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INTENSITY DISCRIMINATION AND ITS RELATION TO THE ADAPTATION OF THE EYE.

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I. INTRODUCTION.

UNDER the above title Wright [1935] has recently published measurements which describe the influence of pre-adapting the eye to high intensities on its capacity to discriminate differences between lower intensities. Wright states that he is unable to describe these measurements in terms of the visual receptor process, and therefore concludes that the basis for intensity discrimination cannot be in the receptor process but must be in some undefined, but more centrally located series of events.

In particular, Wright singles out our ideas [Hecht, 1934*a*] about the nature of the receptor process in the retina, and states that in terms of his new data "the experimental support for" these ideas "has thus largely disappeared".

Examination of existing data on intensity discrimination and their relation to the photoreceptor process shows that (*a*) Wright has missed the meaning of his own measurements; actually they demonstrate almost the opposite of what he supposes; and (*b*) his measurements are easily described in terms of equations already derived for the receptor process in the retina. The two conclusions of Wright's paper are therefore not valid.

II. INTENSITY DISCRIMINATION.

The usual data of intensity discrimination record the intensity I of a test light, and the increment ΔI which must be added to it in order that $I+\Delta I$ may be recognized as just brighter than I. The available data, extending over 70 years, have recently been summarized and critically evaluated [Hecht, 1934*b*, 1935]; they show that $\Delta I/I$ decreases in a regular manner as the intensity I increases. Fig. 1 gives the data of Blanchard [1918] and of Lowry [1931]; the measurements are in modern units, and have been corroborated in our laboratory by J. Steinhardt. These data are significant because they help us to understand the nature of the receptor process, and the meaning of Wright's measurements in relation to it.

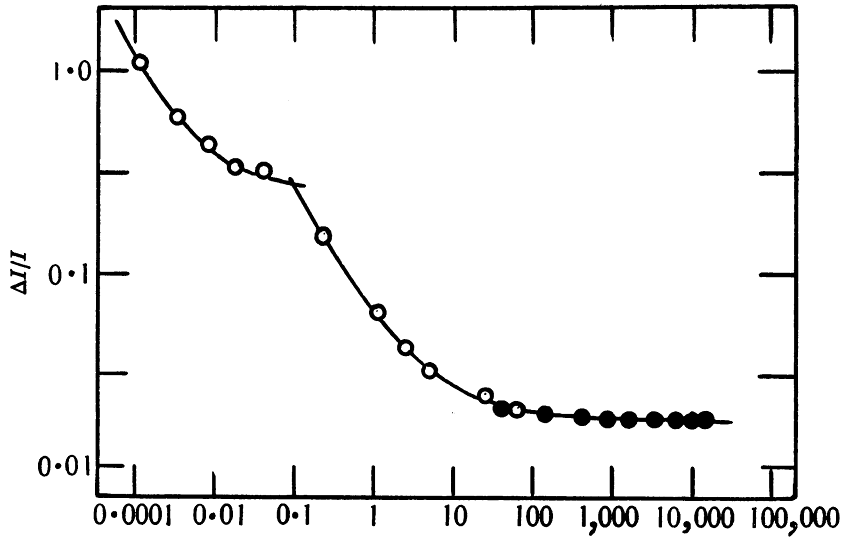

Fig. 1. The data of Blanchard (open circles) and of Lowry (solid circles) for the relation of $\Delta I/I$ to I. The values of I were originally in millilamberts, but since Lowry gives the diameter of his artificial pupil as 5 mm., it has been simple to convert millilamberts into photons by multiplying by 62·5. The two curves are theoretical, and represent equations (6) and (7). For further details see Hecht [1935].

III. The photoreceptor process.

Stated in general terms, photoreception requires the presence of (*a*) an inactive photosensitive substance which absorbs light and is changed by it into one or more active substances which start the train of events ending in an impulse from the receptor cell; and (*b*) some means of maintaining a supply of the sensitive material, since otherwise it would be used up and the process would come to an end.[1] What are the pro-

[1] Obviously the photoreceptor process itself is more complicated than this. Moreover, the process of vision as a whole involves not only the receptor processes in the rods and cones, but the nerve impulses generated by the stimulated elements and by neighbouring elements, as well as all sorts of cortical changes of which we know little or nothing. Since

perties of such a photochemical system under the conditions of intensity discrimination?

Let the total initial concentration of sensitive material be a; let light of intensity I shine on it; let the concentration of photoproducts at the moment t be x; and let it be assumed that some of these products reunite under proper conditions to form again the sensitive material. The velocity of the process as a whole will then be

$$(dx/dt)_I = k_1 I\ (a-x)^m - k_2 x^n, \qquad \ldots\ldots(1)$$

where m and n represent the order of the photochemical and the dark, regenerating reaction respectively; and k_1 and k_2 are their velocity constants, k_1 including the absorption coefficient. On continuous illumination a stationary state is reached in which the opposing reactions become equal; the concentrations of sensitive material and photoproducts become constant; and equation (1) becomes equal to zero. This gives

$$I = k_2 x^n / k_1\,(a-x)^m. \qquad \ldots\ldots(2)$$

If the system is now exposed to intensity $I + \Delta I$, the initial velocity will be

$$(dx/dt)_{I+\Delta I} = k_1\,(I+\Delta I)\,(a-x)^m - k_2 x^n, \qquad \ldots\ldots(3)$$

no changes in concentration having yet taken place. Subtracting equation (1) from (3), we get

$$(dx/dt)_{\Delta I} = k_1 \Delta I\ (a-x)^m. \qquad \ldots\ldots(4)$$

Assume that ΔI is recognized when $(dx/dt)_{\Delta I}$ is constant[1] and equal to c'. Equation (4) then gives $\Delta I = c'/k_1\,(a-x)^m$. Dividing this value of ΔI by the value of I from equation (2) and writing $c'/k_2 = c$, we get

$$\Delta I / I = c/x^n \qquad \ldots\ldots(5)$$

these are all concerned with vision, they surely influence its characteristics to some extent. The question is to what extent; and the answer can be secured only by trial.

Our own viewpoint has been that, no matter what determines the nature of vision, the ultimate place of origin of the impulses passing up the optic tracts is in the action of light on the eye. Therefore, for several years we have measured various properties of vision and photoreception to ascertain whether the data owe any of their quantitative properties to the characteristics of the very first reactions which must take place between light and the sensitive elements concerned with receiving the light. The advantage of dealing with this first process is that it is photochemical, and that the properties of photochemical systems have been much studied and clearly formulated. The present data of Wright are a significant case in point.

[1] This probably means that in a short time Δt, a constant increment of sensitive material Δx, must be decomposed by the addition of ΔI; this small increment Δx may show itself as a given increment in the frequency of impulses leaving the receptor cell to the associated nerve fibre.

as a description of $\Delta I/I$ in terms of the general photoreceptor system.[1]

Equation (5) is important for understanding Wright's measurements, because it defines the relation between $\Delta I/I$ and the concentration x of photoproducts. Since c is constant, $\Delta I/I$ varies inversely with x^n. This means that when x varies $\Delta I/I$ will vary, and when x is constant $\Delta I/I$ is constant.

IV. Wright's experiments.

(1) *First series.*

Wright argued correctly that since $\Delta I/I$ depends on the concentration x, then the value of $\Delta I/I$ should vary with the state of adaptation of the eye, which can be controlled by the adapting intensity. His first experiments were therefore concerned with varying the intensity of the adapting light and determining ΔI for a constant measuring intensity I.

His data are shown in Fig. 2. Consider experiments a and b in which he used adaptation intensities between about 1000 and 40,000 photons and measured ΔI for an intensity $I = 1080$ photons for a, and for $I = 550$ photons for b. He found that ΔI is practically constant at about 70 photons and 50 photons respectively, in spite of the large variation in adapting intensity.

However, it is significant to note in Fig. 1 that $\Delta I/I$ becomes practically constant, and therefore x becomes constant, at about 100 photons. Between 1000 and 40,000 photons, the state of adaptation of the eye as judged by $\Delta I/I$, and of the photoreceptor system as judged by x, is constant. In other words, though Wright thought he had changed pro-

[1] It is interesting to show that equation (5) describes the measurements of intensity discrimination. Since these are given as $\Delta I/I$ against I, it is necessary to replace x by values of I derived from equation (2). When $m = n = 1$, that is when both the light and the dark reactions are monomolecular, equation (5) becomes

$$\Delta I/I = c\,(1 + 1/KI), \qquad \text{......(6).}$$

where $K = k_1/k_2$, and $c = c'/ak_2$. When $m = n = 2$, that is when both reactions are bimolecular, equation (5) becomes

$$\Delta I/I = c\,(1 + [1/KI]^{\frac{1}{2}})^2, \qquad \text{......(7)}$$

where $c = c'/a^2k_2$. Notice that equations (6) and (7) contain two constants c and K, and that these have no influence on the shape of the function if the data are plotted as $\log \Delta I/I$ against $\log I$.

It has been shown [Hecht, 1934*b*, 1935] that equation (6) describes the intensity discrimination of *Drosophila*, and equation (7) the data for the bee and for the clam *Mya*. Moreover, all the critical data for the human eye are described with precision by equation (7) for the cones at high intensities and by (6) for the rods for low intensities, though the rod data are too few for a final choice between (6) and (7). The curves in Fig. 1 are these two equations; the data show clearly the separateness of rod and of cone function.

foundly the state of adaptation of the eye with these high intensities, the fact is that it had remained practically unaltered. This is confirmed by the fact that not only $\Delta I/I$, but visual acuity [Koenig, 1897], and the critical fusion frequency for intermittent stimulation (unpublished experiments) are practically constant in the range of these high illuminations.

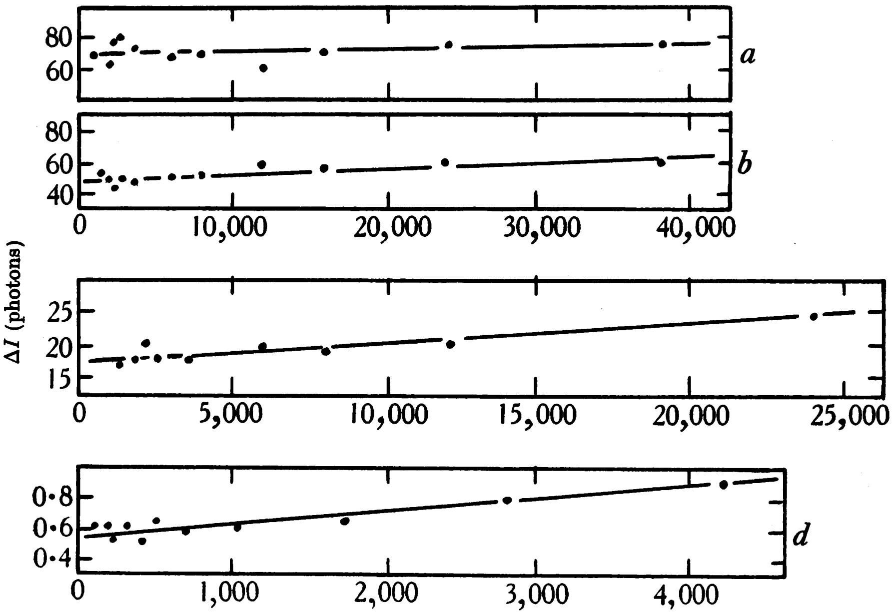

Fig. 2. Wright's data, traced from Figs. 3, 4, 5, and 6 in his paper, are here labelled a, b, c, d respectively.

Let I_a be any one of these very high intensities and let x_a be the concentration of photoproducts at the stationary state when the eye is adapted to I_a. The concentration of sensitive material is then $a-x_a$. In Wright's experiment, the eye was rapidly changed from this intensity I_a to a field of which the intensity on one side is I and on the other the just noticeably brighter one $I+\Delta I$. The action of I and of $I+\Delta I$ on the system is then given by equations (1) and (3) in which $a-x_a$ is the concentration of sensitive material and corresponds to the pre-adapting intensity I_a. Following the steps already given and remembering that $m=n=2$ for the cones, we get

$$\Delta I = c/(a-x_a)^2, \qquad \text{......(8)}$$

where $c=c'/k_1$.

Fig. 1 tells us that x_a is practically constant between 1000 and 40,000 photons; hence $a-x_a$ is constant. In terms of equation (8), ΔI should be practically constant, and this is what Wright found. The values of ΔI in Fig. 2*a* and *b* rise only slightly as I_a mounts to 40,000 photons, as they should since x_a also increases only very slightly.

Returning to Fig. 1, we see that as I goes below 1000 photons, $\Delta I/I$ begins to rise, at first slowly and then rapidly. In terms of equation (5) this means that x decreases in the same way, and that therefore $a-x$ increases similarly. Therefore for adaptation intensities in this range, ΔI should not be constant, but should increase with the adapting intensity. Fig. 2*d* describes just such an experiment made by Wright. I_a varies between 100 and 4000 photons, while I is 6 photons. The data clearly show that over the range covered, ΔI increases about 60 p.c. The measurements in Fig. 2*c* were made by Wright with adaptation intensities intermediate between the lower and higher just discussed, and also show an intermediate rise in ΔI.

All of Wright's first series of experiments thus yield results which are to be expected in terms of the idea that intensity discrimination is mainly determined by the state of adaptation of the photoreceptor system, and may indeed be considered as unexpected and unprejudiced proof of that idea.

(2) *Second series.*

Wright's second series of measurements are the complement of those already discussed. In these he kept the adapting intensity I_a constant and varied the measuring intensity I, and then determined the value of ΔI corresponding to it. In the one experiment given in his paper $I_a = 10{,}000$ photons while I varies between 50 and 550 photons.

What can we expect of the behaviour of $\Delta I/I$ under these conditions? Equation (5) tells us that $\Delta I/I$ is inversely proportional to the concentration of photoproducts at the stationary state. In the present case the adapting light I_a keeps x constant at x_a; therefore $\Delta I/I$ must be constant. This is precisely what Wright found; and here again his data do just what is to be expected of them.

Perhaps the simplest way of realizing what Wright's experiments mean is to look again at the data in Fig. 1. Between 100 and 40,000 photons the eye is in a practically constant state as shown by the constancy of $\Delta I/I$. It matters little how high the adapting intensity is, and whether the measuring intensity is 100 or 1000 photons, because the concentration x is nearly the same for this range, and therefore $\Delta I/I$ will be the same. If the measuring light is below these intensities, say at 50 photons, a slight rise in $\Delta I/I$ may be expected; but Wright's measurements are not critical enough to show this, since they vary between 0·086 and 0·068.

Wright's experiments probably involve a certain amount of dark adaptation. When an eye which is adapted to bright light is suddenly confronted with a much dimmer light, or no light at all, it dark adapts at a tremendous rate [Hecht, 1921]. In the first few seconds, dark adaptation is so fast that it is practically impossible to measure it. Blanchard's observations [Blanchard, 1918] show that when the measuring light is between 1/100 and 1/500 of the adapting light it may still become visible almost instantaneously. Below that fraction, a perceptible amount of dark adaptation is required. Wright's lowest measuring intensities are near this critical region, and may have involved some dark adaptation, which is effective even in 0·1 sec.

Attention is called to dark adaptation not because it is necessary in the explanation of Wright's data, but because it offers rather interesting possibilities for critically testing some of the ideas associated with intensity discrimination, and we hope to follow them.

V. Summary.

Wright has found that (*a*) when the eye is pre-adapted to very high intensities, the instantaneous value of ΔI for a given value of I is very nearly constant when the adapting and measuring intensities are both high, but increases significantly when they are both lower; and (*b*) when the pre-adaptation intensity is high and constant and the measuring intensity I is variable, $\Delta I/I$ remains constant.

It is shown here that the data secured by Wright are easily interpreted by, and necessarily follow from, the equations and ideas previously used to describe intensity discrimination in terms of the photochemical changes in the retinal elements during vision.

Wright's measurements thus furnish fresh and unexpected corroboration of these ideas and equations.

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