .... which vitiate Fechner's law at the upper and lower limits show their influence under accurate observation in the medium illuminations as well, which naturally does not prevent the law from being a first approximation to the truth."

3. Analysis of Evidence.—In view of Helmholtz's criticism it becomes necessary to consider the nature of the original evidence for the Weber-Fechner law. Bouguer, Arago, and Masson state that the ratio $\frac{\Delta I}{I}$ does not vary with the intensity, but none of them presents any data from which to judge independently the range of intensities investigated or the accuracy of the measurements. Steinheil's measurements are excellent; their range of intensities, however, is about 1

to 4. Weber's own data cover a range of 1 to 16, but his judgments with weights vary between 1 and 2 parts in 30. Fechner states that his experiments, conducted by Bouguer's method, yield a constant ratio of $\frac{1}{100}$ for a range of 1 to 40 units. However, a careful analysis of Fechner's method and data by Aubert (1865) shows clearly that, since it is impossible to measure the position of a candle flame with the necessary precision, the results are reliable only over a range of 1 to 10 at best. The evidence from star magnitudes covers even a smaller range. Therefore, all that can be concluded from the evidence is that within *narrow* limits the ratio $\frac{\Delta I}{I}$ may be considered constant.

This conclusion is sustained by all the work on the Weber-Fechner law subsequent to Fechner. It is not relevant to our purpose to review this material here.[1] A good deal of it has been summarized by Exner (1879), and more recently by Wundt (1908). Stripped of controversy, the evidence shows that the Weber-Fechner law holds approximately over a very moderate range of intensities. Kraepelin's (see Wundt, 1908[2]) work is an example. It was carefully done and shows a constant value of $\frac{\Delta I}{I}$ between 300 and 1,000 units of intensity, which Wundt[2] speaks of as proving Fechner's idea "*innerhalb weiter Grenzen.*" We shall see in the next section how $\frac{\Delta I}{I}$ really behaves within wide limits.

4. General Idea Involved.—It is to be regretted that in the controversies over it, the valuable kernel of the Weber-Fechner law should have failed of emphasis. Bouguer, the original discoverer, says, "Un grand bruit nous empêche d'en entendre un autre plus faible; nous

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[1] It is also not in our province to discuss the various theories for the Weber-Fechner law. Most of its philosophical background (*cf.* Müller, 1903) must unfortunately be discarded because of the failure of the law to describe correctly the data of intensity recognition. From our present view-point—that of attempting to work out a mechanism of vision—a fundamental difficulty with the original law and the several modifications and elaborations proposed among others by Fechner (1860) Helmholtz (1866; 1896) and Lasareff (1914) is that, aside from their failure adequately to describe the known data, they rest on no mechanism of vision.

[2] Wundt (1908), p. 659.

ne voyons pas, en présence d'une forte lumière, une autre dont l'intensité est beaucoup moindre, si les deux frappent notre rétine dans le même endroit."[3] Weber similarly understood the matter. Sensory judgments are relative, not absolute. The attempt by Fechner to describe

TABLE I.

Aubert's Data on Intensity Discrimination.*

I	$\frac{\Delta I}{I}$
millilamberts	
0.0005	1/3
0.0006	1/4
0.0013	1/4
0.0025	1/8
0.0056	1/11
0.0156	1/25
0.0351	1/25
0.0506	1/25
0.131	1/31
0.250	1/36
0.316	1/33
0.563	1/31
1.00	1/32
1.37	1/39
2.25	1/45
5.06	1/51
9.00	1/65
20.3	1/112
31.6	1/104
56.3	1/121
136.6	1/146

* Aubert's original figures for the intensities have been divided by 10,000 to convert them into modern units. This factor has been arrived at by comparison of Aubert's data with those of Blanchard and of Koenig and Brodhun as shown in Fig. 1.

by means of a simple formula just how relative our sensory judgments are failed unfortunately to include the full range of the phenomena.

III.

Experimental Data of Intensity Discrimination.

1. Aubert's Work.—The first experiments to determine the manner in which the ratio $\frac{\Delta I}{I}$ really varies over a wide range of intensities

[3] Bouguer (1760), p. 57.

were made by Aubert (1865), who used a procedure which is essentially the two-candles-and-a-shadow method of Bouguer. The lowest intensities were those barely perceptible; the highest were obtained from
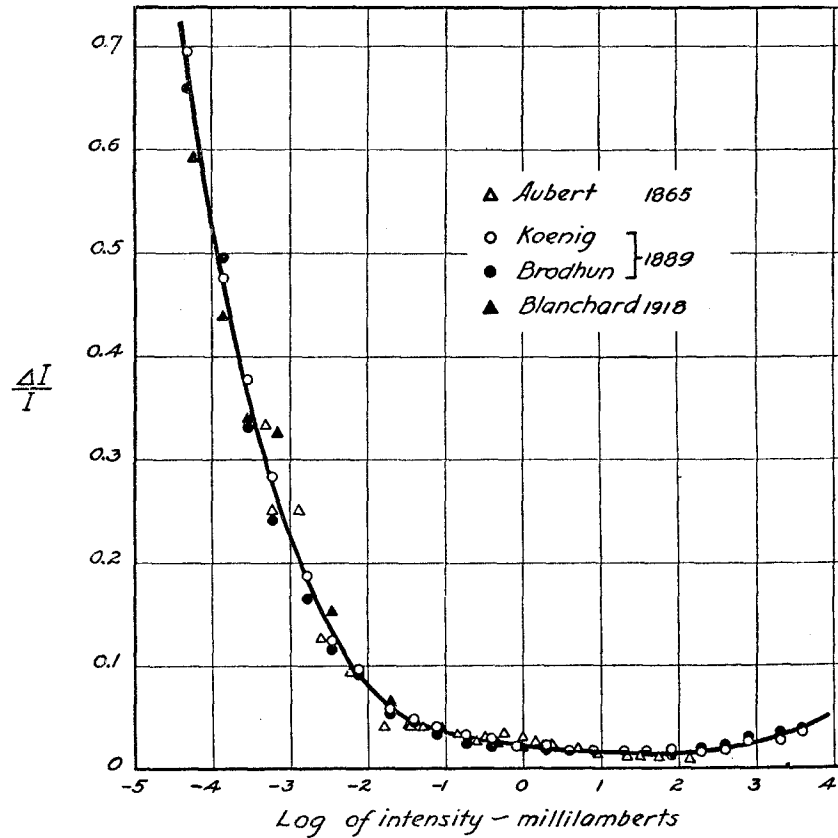

Fig. 1. Intensity discrimination over the total illumination range visible to the eye. Blanchard's data are given in their original units: millilamberts. Koenig and Brodhun's intensities have been divided by 250 in order to convert them into millilamberts. Similarly Aubert's intensities have been divided by 10,000. It is apparent that these three groups of experimenters, working many years apart and independently, have arrived at essentially the same results.

daylight admitted into the dark room. The recorded precautions involving calibration, adaptation, and the like, show a fine appreciation of the sources of error and therefore make Aubert's results reliable.

They are summarized in Table I, and graphically in Fig. 1. It is apparent that over a very limited range of illuminations $\frac{\Delta I}{I}$ may be treated as roughly constant. Viewed as a continuous physiological phenomenon, however, the discrimination ratio decreases steadily as the intensity increases.

2. *Koenig and Brodhun's Work.*—Aubert's work may be thought of as the preliminary experiments for the investigations of Koenig and Brodhun (1889) whose data have become the final statement of the behavior of $\frac{\Delta I}{I}$ for the eye.[4] Koenig and Brodhun determined $\frac{\Delta I}{I}$ over an intensity range from the lowest perceptible illumination to such illuminations that the eye became painfully dazzled—in other words they covered the whole range over which the eye can function. They did this, not only with white light, but with six monochromatic portions of the spectrum. The work as a whole is an extraordinary piece of experimentation.

[4] Koenig and Brodhun studied the problem with a method radically different from that of previous investigators. A parallel beam of plane polarized light is passed through a crystal of Iceland spar so that the emerging ordinary and extraordinary beams partly overlap. Viewed with a properly placed ocular this yields a field of vision, of which the upper half is illuminated by the ordinary beam alone, and the lower half by the ordinary and extraordinary beams combined. The total visual angle of the field is $6° \times 4.3°$. By the rotation of a Nicol prism in the ocular, the intensity of the upper half may be varied while the lower half remains constant, the ratio of the two intensities being proportional to $\cos^2\theta$, where θ is the angle between the ocular nicol and the axis of the calcite crystal. An observation consists in viewing the uniformly illuminated field, and then turning the ocular nicol so that the upper half of the field is just perceptibly darker than the lower. Calling the intensity of the upper half, I, the lower half will then be $I + \Delta I$, and the just perceptible difference between them, ΔI. The minimum discriminable ratio $\frac{\Delta I}{I}$ is easily computed by remembering that I is given by $\cos^2\theta$, and ΔI by $\sin^2\theta$; therefore $\frac{\Delta I}{I}$ is given by $\tan^2\theta$. The data actually secured were the intensity of the field at uniformity and the angle θ when the two halves were just perceptibly different in brightness.

Koenig and Brodhun's data for white light are reproduced in Table II and in Fig. 1.[5] The data for the different colors are essentially the same as those for white light. They may be found in the original

TABLE II.

Data of Koenig and Brodhun on Intensity Discrimination. Brodhun's Eye.

I	ΔI	$\frac{\Delta I}{I}$
millilamberts	*millilamberts*	
0.0000484	0.0000316	0.659
0.0001336	0.0000664	0.495
0.000300	0.000100	0.331
0.000644	0.000156	0.241
0.001716	0.000284	0.165
0.00358	0.000416	0.116
0.00732	0.00068	0.0912
0.0190	0.0010	0.0533
0.0382	0.0018	0.0457
0.0776	0.0024	0.0332
0.1948	0.0052	0.0270
0.3912	0.0088	0.0228
0.784	0.016	0.0223
1.956	0.044	0.0221
3.928	0.072	0.0185
7.86	0.14	0.0180
19.69	0.31	0.0158
39.36	0.64	0.0163
78.76	1.24	0.0156
196.2	3.8	0.0193
391.6	8.4	0.0215
776.8	23.2	0.0297
1,935.	65.	0.0336
3,853.	147.	0.0380

[5] The intensities given in Table II are in millilamberts, derived by multiplying Koenig and Brodhun's original figures by 0.004. They describe their unit as the brightness of a magnesium oxide screen illuminated by one tenth of a Violle standard and viewed through a 1 sq. mm. artificial pupil. The Violle standard is 23 candle power, and the reflecting power of a magnesium oxide surface is 85 per cent. The brightness of the screen is therefore 0.2 millilambert. A normal pupil at such an intensity has an effective area of about 50 sq. mm. Therefore the light reaching the eye is reduced to 1/50, which makes the unit approximately 0.004 millilambert. Blanchard's (1918) independent repetition of Koenig and Brodhun's experiments confirms the correctness of this calculation.

paper and are not reproduced here because their analysis is identical in principle with that for white light, which alone concerns us in the present paper.

3. Corroborative Evidence.—These data support those of Aubert in showing that the ratio $\frac{\Delta I}{I}$ not only is not constant as demanded by the Weber-Fechner law, but that it varies in a definite way. Koenig and Brodhun's work covers intensities much higher than those of Aubert, and at these, the ratio, after first decreasing now begins to increase.

This rise at high intensities is undoubtedly a real phenomenon, first because of the intrinsic excellence of the experiments themselves, and second because the same increase had been found for intensity discrimination in *Mya* (Hecht, 1923-24, *a*) by a method entirely different. That the other parts of the data are also not open to question has been shown by Blanchard (1918) who repeated the experiments in still another way. Blanchard gives $\frac{\Delta I}{1+\Delta I}$ but from his published data it has been simple to compute $\frac{\Delta I}{I}$. These values are plotted in Fig. 1. The points in Fig. 1 show clearly that the three groups of independent experiments covering half a century have yielded identical results.

We possess, therefore, a reliable set of figures, free from preconception, which record accurately the discrimination threshold at all intensities at which the eye can function. In the further treatment of these data, we shall confine ourselves to those for Brodhun's eye alone. The data for Koenig's eye are practically the same, and their theoretical analysis is identical.

IV.

Influence of Pupillary Size.

1. Principle of Analysis.—The experiments of Koenig and Brodhun measure the discriminating power of the eye as a whole. The data are thus a synthesis of the effect of light on at least three structures in the eye: the iris, the rods, and the cones. It is our object to describe these data in terms of a mechanism of vision. There-

fore, it becomes necessary to isolate the individual contribution
of each of these three systems toward their combined effect. In
this way it will be possible to analyze the actual relations between
light and the photosensory process in the retina.

Intensity discrimination is obviously determined by the amount
of light which enters the eye and falls on the rods and cones. How-
ever, the data as they stand record the outside intensities and do
not give the real sequence of illuminations at the retina, because
between the light outside and the retina inside there is a variable
diaphragm—the iris—whose opening itself varies with the intensity.
The pupil is therefore the first system whose contribution must be
isolated and eliminated.

TABLE III.

*Relation between Intensity and Pupil Area during Monocular Illumination as
Computed from Reeves' Data.*

I	Area.
millilamberts	*sq. mm.*
0.0	50.9
0.00015	48.4
0.01	48.4
0.6	40.2
6.3	26.4
126.0	8.55
355.	6.60
2,000.	3.14

2. Elimination of Pupil as Factor.—The removal of the iris as a
factor is accomplished by means of the work of Reeves (1918).
Koenig and Brodhun's experiments involve looking with one eye
through a telescope. The other eye, whether open or shut, is in the
dark. Table I of Reeves' paper records the relation between inten-
sity and pupil width under monocular illumination. From these
figures the area of the average pupil at different illuminations has
been calculated; the results are given in Table III and graphically
in Fig. 2.

With any value of the intensity for Brodhun's eye one can find
by graphic interpolation the corresponding pupil area. These
areas are in Column 3 of Table IV. The product of the outside

intensity and the resulting pupil area gives the figures in Columns 4 and 5 of Table IV. These then represent the actual sequence of illumination intensities at the retina corresponding to the series of discrimination ratios in Table II.

Having in this way removed the iris as a variable in these data, we must now consider their meaning in terms of the effect of light on the rods and cones.
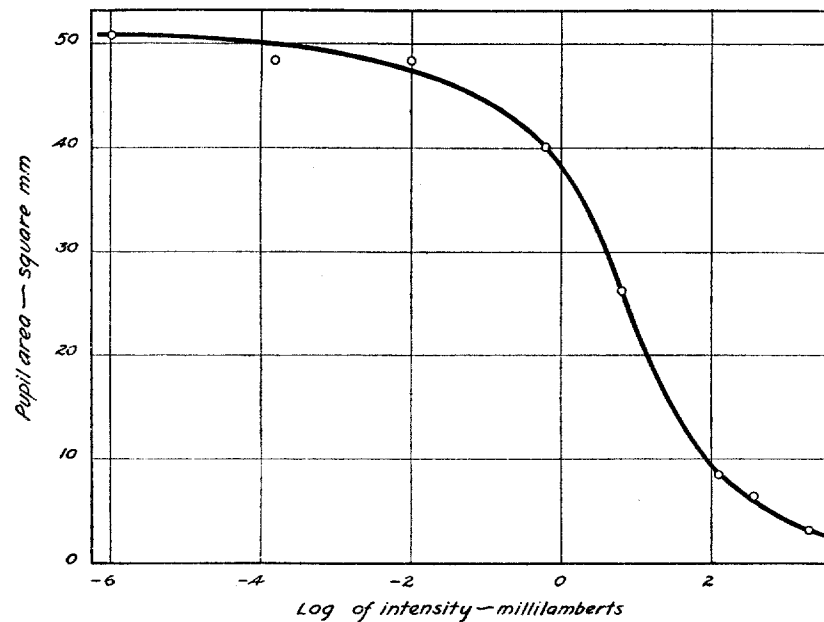

FIG. 2. Relation between intensity and pupillary area with monocular illumination. The points are computed from Reeves' data, and are the averages of two observers.

V.

Retinal Basis of Intensity Discrimination.

1. Separation of Rods and Cones.—The rods and cones of the retina are two separate photosensitive systems, with different thresholds, different rates of dark adaptation, and in general different functions. They possess in common, however, the capacity for intensity discrimination, because intensity differences can be observed with the

fovea alone, which contains only cones, as well as at such low illuminations that only the rods function. It may be possible to identify the separate contribution of each of these two systems in intensity discrimination with the aid of their differences in other respects.

The visual field in the experiments of Koenig and Brodhun includes both retinal elements. At the lowest perceptible intensities the rods alone mediate intensity discrimination. As the intensity increases a point is reached which lies at the cone threshold. From then on, either the value of ΔI is determined as a sort of average between the rods and cones, or at some point the cones take over completely the function of intensity discrimination, provided the necessary increase ΔI is less for the cones than for the rods. The first alternative, though possible, is complicated, and does not help us to separate the action of the two types of sense cells. The second alternative—a sharp division—is simpler, and more useful because its consequences are clear. As the intensity increases, analysis must show a break at some point, preceding which ΔI has been determined by the rods, and beyond which it is controlled by the cones.

The separation of the two retinal elements in this way is a cardinal feature of the present treatment of the data. It leaves us free to consider the rods and cones as separate systems and to study the action of light on each independently.

In order to do this effectively, we shall find it convenient to examine intensity discrimination in *Mya*, where its nature and mechanism have already been described (Hecht, 1923–24, *a*). The significance of *Mya* for the study of the visual process lies in the fact that its photosensitive system is a simplified version of the eye. It possesses neither lens nor iris, and apparently only one kind of photosensitive cell. Its outstanding qualification is that the chemical mechanism underlying its photic sensitivity corresponds in many essentials to that of the rods and cones. The properties of the mechanism in *Mya* have been studied in a variety of ways, and in the present instance of intensity discrimination the behavior of the mechanism will serve as the basis for the analysis of the similar discrimination by the retina.

2. *Intensity Discrimination in Mya.*—*Mya*, when first exposed to a given illumination, responds by the retraction of its siphon. Continued exposure produces no further reponse, and the animal, after extending its siphon again, comes into sensory equilibrium. If the intensity of the illumination is raised by a certain increment, another response occurs. *Mya* can therefore distinguish between two intensities to which it is successively exposed, and indicates this discrimination objectively by the retraction of its siphon. When studied over a large range of intensities the quantitative results show an extraordinary similarity to the data for the eye. As the intensity rises, the ratio $\frac{\Delta I}{I}$ gradually decreases to a certain point, after which it increases again. It fact, the curve for the relation between $\frac{\Delta I}{I}$ and log I (Fig. 1) for the eye and for *Mya* are almost identical (*cf.* Figs. 4 and 5 in Hecht, 1923–24, *a*).

The analysis of the results on *Mya* is secured in terms of its underlying photochemical mechanism. This system may be represented for mathematical convenience as a reversible reaction of the type

$$S \underset{\text{``dark''}}{\overset{\text{light}}{\rightleftharpoons}} P + A \tag{3}$$

whose properties have been derived from the responses of *Mya* under conditions designed for that purpose. A characteristic of this reaction system is its capacity to come into an apparently stationary state under continued illumination. This results in the light adaptation of the animal. When illuminated, the sensitive material S absorbs light and is changed into P and A, the velocity of the reaction depending on the concentration of S and on the intensity of the light. The reverse reaction, being independent of light, sets in as soon as some P and A are formed, the velocity of recombination being proportional to the concentrations of P and A. If the illumination is maintained, the two opposing reactions quickly strike a stationary condition in which the concentrations of S, P, and A remain constant. This point is determined by the intensity of the illumination, and may be described in terms of a simple equation.

The data on *Mya* show that when the animal discriminates between one intensity and another, the transition from the stationary state of the reaction $S \rightleftharpoons P + A$ at one intensity to the stationary state at the other is accompanied by the decomposition of a definite quantity of photosensitive substance. Thus, discrimination between two intensities involves a constant amount of photochemical decomposition, regardless of the numerical values of I and ΔI and their ratio.[6]

3. Outline of Analysis in Eye.—Studies of the dark adaptation of the eye (Hecht, 1919–20; 1921–22) have shown that a reversible photochemical reaction similar to that in *Mya* exists in the rods and in the cones. Our treatment of intensity discrimination in the eye may then be expressed in terms of its two photochemical systems with reference to their resemblances to that of *Mya*. At low intensities the rods alone determine discrimination. The photochemical system comes to a stationary state at a given value of I. Then, in order for the rods to recognize a further increase in intensity the additional light ΔI must be of such magnitude as to decompose a given amount of photosensitive material. This results in a constant difference in the concentration of sensitive material between the stationary state determined by I and that determined by $I + \Delta I$. For the rods the absolute magnitude of this constant increment in decomposition is larger than it is for the cones. Therefore the recognition of intensity differences shifts to the cones at an illumination where ΔI furnishes sufficient energy to produce in them the necessary decomposition but not enough to produce the corresponding change in the rods. From then on the cones continue to determine intensity discrimination until the concentration of S at the initial stationary states is so low that ΔI, no matter how great, cannot decompose the necessary amount of sensitive material.

It is apparent from even this general statement of the retinal basis of intensity discrimination that a mechanism as simple as this

[6] The idea that a constant increment in photochemical decomposition is the condition for a threshold difference in sensation has already been put forward by Cobb (1916). In addition Cobb conceived the notion of a reversible reaction as the basis for a visual mechanism, and even derived an equation for its stationary state.

cannot be complete. The phenomena involved are diverse and complex. The best that can be done at present is to use these ideas as the basis for a first approximation, simple enough for rigorous, quantitative consideration but broad enough for the necessary future modifications. The mechanism here proposed obviously involves a number of aspects of vision, the exact properties of which will have to be in harmony with the results of a quantitative treatment of the data. We shall return to this phase of the matter after first subjecting the data of Koeing and Brodhun to such an analysis.

VI.

Quantitative Analysis of Intensity Discrimination.

1. Calculations and Results.—The photochemical system in the rods and in the cones both may be represented for convenience as reversible reactions of the type

$$S \overset{\text{light}}{\underset{\text{"dark"}}{\rightleftharpoons}} P + A. \tag{4}$$

Let such a system be exposed to light of intensity I, and let the illumination be maintained until x per cent of P and A has been formed, leaving $(a - x)$ per cent of S, the original concentration of which was a. At that moment the velocity of the light reaction alone, $S{\rightarrow}P{+}A$, since it is proportional to the concentration and to the intensity (Hecht, 1923–24, b), is given by

$$v_1 = k_1 I (a - x). \tag{5}$$

Because the complete reaction is reversible, P and A reunite to form S independently of light. The velocity of their recombination is proportional to the concentrations of P and A, and is given by

$$v_2 = k_2 x^2. \tag{6}$$

As the illumination is continued the two velocities become equal, and the resulting stationary state is described by

$$K I = \frac{x^2}{a - x} \tag{7}$$

in which $K = \dfrac{k_1}{k_2}$. This equation[7] of the stationary state is all that is necessary for the computation of the data in terms of our analysis. It contains only two variables—I, the intensity, and x, the concentration; of these, I is clearly the independent variable, and its value at once determines the equation.

In the retina let x_1 be the concentration of P and A at the stationary state of the intensity I, and let x_2 be the corresponding concentration for $I + \Delta I$. Then a value of the constant K can be found for which the quantity $x_2 - x_1$, computed from the data, is constant for a series of intensities beginning with the lowest. As the intensity increases the value of $x_2 - x_1$ should fail to conform at a certain point, which represents the illumination where the rods cease to determine intensity discrimination. Beginning with this intensity a new value of the constant K should be found which will again render $x_2 - x_1$ constant but of smaller magnitude than before.

Computation of the data yields a set of figures which support such a line of reasoning. Table IV contains the intensities I and $I + \Delta I$ at the retina, the values of x_1 and x_2 of the two corresponding stationary states, and the two values of K. Taking $K = 100$, it is plain that the first seven intensities yield practically constant values of $x_2 - x_1$. The average value for the seven is 1.56, which repre-

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[7] Equation (7) describes the stationary state in the simple terms of a completely reversible reaction. Very likely the system is really more complicated, and is probably only pseudoreversible, such as

$$\begin{array}{c} \text{light} \\ S \longrightarrow P + A + B \\ S \longleftarrow P + A + C \\ \text{``dark''} \end{array} \qquad (8)$$

in which B is different from C, and C is present in excess. The mathematical treatment for the two, however, is the same. In case of the pseudoreversible reaction the stationary state represents not only a constant concentration of S, P, and A, but in addition a steady production of B at a rate proportional to the concentration of P and A. Probably it is this continuous formation of B, and its effect on the nerve which enable us to see an illumination to which the eye is adapted. It is possible that a similar pseudoreversible reaction underlies the behavior of many animals which continue to orient to light after they have become adapted to it.

sents the unitary change for rod vision. For the next few intensities, if calculated with $K = 100$, the quantity $x_2 - x_1$ drops sharply first to 0.90 and rapidly almost to 0. If now the value of K be put at 0.25 a new series of values of $x_2 - x_1$ is secured, smaller in magnitude and roughly constant at an average value of 0.21. In terms of the analysis this is the unitary change for the cones.

TABLE IV.

Concentrations of Sensitive Substance Decomposed at Different Outside Illuminations.

Illumination outside.		Pupil area.	Illumination at retina.		Concentration.			K
I	$I + \Delta I$		I	$I + \Delta I$	x_1	x_2	$x_2 - x_1$	
0.0000484	0.0000800	50.3	0.00243	0.00402	4.81	6.14	1.33	100
0.0001336	0.000200	49.7	0.00664	0.00994	7.83	9.48	1.65	
0.000300	0.000400	49.5	0.0149	0.0198	11.48	13.12	1.64	
0.000644	0.000800	49.0	0.0316	0.0392	16.27	17.94	1.67	
0.001716	0.00200	48.6	0.0834	0.0972	25.01	26.69	1.68	
0.00358	0.00400	48.0	0.172	0.192	33.76	35.26	1.50	
0.00732	0.00800	47.7	0.349	0.382	44.15	45.59	1.44	
0.0190	0.0200	47.4	0.901	0.948	4.63	4.75	0.12	0.25
0.0382	0.0400	46.9	1.79	1.88	6.47	6.63	0.16	
0.0776	0.0800	46.3	3.59	3.70	9.04	9.17	0.13	
0.1948	0.2000	44.3	8.63	8.86	13.65	13.81	0.16	
0.3912	0.4000	42.0	16.43	16.80	18.32	18.50	0.18	
0.784	0.800	38.6	30.26	30.88	23.75	23.95	0.20	
1.956	2.000	33.6	65.72	67.20	33.14	33.45	0.31	
3.928	4.000	29.2	114.7	116.8	41.12	41.37	0.25	
7.86	8.00	24.4	191.8	195.2	49.30	49.59	0.29	
19.69	20.00	18.3	360.3	366.0	60.02	60.28	0.26	
39.36	40.00	14.2	558.9	568.0	67.45	67.71	0.26	
78.76	80.00	10.7	842.7	856.0	74.00	74.24	0.24	
196.2	200.0	7.4	1,451.9	1,480.0	81.64	81.88	0.24	
391.6	400.0	5.7	2,232.1	2,280.0	86.57	86.79	0.22	
776.8	800.0	4.5	3,495.6	3,600.0	90.61	90.83	0.22	
1,935.0	2,000.0	3.2	6,192.0	6,400.0	94.26	94.43	0.17	
3,853.0	4,000.0	2.2	8,476.6	8,800.0	95.68	95.83	0.15	

The values of $K = 100$ for the rods and $K = 0.25$ for the cones were found by trial, and are obviously round numbers. They show clearly, first that $x_2 - x_1$ is smaller for the cones than for the rods, second that there is a sharp break at a certain illumination when intensity discrimination shifts from the rods to the cones, and third that $x_2 - x_1$ for the rods and the cones has in each case a constant

order of magnitude which represents the unitary minimal decomposition of sensitive substance necessary for intensity discrimination.

2. Sources of Error.—The values of $x_2 - x_1$ for the rods though perhaps varying in a regular way, on the whole are reasonably constant. The values of $x_2 - x_1$ for the cones—all within another order of magnitude—do, however, vary definitely in a regular manner. In the computations the values of x are obtained as differences between two larger numbers. Too much reliance, therefore, is not to be placed on the precise numerical values of $x_2 - x_1$ for the cones, because they are second order differences, and lie at the limit of accuracy of the data. They show a reasonable similarity and a constant order of magnitude, and satisfy the requirements of an analysis which is a first approximation.

There are several aspects of the experiments which would influence the data and hence the constancy of $x_2 - x_1$. In the first place the values of Koenig and Brodhun were corrected by means of the data of Reeves on pupil size. Koenig and Brodhun looked through a telescope at a small illuminated area surrounded by darkness, whereas Reeves used a large illuminated surface. The two are therefore not strictly comparable measurements (Cobb, 1916). In the second place it is possible that the ocular opening of the telescope used by Koenig and Brodhun was smaller than the pupil at maximum dilatation. This would influence the measurements at low intensities. These two sources of error are probably small in magnitude and their existence may even be doubtful.

A more serious matter concerns the relation of the two halves of the field as projected on the retina. Our analysis tacitly assumes that when two contiguous parts of the retina are illuminated one by I and the other by $I + \Delta I$ the same results obtain as when the same area is subjected successively to these just discriminable intensities. Cobb (1916) has shown that the part of the retina which surrounds an illuminated area plays a distinct rôle in intensity discrimination. A similar effect is to be deduced from the work of Lasareff (1911) on the influence of the size of the field on intensity discrimination. Very likely two differently illuminated contiguous areas in the retina affect each other, and this influence would distinctly depend on the intensity, and hence would be different for different parts of the data.

Still another influence in the constancy of $x_2 - x_1$ concerns the

method of deriving the equation for the stationary state. In writing the velocity of the light reaction alone as directly proportional to the incident intensity it has been assumed (Hecht, 1923–24, b) that the absorption coefficient of the sensitive substance is small. This, though accurate for first order results, is probably inaccurate for second order computations such as those represented by $x_2 - x_1$ for the cones. For the sake of simplicity the assumption is retained, but it must be borne in mind as a source of error.

3. Trimolecular Assumption and Results.—Nevertheless there is a slight modification in the detail, but not in the principle, of the analysis which eliminates at once the regular variation in $x_2 - x_1$ for the cones. The bimolecular nature of the "dark" regeneration reaction rests on the kinetic interpretation of dark adaptation data (Hecht, 1921–22) and represents the simplest reaction order compatible with the observations. Within the experimental error there is no great difference between the kinetics of a bimolecular reaction and a trimolecular one. If we assume the dark reaction to be trimolecular the equation for the stationary state becomes

$$K I = \frac{x^3}{a - x}. \tag{9}$$

The values of $x_2 - x_1$ for the cones derived from this equation show an excellent degree of constancy.

Using $K = 20$ for the cones, the following values of $x_2 - x_1$ are obtained[8] corresponding to every other set of cone intensities in

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[8] Since the direct computation of x from equation (9) is not possible, a graphic method has to be used. Giving for the moment a value of 1 to K, and assuming a series of values for x between 0 and 100 per cent, the resulting values of I are calculated. A large scale curve relating x and $\log I$ is then plotted. The curve has an S shape similar to those in Fig. 3. The distance on this curve between any pair of values of $\log I$ and $\log (I + \Delta I)$ is so small that it may be considered with great accuracy as part of a straight line. From this the value of x can be found as

$$x = a \log I + b \tag{10}$$

in which a is the tangent of the curve at the point under consideration. The difference between x_2 and x_1 is then

$$x_1 - x_2 = a \log (I + \Delta I) - \log I. \tag{11}$$

The first differential of the large scale curve is constructed giving the relation between $\log I$ and the tangent a, after which it is simple to choose a proper value for K and to compute $x_2 - x_1$ for the values of I and $I + \Delta I$.

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Table IV: 0.20, 0.17, 0.19, 0.23, 0.21, 0.22, 0.23, 0.20, 0.19. These values are obviously constant. Their average is 0.20 representing the unitary difference in stationary state between x_1 and x_2, and is probably identical with the average of 0.21 found by use of the bimolecular assumption.

The reasons that the bimolecular assumption is used in presenting the data are, first, that it is simpler to handle, and was the one found for dark adaptation; second, as far as the general analysis is concerned, the differences in the two results are really matters of detail and not very significant; third, the trimolecular assumption breaks down with the rod data: it has not been possible to secure constant values of $x_2 - x_1$ for the rods by the use of equation (9). The choice is therefore between an approximately good fit for both rods and cones with a bimolecular assumption, or a good fit for the rods with the bimolecular and for the cones with the trimolecular. We have adopted the first. If the second alternative has to be chosen later nothing is lost, and much is gained in an understanding of the situation. The theoretical consequences are practically the same for the two.

The main point to be brought out is that a quantitative treatment of the data of intensity discrimination yields results which fit with a reasonable degree of accuracy the significant features of the mechanism outlined for the photochemical basis of intensity discrimination.

VII.

Facts Related to Present Analysis.

1. Threshold of Rods and Cones.—There are a number of facts of vision which can be applied as tests for the consistency of the present treatment of intensity discrimination. We have assumed—and the analysis of the data has borne it out—that the differential threshold ΔI is smaller for the cones than for the rods. How does this agree with the fact that the cones are known to have a higher *absolute* threshold than the rods? Fortunately there is not only no contradiction between these two facts, but the analysis here proposed actually calls for the higher absolute threshold.

The simplest way of showing this is by plotting equation (7) of the stationary state using x as ordinates and $\log I$ as abscissæ. Put-

ting K = 100 gives the left hand curve in Fig. 3, and putting K = 0.25 gives the right hand curve. The curves are parallel and represent the behavior of the photochemical system in the rods and cones respectively. The points are the computed values of x_1 of Column 6 corresponding to I in Column 4 of Table IV.

The values of K used in the calculations in this paper were chosen with no other desire than to get the most constant values for $x_2 - x_1$
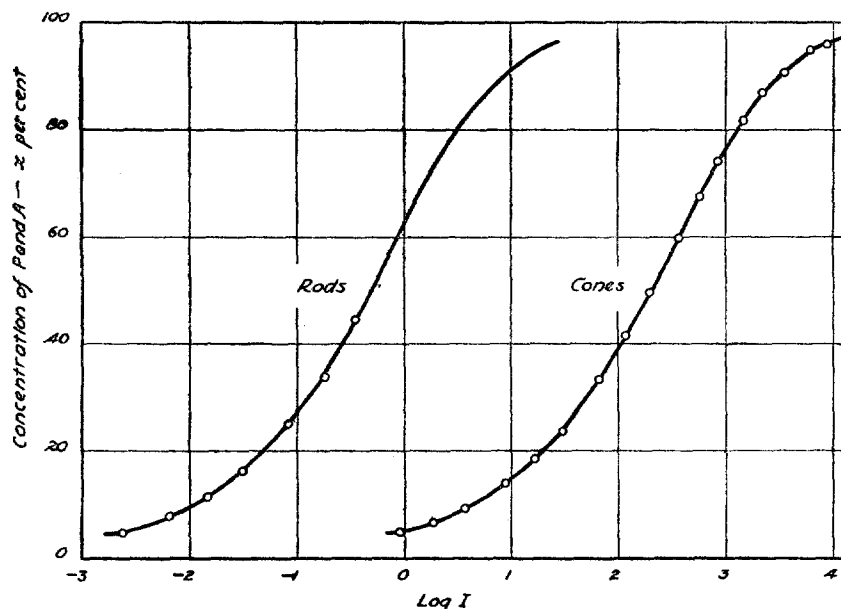

FIG. 3. Relation between retinal illumination and the amount of photochemical action at the stationary state of the reaction $S \rightleftharpoons P + A$. The curves represent the equation $K I = \dfrac{x^2}{a-x}$, in which K = 100 for the rods, and K = 0.25 for the cones.

for the two systems. It is significant that the curves which result from the use of such values of K indicate a higher absolute threshold for the cones than for the rods. The whole cone system seems to be pitched at a higher intensity than the rods. The analysis of the data in terms of the suggested mechanism is therefore in harmony with this familiar truism of retinal physiology.

2. Dark Adaptation.—The relative values of K for the rods and cones have an interesting bearing not only on the absolute thresholds of the two systems, but on their dark adaptation as well. It will be remembered that $K = \frac{k^1}{k^2}$ in other words that K is the ratio of the velocity constants of the light and "dark" reactions in the photochemical system. For the rods $k_2 = 0.01\ k_1$, whereas for the cones $k_2 = 4\ k_1$. These do not tell us the absolute values of k_2 for the rods and cones because k_1 is probably different for the two. But they create a strong presumption that k_2 for the cones is larger than for the rods. The rate of dark adaptation is a function of the "dark" reaction whose speed is determined among other things by the magnitude of k_2. From this it follows that the cones should have a more rapid rate of dark adaptation than the rods. The data on this point are unequivocal. The dark adaptation of the cones is practically complete in 3 minutes (Hecht, 1921–22) whereas the same process in the rods is not complete in 30 minutes (Hecht, 1919–20).

An additional point of interest in regard to dark adaptation is the relation between intensity and photochemical effect. It is apparent from Fig. 3 that between 10 and 90 per cent both curves may without great distortion be treated as straight lines. Therefore, within a reasonable experimental error the effect of light may be considered as proportional to the logarithm of its intensity. This holds true also when the dark reaction is trimolecular. It is to be noted that in order to interpret the data of dark adaptation of the rods in terms of a reversible photochemical reaction this is precisely the relation which we assumed between intensity and photochemical effect.

For the cones the simplest assumption to fit the data (Hecht, 1921–22) is that the effect is directly proportional to the intensity. Recomputation of the data in terms of the log I relation, however, also gives a bimolecular order to the dark reaction.[9] The linear

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[9] The reason that both assumptions yield similar results lies in the fact that the range of threshold intensities, and therefore of the photochemical effects for cone dark adaptation are comparatively small. Combining equations (5) and (6) for the light and dark reactions respectively the velocity of the process as a whole can be expressed as

$$v = k_1 I\ (a - x) - k_2 x^2. \tag{12}$$

If the amount of photochemical change x is small, say less than 10 per cent, x^2

relation and the logarithmic relation are both approximations, the latter being more nearly correct, since it covers a much larger range. However, the only strictly exact relation between intensity and photochemical effect is equation (7) for the stationary state on the one hand, and on the other the integral of equation (12) for the course of the reaction. This integration has been carried out and tested experimentally (Hecht, 1922-23).

Free from any assumptions, however, the experimental data of dark adaptation show clearly that the cone process is faster than the rod process. And this is the main point relevant to our present analysis.

3. Transition Point in Visual Acuity.—Perhaps the most striking outcome of our analysis is the presence of a sharp change in the magnitude of $x_2 - x_1$ representing the transition from rods to cones. The data themselves present no such break (*cf.* Fig. 1). The presence according to our analysis of such a clean break in the calculations, therefore, requires substantiation from some other source in order to render its reality more probable. Fortunately there exists a set of data which furnishes precisely this corroboration.

Koenig (1897) investigated the relation between visual acuity and intensity of illumination. The range of intensities in the experiments covers the interval from the lowest utilizable intensities to those which result in no further increase of visual acuity. The results show that visual acuity is proportional directly to the logarithm of the intensity. For white light, beginning with the lowest intensity ($I = 0.00036$ unit) the data, plotted as acuity against log I, fall on a straight line whose tangent is 0.0414. At very nearly 0.1 unit of intensity, the data sharply diverge, and from now on fall also on a straight line whose tangent, however, is 0.434 or about ten times that for the low intensities.

For intensities below the intersection of the two lines Koenig found that visual acuity is controlled by the periphery of the eye,

becomes less than 1 per cent, and the minus term may be neglected. At the same time $(a - x)$, being ever 90 per cent, may be considered constant. This yields that the velocity of the reaction, and therefore the amount of decomposition for comparable exposures is directly proportional to the intensity.

fixation with the fovea being impossible; but above the intersection the cones come into play and fixation is entirely foveal. These observations were confirmed beautifully by Koenig in a similar investigation of visual acuity in a totally color blind person. In this case the relation between visual acuity and log I is given by a *single* straight line identical in slope and position with the lower straight line for Koenig's own eye.

From our standpoint the implications of all this are clear, because visual acuity is an indirect manifestation of intensity discrimination. Up to a certain point in the intensity scale, acuity is determined by the rods; above that point it is determined by the cones. The point of transition should correspond in some way with the one determined in our analysis of intensity discrimination. The transition intensity is 0.1 units, and is therefore 278 times the threshold intensity. The threshold for intensity discrimination is 0.0000484 millilambert, (Table IV), and 278 times this threshold gives 0.0134 millilambert, a value midway between the last intensity for the rods (0.00732 millilambert) and the first intensity for the cones (0.0190 millilambert).

The transition point from rods to cones as derived from acuity and discrimination data is obviously the same *relative* to the threshold of visibility in the two cases. It would be added evidence to determine whether the *absolute* values of the transition intensity in the two cases are of the same order of magnitude. The units in the data for intensity discrimination have been defined. It is necessary only to find the unit of intensity for the acuity data. Koenig defines this as the illumination by a Hefner lamp at a meter distance. This is 0.9 meter candle; and if the surface reflects 100 per cent, corresponds to 0.09 millilambert. Obviously white paper reflects less than that; how much less we cannot tell from the information furnished. Assume 80 per cent reflection[10] since the paper was evidently chosen with care. This gives the unit a value of 0.072 millilambert. The transition point at 0.1 unit then becomes 0.0072 millilambert, which (Table IV) is exactly the value of the last intensity controlled

[10] Sumpner (1893) found that white blotting paper reflects 82 per cent; white cartridge paper 80 per cent; and ordinary foolscap 70 per cent of the incident light.

by the rods. A slight difference is to be expected between the two groups of results in view of Cobb's work on the influence of the background on intensity discrimination. The acuity work was done with a field of vision most of which was uniformly illuminated, whereas intensity discrimination was measured with a small illuminated area against a background of physical blackness. Nevertheless the agreement is surprisingly close.

An additional point of significance in Koenig's acuity measurements is the position of the transition point in relation to the total range over which the rods can function. From Table IV and Fig. 3 it is apparent that the transition point corresponds to a condition in which approximately half the sensitive substance of the rods has been decomposed, and therefore lies about midway between the limits over which the rods can function. The straight line which describes the acuity data of the color blind individual in Koenig's experiments, and consequently corresponds to the activity of the rods, is almost accurately bisected at the transition point in the data of Koenig's own eye.

Such a series of correspondences between acuity measurements and the calculations from the intensity discrimination data in terms of our analysis can hardly be mere coincidences. When there is added the evidence of the relative thresholds and the agreement with adaptation data, it seems fair to conclude that the assumptions on which our analysis is based as well as the results calculated in terms of it from the data of Koenig and Brodhun probably represent something real in the composition and action of the rods and cones in the visual discrimination of intensity.

VIII.

Discontinuity and the Structural Basis for Intensity Recognition.

1. Discontinuity of Intensity Recognition.—Historically, the idea behind the Weber-Fechner law was an effort to describe the nature of intensity recognition in terms of intensity discrimination. There are two reasons for the failure of the law to do this. First, as must be abundantly clear from our present paper, it was based on data which do not describe intensity discrimination correctly. Second,

it omitted recognition of the obvious discontinuity of intensity perception. This is particularly true of the integrated form—the psychophysical law of Fechner—since the very act of integration assumes infinitesimal changes rather than crude discontinuities.

However, the fact that visual recognition of intensity proceeds in a series of discrete steps is of fundamental importance and must form the basis of any acceptable analysis of the phenomena. Koenig (1895) calculated from the data of Koenig and Brodhun that 572 such steps cover the perception of the entire range of intensities. Our own calculations (Table IV and Fig. 3) indicate that about one-third of these steps are discriminated by the rods, the rest by the cones.

2. Basis of Discontinuity in Retina.—In terms of our analysis, each of these perceptible steps in intensity recognition represents a unitary increase in the quantity of sensitive material decomposed in the retina. It is important to consider the exact nature of these unitary increases. We have pictured them as occurring in the retina. The experiments of Müller (1897) and more recently of Brückner and Kirsch (1913) and of Lasareff (1923, *b*) have made it certain that even extreme changes in the light and dark adaptation of the eye do not influence its threshold for electrical and mechanical stimulation. These, therefore, represent the threshold of the structures which lie central to the rods and cones, since during adaptation the peripheral sense cells undergo enormous changes in sensitivity to light. Intensity differences on the retina result in local differences in adaptation. Since these cause no changes in the sensitivity of such structures as the ganglion cells and the optic centers in general, it follows that changes in sensitivity to light which do exist must be caused by the changes in the retina alone.

Aside from the direct bearing that this conclusion has on the matter in hand, it is also interesting as demonstrating (*cf.* Hecht, 1922–23) that a sense organ like the eye acts as a sort of buffer between the environment and the central nervous system.

3. Entire Process in Each Retinal Element.—One way of conceiving the nature of these unitary increments in photochemical decomposition in the retina is to consider each rod and cone as a complete system capable by itself of covering the range of intensity perceptions

and discriminations indicated by the two curves in Fig. 3. Transmission to the respective nerve fiber of such a series of unitary increases may be pictured in a speculative way as follows: Each intensity is represented by a discontinuous, all-or-nothing discharge from the sense cell, the rhythm of which is determined in part by the concentration of decomposed material, or more likely by the rate of energy liberation in the process of decomposition.[11] A unitary increase in this rhythmic discharge means a minimal increase in intensity, and the frequency corresponding to any stationary state would determine intensity perception as a whole. This is essentially the idea proposed by Forbes and Gregg (1915–16) to account for intensity transmission in reflexes, but modified to correspond with unitary increments (cf. also Adams and Cobb, 1922).

4. Each Element Represents One Step.—Such a conception of intensity recognition would mean that in a given illuminated retinal area all the rods and all the cones, even at their thresholds, function at the same time. This accounts not only for the present data, but also for those of dark adaptation. It must be apparent nevertheless, that this is probably one of those simplifications of the problem to which reference was made at the outset of our analysis. On such a basis it would be difficult to understand so patent a fact as the increase of acuity with intensity. It may be that more cones and more rods are functional at the higher intensities than at the lower.

This reasoning can be carried to its logical end by assuming that each sensory element behaves strictly in an all-or-nothing manner and that unitary increments in the retina represent the addition of a group of sense cells to those already functioning. In this case intensity recognition would be determined solely by the number of sensory elements acting in a given area. Such an idea, following from the development of the all-or-nothing hypothesis in nerve (Adrian, 1913–14) has been suggested frequently before (*e.g.* Forbes and Gregg, 1915–16), but more recently again by Lasareff (1923, *a*),

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[11] Such a scheme is particularly consistent with a pseudoreversible reaction like the one suggested in Section VI. At the stationary state, light is being steadily poured in at one end of the sense cell. The result is a continuous production of *B*, which heaps up and discharges rhythmically, and stimulates the nerve ending at the other end of the cell.

who derives it from the anatomical discontinuity of the retina and the quantal discontinuity of light. This kind of hypothesis is very attractive, though unfortunately its quantitative implications have never been described concretely with reference to any series of data.

In considering the quantitative consequences of such an interpretation it clearly is ·insufficient to rely, as Lasareff has done, merely on the all-or-nothing character of the nerve impulse plus the discontinuity of both retina and light. There must be made the additional and more critical assumption that the sensory elements in the retina differ widely in their threshold. It is on the basis of this quantitative variation in sensory threshold that such an idea can be used to describe the data of intensity discrimination.

It is simple to show that because of this variability in the sensory elements this type of arrangement can also be based on the photochemical mechanism derived in this paper to account for intensity discrimination. Assume that when they differ in threshold at all, the sense cells differ by the unitary amount $x_2 - x_1$ in the quantity of decomposed photosensitive material necessary to set off an impulse from the cell. If there are the same number of sense cells corresponding to each unitary step in concentration, their distribution *with relation to the intensity* will be such as to give the two curves in Fig. 3. The resemblance of these two curves to integral distribution curves is striking. The form of their first differential is distinctly that of the usual frequency curves of populations, errors, and the like. It is not symmetrical, as is apparent from the point of inflection which lies not at 50, but near 60 per cent. This is a consequence of the fact that equation (7) which determines the curves is itself unsymmetrical. In the case of the excellent fit for the cones given by equation (9) the first differential curve is still more skew, since the equation is obviously still less symmetrical. It is therefore clear that these consequences of our analysis can easily serve as the ultimate basis for an interpretation of the variability of the sense cells. The present photochemical analysis may thus be considered basic.

5. Combination of Two Extreme Ideas.—The obvious notion that each cone and each rod can cover the whole range of intensity discrimination is probably too simple to be the correct expression of our analysis. The opposite idea that each cone and each rod can cover

only one step in the series of intensity discriminations seems an extreme form of functional limitation, for which there is no proof. Moreover, it fails to explain the phenomena of dark and light adaptation.

It is possible of course to consider a compromise between these two plans. In this each cone and each rod would contain a complete photochemical system capable of discriminating intensities over a small range, say five or ten unitary steps, and in addition different individuals would be pitched at higher intensity levels somewhat as the cones as a whole are higher than the rods. The levels between the individual cells would be less than the range that can be covered by a single cone or rod. In this way a step in intensity discrimination would mean a unitary step in a given sense cell or the addition of a new one to those already affected; and in an area under illumination probably both of these would occur at once. The curves in Fig. 3 would then represent the smoothed result of the combined effects. This compromise mechanism explains not only such things as the dependence of acuity on intensity and the variation of the discrimination ratio with the size of the visual field but also the curious interchangeability of intensity and the size of the visual area (cf. Parsons, 1915[12]). Such an idea receives additional support from the fact that several rods may be supplied by a single nerve fiber.

At present there seems to be no means of choosing among these structural interpretations of our analysis. Experiments must therefore be devised whose purpose will be to throw light on these fundamental aspects of vision. Such experiments have already been planned, and it is hoped that the results and their interpretation will be forthcoming in the near future.

SUMMARY.

1. A study of the historical development of the Weber-Fechner law shows that it fails to describe intensity perception; first, because it is based on observations which do not record intensity discrimination accurately, and second, because it omits the essentially discontinuous nature of the recognition of intensity differences.

[12] Parsons (1915), p. 117.

2. There is presented a series of data, assembled from various sources, which proves that in the visual discrimination of intensity the threshold difference ΔI bears no constant relation to the intensity I. The evidence shows unequivocally that as the intensity rises, the ratio $\dfrac{\Delta I}{I}$ first decreases and then increases.

3. The data are then subjected to analysis in terms of a photochemical system already proposed for the visual activity of the rods and cones. It is found that for the retinal elements to discriminate between one intensity and the next perceptible one, the transition from one to the other must involve the decomposition of a constant amount of photosensitive material.

4. The magnitude of this unitary increment in the quantity of photochemical action is greater for the rods than for the cones. Therefore, below a certain critical illumination—the cone threshold— intensity discrimination is controlled by the rods alone, but above this point it is determined by the cones alone.

5. The unitary increments in retinal photochemical action may be interpreted as being recorded by each rod and cone; or as conditioning the variability of the retinal cells so that each increment involves a constant increase in the number of active elements; or as a combination of the two interpretations.

6. Comparison with critical data of such diverse nature as dark adaptation, absolute thresholds, and visual acuity shows that the analysis is consistent with well established facts of vision.

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