

The apparent rarity of geometric effects in environmental variability is perhaps due to the fact that some environmental factors are stimulatory and some inhibitive in effect. A geometrically progressive inhibiting factor would tend to result in negative skewness. Possibly the apparent absence of skewness may be the result of the cancellation of one type of effect by the other. Such speculations are rather fruitless in the absence of more definite evidence.

Summary.—Evidence is presented that in the inheritance of fruit size in *Cucurbita Pepo* the genes have a geometrically cumulative effect, resulting in a positively skewed distribution in F_2 . Much more nearly symmetrical distributions are obtained by plotting in logarithmically equal classes. The suggestion is made that this type of gene action results from the fact that many processes, independent genetically and developmentally, are concerned in the determination of size, and that these interact in a multiplicative fashion.

¹ East, E. M., *Bot. Gaz.*, **55**, 177–188 (1913).

² Rasmusson, J., *Hereditas*, **18**, 244–261 (1933).

THE INSTANTANEOUS VISUAL THRESHOLD AFTER LIGHT ADAPTATION

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One of the satisfactions in applying a theory comes from its unexpected illumination of data which, though well known, have long remained obscure in their interpretation and unrelated to the rest of the field. The measurements of visual intensity discrimination are a case in point. Though accumulated^{1,2,3} over a period of 75 years, they have only recently been recognized⁴ as falling into (a) the physiological scheme of the duplicity theory⁵ which separates vision into cone function at high illuminations, and rod vision at low illuminations, and (b) the mathematical pattern which describes the first steps of photoreception in terms of photochemical and dark reactions arranged as a cyclic pseudoreversible system.⁴ The familiar data of Blanchard³ on instantaneous thresholds bear on precisely the same ideas, but have failed of interpretation until now.

In Blanchard's measurements the eye is adapted to a given intensity by looking for some time at a large suitably illuminated area. At a specific moment this adapting light is cut off, and the minimum illumination is

determined at which a centrally fixated 5° area becomes visible at the same moment. This requires several trials, each preceded by proper adaptation, until the precise intensity is found which renders the central area just visible instantaneously on shutting off the adapting light.

Blanchard made these measurements over a large range of adapting intensities, using white light as well as the red, yellow, green and blue portions of the spectrum isolated by roughly monochromatic filters. He found that the instantaneous threshold intensity increases with the adapt-

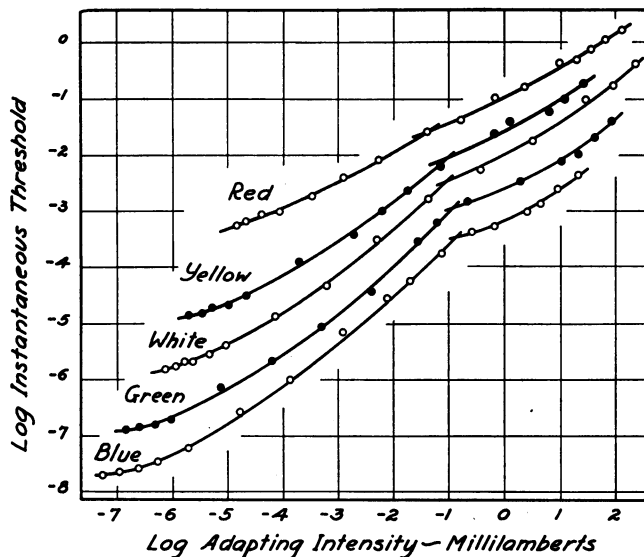


FIGURE 1

Blanchard's measurements of the instantaneous threshold following light adaptation to various intensities and colors. The adapting intensity axis is the same for all the data. The numbers on the instantaneous threshold axis apply only to the white data because, to avoid confusion in plotting, the yellow data have been displaced upward 0.5 log unit and the red 1 log unit; the green data have been displaced downward 0.5 log unit and the blue 1 log unit.

ing intensity, and states that on a double logarithmic plot the data, except at the extreme intensities, lie on practically straight lines which he represents by the appropriate equation for a straight line. Blanchard notes that the data for the different colors are very similar at moderate and high brightnesses, but that they diverge at the lowest brightness, and he correctly attributes the latter fact to the Purkinje phenomenon.

Blanchard adds the pertinent observation that "all the color curves except red show a decided dip, indicating a depression of sensibility, in a

region roughly between 0.01 and 1 millilambert, a region corresponding to about the average range of interior brightnesses at night," but fails completely to appreciate the meaning of his observation. I have replotted his data in figure 1, from which the significance of his "dip" is at once apparent in terms of the duplicity theory. The reason that Blanchard speaks of the region of the rod-cone transition as a dip rather than as a rise is that he actually plotted the negative logarithm of the instantaneous threshold (calling it the sensibility), and thus his curve is reversed in direction of the ordinates.

Figure 1 shows that with red light the measurements form an almost continuous function. Indeed, when plotted by themselves, the red data may easily be fitted with one line; it is only when the data for the other colors are added that the double nature of the function becomes apparent because the inflexion point in the red data, though gentle, corresponds so obviously with the point of striking change in slope shown by the yellow, white, green and blue data. Judged by the transmission data published by Blanchard, his red light begins at 600 $m\mu$; it would therefore stimulate the rods as well as the cones in this 5° centrally fixated area.

In figure 1 it is apparent that the high intensity portions for all the colors and for white are much the same, indicating their common origin in cone function. Except for red, the low intensity sections drop sharply away, also in a form which is approximately the same for all the measurements. Note particularly that the low intensity rod section is largest for blue light and becomes smaller through the spectrum to the red, as is to be expected from the spectral sensibility curves of the rods and cones as separately determined. Attention has already been called to this situation in dark adaptation,⁶ in intensity discrimination⁴ and in flicker,⁷ and it is unnecessary to labor the point here. The instantaneous threshold measurements fit directly into the pattern of the duplicity theory, and serve to strengthen the force and validity of that generalization.

These data of Blanchard's are significant beyond their rod-cone interpretation because of their quantitative numerical relations. In this respect, they are like the data of intensity discrimination and flicker, since they fall into the photochemical scheme proposed for the initial events in the photoreceptor process.⁴

In general terms this scheme supposes that the photoreceptor process is composed of (a) a primary photochemical reaction in which an inactive photosensitive material absorbs light and is converted by it into one or more active products; (b) a primary dark reaction which maintains the supply of sensitive material, since otherwise it would be used up and vision would cease; and (c) a secondary dark reaction in the course of which the active photoproducts of the primary photochemical reaction undergo some

change, the end result of which is an impulse from the receptor cell to the attached nerve.

Of course the photoreceptor system is more complicated than this, and to describe some visual data it may be necessary to make further suppositions. For dealing with the present data, however, it is not necessary to consider even the whole of the suggested system; we need to study only the primary light and the primary dark reactions. In such a simplified arrangement, the sensitive material S is changed by light into the photo-products P, A, \dots some of which may under proper conditions reunite to form the sensitive material from which they were derived.

Let the total initial concentration of S be a , and the concentration of P, A, \dots at the moment t be x . Under the influence of light of intensity I the photochemical process will have a velocity

$$(dx/dt)_1 = k_1 I (a - x)^m \quad (1)$$

where k_1 is the velocity constant which includes the absorption coefficient, and m is the apparent order of the reaction. The simultaneous dark or thermal reaction which furnishes the sensitive material S from the main photoproducts P, A, \dots has a velocity

$$(dx/dt)_2 = k_2 x^n \quad (2)$$

where k_2 is a velocity constant and n is the order of the reaction. If the light I continues to illuminate the eye, the two velocities become equal. Putting equation (1) equal to (2) gives

$$KI = x^n / (a - x)^m, \quad (3)$$

the familiar stationary state equation in which $K = k_1/k_2$.

After producing this stationary state, the light I is sharply cut off; the instantaneous threshold I_0 is then the least intensity of light which is visible to the eye at the very first instant of darkness. At this first moment, before the stationary state has undergone any change, the receptor system becomes exposed to the instantaneous threshold intensity I_0 . The velocity of the resulting photochemical action is

$$(dx/dt)_{I_0} = k_1 I_0 (a - x)^m \quad (4)$$

where $(a - x)$ is still the concentration of sensitive material in the stationary state. In treating intensity discrimination⁴ we assumed that to produce a minimal visual effect, the initial velocity of this photochemical reaction is constant and equal to c' . To make the same assumption here means putting equation (4) equal to c' , and gives

$$I_0 = c' / k_1 (a - x)^m. \quad (5)$$

For this expression to be useful with measurements, we need to substitute

for $(a - x)$ the value of the corresponding adapting intensity I in the stationary state equation (3). When $m = n = 1$, equation (3) yields $(a - x) = a / (1 + KI)$, which when introduced in (5) gives

$$I_0 = c(1 + KI) \tag{6}$$

where $c = c'/k_1a$. When $m = n = 2$, equation (3) yields $(a - x) = a / [1 + (KI)^{1/2}]$; after this value is put into equation (5) we get

$$I_0 = c[1 + (KI)^{1/2}]^2 \tag{7}$$

where $c = c'/k_1a^2$.

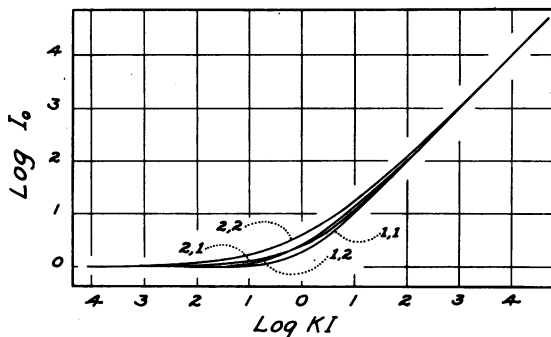


FIGURE 2

Theoretical relation between the instantaneous threshold I_0 and the adapting intensity I in terms of equations (6) and (7). For completeness the curves corresponding to $m = 2, n = 1$, and $m = 1, n = 2$, have been added. Because they are plotted on a double logarithmic grid, the shape of the curves is invariant in relation to the constants c and K which merely determine the position of the curves on the ordinates and abscissas, respectively.

The curves which correspond to equations (6) and (7) are plotted in figure 2; the two curves showing the situation when $m = 1, n = 2$, and $m = 2, n = 1$ are also included. The curves are plotted as $\log I_0$ against $\log KI$, a procedure which renders their form invariant. The shape of the relation between the two variables remains the same regardless of the constants involved; changes in the constant c merely move the curve as a whole along the ordinates, while changes in K move the curve along the abscissas.

Examination of the theoretical curves in figure 2 shows their similarity to Blanchard's actual measurements in figure 1. However, a direct comparison of theory and data is not immediately possible because the measurements were made with the natural pupil, which varies enough over this

large range of intensities to distort the actual relationship. Fortunately Blanchard records his own pupil diameter at different illuminations. The corresponding pupil areas can then be corrected for their relative efficiency in brightness transmission as determined by Stiles and Crawford,⁸ and the resulting effective pupil areas used for converting millilamberts, which are brightness units, into effective photons which are retinal units.⁹ Since the instantaneous threshold represents a measurement made at the first instant after light adaptation when no pupil change can as yet have oc-

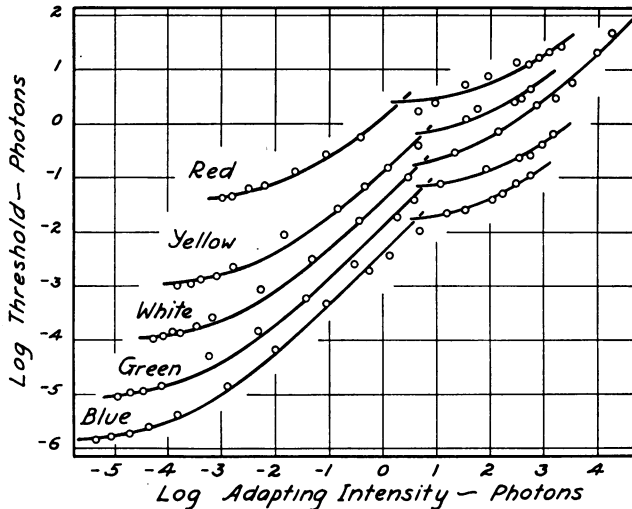


FIGURE 3

Blanchard's data corrected for pupil area from his own measurements, and for relative effectiveness of pupil area from the work of Stiles and Crawford. The curves through the points are all the 2, 2 function in figure 2, corresponding to equation (7). As in figure 1, the data for yellow and red have been displaced upward 0.5 and 1 log unit, respectively, and the data for green and blue downward 0.5 and 1 log unit, respectively.

curred, the same effective pupil area correction applied to the adapting intensity must also be applied to the corresponding instantaneous threshold intensity.

Blanchard's data corrected in this manner are shown in figure 3. The high intensity sections, representing cone vision, contain too few points (except for white) for a critical choice among the four curves of figure 2. The $m = n = 1$ curve is definitely excluded; and since for intensity discrimination the 2, 2 curve gave the best fit, the 2, 2 curve has been drawn through the present cone data as well. The fit of the data by the theoretical curve is obvious. The rod data at low intensities are numerous enough

to exclude the 1, 1 formulation. Flicker measurements¹⁰ would encourage the use of the 2, 1 curve for the rods. Though this is not excluded here, the 2, 2 fits distinctly better; its curve is therefore drawn through the rod data also.

One must treat this choice of exponents as distinctly preliminary. The data are for one person only and have had to be corrected; additional measurements made with a fixed pupil are necessary before serious attention can be paid to the specific values of m and n . However, the measurements are good enough to show their agreement with theoretical expectation, especially since their precise form could not be predicted intuitively.

Summary.—Blanchard's measurements of the instantaneous visual threshold following light adaptation to different intensities and colors are shown to fit directly into the pattern of the duplicity theory which separates vertebrate vision into cone and rod functions. Moreover, the numerical values of the measurements and the precise form of their relations are found to conform to the mathematical predictions from a reversible photochemical system previously used for describing other properties of vision and photoreception.

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