INTERMITTENT STIMULATION BY LIGHT

I. The Validity of Talbot's Law for Mya

By SELIG HECHT and ERNST WOLF*

(*From the Laboratory of Biophysics, Columbia University*)

(Accepted for publication, January 8, 1932)

I

Talbot's Law

When the illumination of a visual field is interrupted with sufficiently high frequency, it appears to the human eye as continuous. Talbot (1834) first pointed out that the brightness of such a field now corresponds to the original illumination multiplied by the fraction which the actual duration of illumination is of the total duration of a complete cycle of illumination and darkness. Thus, a reduction in the time of action of the light is equivalent *visually* to a corresponding reduction in its intensity.

Talbot, himself, records no measurements in terms of which the validity of his law may be judged, though his paper clearly indicates that he made such measurements. These were first given by Plateau (1835) who compared the brightness of rotating white discs containing black sectors with the brightness of the same white cardboard at different distances from a source of light. At equal brightness, he found that the square of the distance of the rotating disc from the light is to the square of the distance of the white paper as the angle of the white sector is to 360°. The measurements are limited, but adequate. Later, Helmholtz (1865) described several additional ways of demonstrating Talbot's law, and appears to have tried them; but he gives no measurements.

The first to doubt the validity of Talbot's law was Fick (1863) who, in thinking about the matter, laid down a surprisingly adequate mathematical basis for the whole process. Fick recognized that at the stationary state, when an intermittent illumination produces a con-

* Fellow, International Education Board, 1927–28.

tinuous impression, the velocities of the rise and of the decay of the excitatory process (An—und Abklingen) must be equal regardless of the relative durations of light and dark exposures. But that this should result in so simple a mathematical relation as Talbot's law seemed impossible to Fick in the light of what was to him the obviously complicated nature of the light and dark processes themselves.

Fick's own measurements, using essentially Plateau's technic, convinced him that Talbot's law is not valid. However, as Aubert (1865) clearly showed, Fick's own measurements do not support his contention. They are indeed quite adequate to verify the law within the rather large experimental error incident to his method of measurement.

It may be added that Fick's ideas of the complexity of the retinal processes, though justified on general principles, have not been borne out by later developments. Modern work on the physiology of vision, notably on light and dark adaptation (Hecht, 1931; Kohlrausch, 1931), has shown these processes to be much simpler than Fick could have anticipated.

The position of Talbot's law remained where Fick and Aubert left it until Kleiner reinvestigated the whole matter in 1878, using Zöllner's polarization photometer. His data show quite clearly that within a photometric error of a few per cent Talbot's law holds for the sector openings he measured, which ranged from 180° to about 1.5°. These results have been confirmed by Wiedemann and Messerschmidt (1888) using only a few sectors, by Ferry (1893), and by Lummer and Brodhun (1896). Lummer and Brodhun state that according to their extensive measurements, made at the Reichsanstalt, Talbot's law holds to within 0.5 per cent, but neither they nor Ferry record any of their data.

Apparently the doubt raised by Fick seems still to have persisted, because in 1906 Hyde deemed it necessary to study the situation all over again in full detail. Hyde's work, done at the Bureau of Standards, is a model of precision. He investigated sector openings between 10° and 288° and found the results to be in agreement with expectation from Talbot's law within a photometric error of 0.5 per cent. For the human eye, therefore, there can no longer be any doubt of the validity of Talbot's law.

Certain points, however, remain to be noted. Though the deviations from Talbot's law found by Hyde are below 0.5 per cent, they are not haphazard, but systematic. This is true also of Kleiner's measurements, and of Fick's before him. Similarly, Grünbaum (1898) noted rather large deviations (12 to 14 per cent) at extremely high intensities, though he found Talbot's law to hold within about 1 per cent at ordinary illuminations. These deviations are undoubtedly significant, and may serve to give second order information about the visual process.

A completely different matter is the work of Parker and Patten (1912) which has been taken as contradicting Talbot's law. Parker and Patten found that two lights—one continuous and one intermittent—which had been made equal in brightness visually, gave different "energy" values when measured by a radiomicrometer, the intermittent light giving a reading about 5 per cent greater than the continuous.

In explanation of Parker and Patten's findings, it should be emphasized, as indeed Talbot himself emphasized it nearly one hundred years ago, that Talbot's law is a *physiological* generalization, not a physical one. A physical arrangement which will follow Talbot's law must be constructed in certain essentials like the eye and brain. A radiomicrometer is not such an arrangement because its response to light and its recovery are both slow in comparison to the frequency of flicker required by the eye for fusion. A photoelectric cell, which can follow faithfully the rapid alternation of light and dark, is a more likely instrument for recording the energy content of a beam of intermittent light.

Of Talbot's law for animals other than man, enough is known to make its general validity probable. Ewald (1913–14) found that the eye of *Daphnia* could not discriminate between continuous light whose intensity was reduced with a diaphragm and intermittent light reduced by a sector of corresponding magnitude. The same is stated by Patten (1914) to be true for the orientation to light of the blowfly larva. Ewald investigated only three discs, transmitting $\frac{1}{2}$, $\frac{1}{4}$, and 1/10 of the light, whereas Patten apparently used only one sector disc of unspecified aperture. Later measurements by Loeb and Northrop (1917) and by Northrop and Loeb (1923) showed that

barnacle larvae and *Limulus* follow Talbot's law in their phototropic behavior to light. In both cases Loeb and Northrop used only two sector openings: 90° and 144° with the barnacle larvae, and 90° and 180° with *Limulus*. Patten as well as Loeb and Northrop refer to their results as proving the Bunsen-Roscoe law; however, it is apparent, as Ewald (1913) has already pointed out, that they mean Talbot's law.

With *Daphnia*, Ewald had found that Talbot's law held only when the alternation of light and dark was greater than thirty times per second. At frequencies below thirty per second, the intermittent light became less or more effective depending on the particular reflex chosen for measurement. Apparently thirty cycles per second is the critical fusion frequency for *Daphnia* for the illuminations used. Below the critical fusion point other phenomena probably come in.

This is borne out by the work of Dolley (1923) and of Mast and Dolley (1924), who found with several species of insects that the effectiveness of interrupted light at low frequencies of interruption varies with the rate of flicker. At some middle rate the animals are stimulated more than at a higher or a lower flicker rate. These phenomena occur at rather low frequencies of interruption—between 12 and 20 per second, and are most likely below the point of fusion. A similar situation seems to occur in human vision when, as first found by Brücke (1864) and later confirmed by Exner (1870), an interrupted light *while it still appears flickering*, seems brighter than when it has fused. This phenomenon is therefore not strictly related to Talbot's law which deals only with illuminations interrupted with frequencies sufficiently above the fusion point to give a continuous visual effect.

II

Physiological Significance of Talbot's Law

Talbot realized that the law which has come to bear his name is a physiological generalization, and depends on the properties of the visual mechanism. Since little knowledge of retinal physiology was then available, he could not deduce such a relationship, and therefore stated that "its proof can rest upon experiment alone." He added that "by that it appears to be most satisfactorily established," a

statement in which we can concur as a result of the work just enumerated.

For us the validity of Talbot's law is important, because it can serve to define those kinetic aspects of the visual mechanism which are responsible for its validity. This was recognized by Fick (1863), who, it will be recalled, was so certain of the complexity of the visual process that he denied *a priori* the validity of Talbot's law. Exner (1870), being deterred by no such limitations, tried to derive from Talbot's law the curves for the rise and fall of the sensation produced by light. Because of the arbitrary nature of the details of these curves, they have been of only limited use. They are of importance, however, in indicating that the significance of Talbot's law as a tool for understanding the retinal processes was fully appreciated fifty years ago.

Our approach to Talbot's law is a different one from Fick's and Exner's. We shall try to do what Talbot, for complete lack of data, could not do, namely, to start with the known properties of the photosensory process and to derive Talbot's law from them.

In the course of the last few years the nature of the processes concerned with photoreception has received a certain clarification by the construction of tentative hypothetical systems dealing with the physical chemistry underlying the photosensory process (Hecht, 1931). If these hypothetical systems have more than *ad hoc* value, it should be possible to derive from them expressions for the effects of intermittent light, and in particular for the validity and limitations of Talbot's law.

The present paper records our work with the clam, *Mya arenaria.* We propose first to show how Talbot's law may be derived on purely theoretical grounds from the equations which have been previously found to describe measurements of different aspects of the photosensory behavior of *Mya*; and second, to present the details and measurements of our experiments made to test in two ways the validity of Talbot's law for *Mya.*

III

Theoretical Derivation of Talbot's Law

Many previous measurements have shown that the primary process in the photoreception of *Mya* behaves like a reversible photochemical reaction. It is supposed that a photosensitive substance S is decom-

posed by the light, and that the major decomposition products P and A by themselves or with the help of another substance or source of

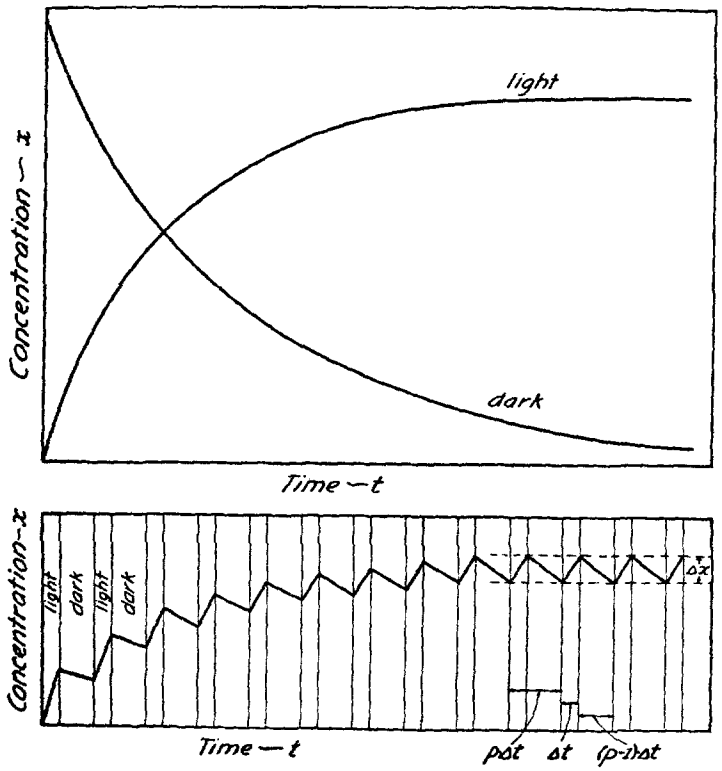

FIG. 1. Diagrammatic derivation of Talbot's law. The upper two curves represent the course of light adaptation and of dark adaptation. For *Mya*, dark adaptation is in reality many times slower than light adaptation. The two processes are made roughly alike in speed here purely for diagrammatic purposes, since the actual values do not enter into the derivation of Talbot's law as given in equations (1) to (9). In the lower part, the alternation of light and dark periods is such that the light period is given by the small time Δt, the total cycle of light and dark periods by $p\Delta t$, and the dark period by $(p\text{-}1)\Delta t$. The jagged line is constructed from the two upper curves of light and dark adaptation by drawing for each light and dark period that portion of the upper curve which corresponds to the particular value of the ordinate x which the jagged line reaches at each light and dark period. The fluctuation in concentration, Δx, at the final period of the stationary state is to be considered quite small in relation to the concentration x.

energy reunite to form S by means of an ordinary dark reaction. The reaction as a whole is a reversible one, possibly completely, but more likely only pseudoreversible.

Consider then the kinetics of such a photochemical reaction $S \rightleftarrows P+A$. Let a be the initial concentration of S in the dark. The system is exposed to light whose intensity is I. Let x be the concentration of S which has been transformed to form a corresponding concentration of P and A. The amount of S remaining is $a-x$. The velocity of decomposition of S is then

$$\frac{dx}{dt} = k_1 I(a - x) - k_2 x^2 \tag{1}$$

where k_2 is the velocity constant of the dark reaction and k_1 is the velocity constant of the photochemical reaction proper and already includes the absorption coefficient of the sensitive material S (Hecht, 1924). That the "dark" effect must be included in a description of the light effect was apparently first recognized by Exner (1870). The course of this light reaction is shown in Fig. 1. If the light is permitted to shine indefinitely, it will induce a stationary state in which the concentrations of S, P, and A remain constant since $dx/dt = 0$. Equation (1) becomes then

$$\frac{k_1}{k_2} I = \frac{x^2}{a - x} \tag{2}$$

the familiar expression for the stationary state.

Corresponding to any value of I in equation (2) there is a given concentration of x. Thus a reduction of the intensity to I/p by some purely physical means such as a diaphragm or a filter will yield

$$\frac{k_1}{k_2} \cdot \frac{I}{p} = \frac{x_p^2}{a - x_p} \tag{3}$$

which describes a specific value of x in equation (2) as determined by I/p.

What effect will there be on this photochemical system when we reduce not the intensity, but the time during which the intensity acts, by means of a sector disc? The system is now subjected to alternating periods of illumination by intensity I and of darkness. Fig. 1 will

help in describing what happens. During the light period the velocity of the process will follow equation (1) and the concentration x will increase; while during the dark period, only the "dark" reaction, whose velocity is given by

$$\frac{dx}{dt} = k_2 x^2 \tag{4}$$

will proceed. This is essentially a short period of dark adaptation during which x will decrease. If the alternation of light and dark periods is maintained, a pseudostationary state is reached in which the dark recovery becomes equal to the light effect, and x fluctuates equally above and below a mean value. With rapid alternation of light and dark periods the rise and fall in concentration x becomes small until, when flicker disappears, the change in concentration of x, which we may now call Δx, becomes too small to be effective in producing a change in the sensation of brightness.

Fig. 1 makes the matter clear. The vertical distance is Δx and is to be considered as very small. Let the light period be Δt, a short interval of time, and let the dark period be $(p-1)\,\Delta t$. The total time of a cycle of light and dark exposures is $p\Delta t$ and $1/p$ is the fraction of the total exposure time occupied by the light exposure alone. During the short time Δt the velocity of the light reaction will be

$$\frac{\Delta x}{\Delta t} = k_1 I(a - x) - k_2 x^2 \tag{5}$$

whereas the velocity of the dark reaction during the short time $(p-1)$ Δt will be

$$\frac{\Delta x}{(p - 1)\,\Delta t} = k_2 x^2 \tag{6}$$

since as much recovery must take place during the dark as decomposition in the light. Equation (6) may be transformed into

$$\frac{\Delta x}{\Delta t} = (p - 1) k_2 x^2 \tag{7}$$

which can now be equated to (5). This relation is

$$k_1 I(a - x) - k_2 x^2 = (p - 1) k_2 x^2 \tag{8}$$

which on combination of terms and solving, becomes

$$\frac{k_1}{k_2} \cdot \frac{I}{p} = \frac{x^2}{a - x} \tag{9}$$

an equation identical with (3). In other words, a reduction to a given fraction $1/p$ in the time of action of a light by alternating it rapidly with periods of darkness is exactly equivalent to a reduction to the same fraction of the intensity of a continuously acting light. This is Talbot's law, which has now been derived from previous work with *Mya* without the addition of any new information or assumptions.

A word of caution may be added here with regard to the meaning of the equations and symbols used in this derivation and in previous work with *Mya*, and indeed with the human eye as well. We have referred to substances S, P, A, and to their concentrations a and x. If it pleases any one better, these may be considered as the various levels or intensities of the rise and fall of the "excitatory" process; the quantitative relationships will maintain their validity, though no picture will be available for the mechanism.

Indeed one need refer neither to a photochemical reaction nor to an "excitatory" process, but to the original measurements of light and dark adaptation. It is found by direct measurement that dark adaptation follows a certain course, and may be described quite empirically by an expression like equation (4) in which x refers to measurements of reaction time, or of intensity thresholds. Similarly the course of light adaptation may be measured, but not so directly. Its kinetics may be described in terms of equation (1) in which here again x will be some function of the measured values of the reaction time or of the threshold intensities. The remaining algebraic manipulations follow exactly as before, and the result is that in terms of measurements of light and dark adaptation one may predict the validity of Talbot's law. We ourselves prefer to interpret the equations in terms of a photochemical system, purely for the convenience in thinking concretely about the receptor process.

A similar situation concerns the precise meaning of the value Δx. We have described it here as that fluctuation in concentration x which becomes too small to be effective in producing a sensory change in intensity reception. It is not possible at present to say whether this

corresponds to a non-effective fluctuation in the frequency of impulses which pass over the nerve fiber from the sense cell, or whether it corresponds to that value of the intensity fluctuation which will fail to elicit a change in the number of elements functional in the sensory layer. It may mean any of these three aspects of the matter—concentration, frequency, or number—or all of them, or perhaps some other, still unknown aspect of the sensory process. The derivation of Talbot's law as here given remains unaffected.

IV

Nature of Measurements

Having deduced Talbot's law for the photosensory behavior of *Mya*, we then devised two series of experiments for testing this deduction. The first series was made with seven discs having openings ranging from 2 per cent to 100 per cent of the disc. For each disc the intensity of light was computed which, when combined with the rapidly rotating disc, will furnish a given amount of energy. The light from each combination now appears the same to the human eye, and is indistinguishable from a continuous light delivering the same energy over the same period of time. If Talbot's law holds for *Mya*, the photosensory behavior of an animal exposed to such lights should always be the same regardless of the combination of light and sector opening producing the illumination, and should also be indistinguishable from its behavior to a continuous light of corresponding energy content. This was found to be true.

In the second series of measurements the same discs were used with a constant outside intensity so as to produce a series of beams differing in energy content. Each beam of interrupted light was matched in energy content by a beam of continuous light, and the photosensory effect of the two groups of lights were compared. The results showed that, judged by its photosensory behavior, *Mya* could not distinguish between intermittent light and continuous light of the same energy content.

The particular aspect of the photosensory behavior of *Mya* which we used in these experiments is the capacity of *Mya* for intensity discrimination. It has been shown (Hecht, 1923) that the clam, when exposed to sustained illumination, at first responds by contracting its

siphons, and then rapidly comes into sensory equilibrium with the light. This is of course the process of light adaptation. To produce another contraction of *Mya's* siphons, the light must be suddenly augmented. The reaction time to this added illumination depends on the intensity of the adapting light and on the intensity of the added (or stimulating) light. With a constant stimulating intensity the reaction time increases in a specific way as the adapting intensity increases. Our purpose then was to compare the reaction time of *Mya* to a stimulating light of constant intensity after it had been adapted for some time to an illumination of given energy content furnished on the one hand by intermittent light secured by a variety of sectors and on the other hand by continuous light.

V

Apparatus and Calibrations

The measurements were made at the Marine Biological Laboratory, Woods Hole, Massachusetts, during the summer of 1928. The experimental arrangements may be made out by means of Fig. 2. We used two dark rooms separated by a wall, and communicating through an opening in the wall. In dark room A were placed the adapting light, its metal housing, the motor, the sector discs, as well as various screens for keeping all but the direct light of the lamp from entering the second dark room B through the opening in the wall. The second dark room contained a long, solidly mounted, black table on which there was a board about 30 cm. square which could be moved along the table and placed in any position on it. On this black painted board there were marked cross-lines as shown in Fig. 2 which indicated the exact position and direction for the placing of the siphon of an animal in a rectangular glass dish. About 20 cm. away and in the position indicated in Fig. 2 there was mounted on the board a 100 watt, concentrated-filament lamp in a light-tight container with an opening 3 cm. square facing the animal This was the stimulating light. A shutter in front of the opening served to expose the animal to the stimulating light at the proper time and with proper precision, the light having been first turned on by a switch.

The sector discs were made of aluminum 2 mm. thick and 200 mm. in diameter. Each disc had two sector openings 180° apart. The

discs were painted dead black. Each disc could in its turn be mounted directly on the shaft of the motor which was rotated at a speed of 4000 R. P. M. Thus during the experiments there were approximately 130 cycles of light and dark flashes per second, a rate well above any recorded value of the critical frequency for fusion at the highest brightness for the human eye.

In view of the complete validity of Talbot's law for the eye we calibrated the sector openings photometrically. The diffusely reflecting plate of a Macbeth illuminometer was placed in the position of the animal, and at 45° to the direction of the beam of light. The

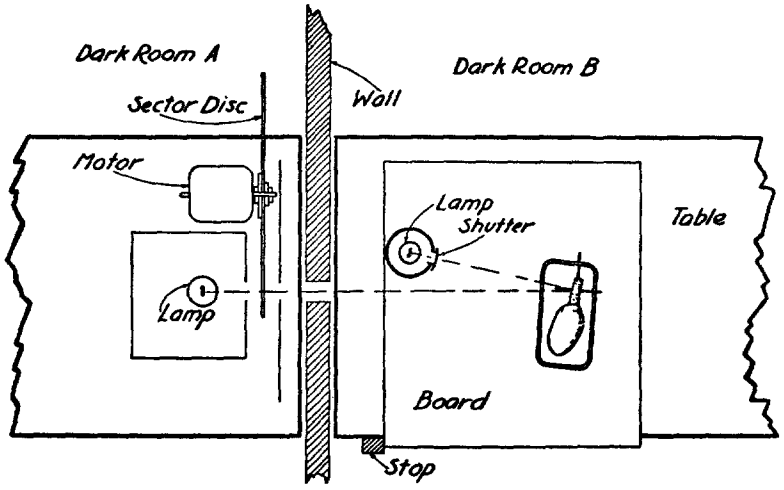

FIG. 2. Arrangement of apparatus.

light was a 400 watt, concentrated-filament lamp, and was run on 110 volts direct current; the current was kept constant with a rheostat and an ammeter. The Macbeth illuminometer itself was securely clamped at right angles to the beam of light so as to view the center of the illuminated diffusing plate. With everything clamped in position we made three separate series of calibrations of the brightness of the plate in the direct light of the adapting lamp, and with the various sector discs in operation. We each made ten readings of the brightness for each sector disc. The results of the three series agreed satisfactorily; we have therefore averaged them. The transmissions of the sector discs given in Table I are thus the averages of 60 readings each.

In order to make up combinations of sector disc and intensity so as to yield a given value of energy with which to adapt *Mya*, we needed a variable intensity. This we wished to secure by placing the board, on which rested the animal and the stimulating light, at different

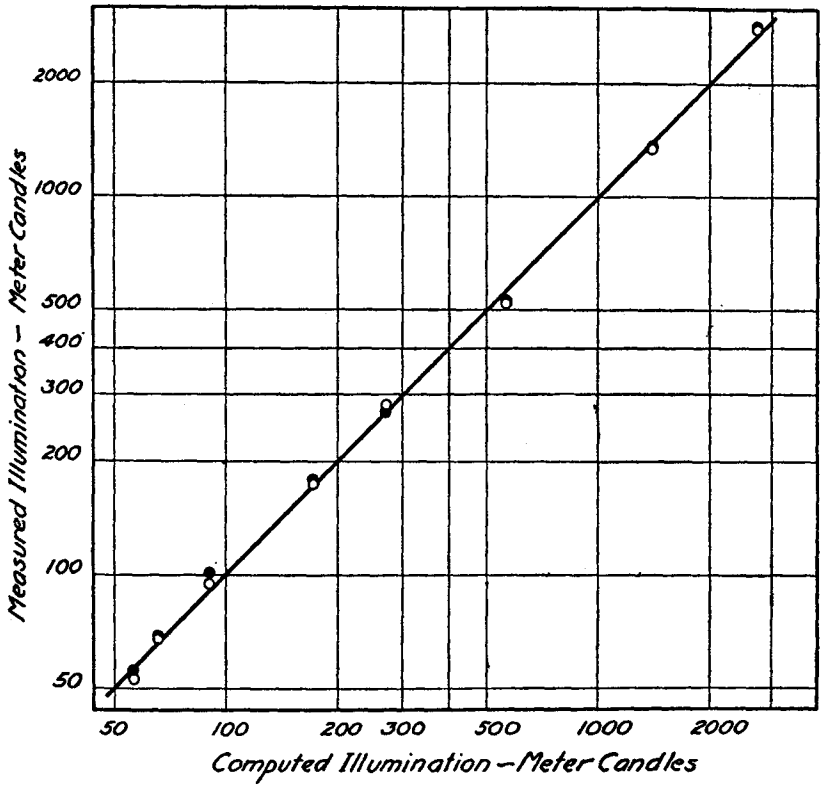

FIG. 3. Relation between illumination and distance from the adapting lamp. The ordinates are the measured values for H (open circles) and for W (solid circles) whereas the abscissas are computed from the inverse square of the distance. The coordinates are logarithmic, the better to show up the errors at low intensities.

distances from the adapting light in the next room. Using the same Macbeth illuminometer, the same 400 watt lamp, and the same diffusing plate in the same position on the board as before, we determined the brightness of the diffusing plate at different distances from the lamp.

In making these measurements we had no idea other than to construct a calibration curve relating distance from the lamp along the table and resulting intensity of illumination. In computing the measurements we found that under the circumstances (a concentrated filament lamp, and complete screening of extraneous and reflected light) the data followed the inverse square law well within the limits of our photometric error. This is not unexpected in view of the thorough test to which Hyde (1906) has subjected the inverse square law for other than point sources. However, since the statement is so frequently made that the inverse square law does not apply, we give our measurements in Fig. 3. The figure shows a comparison between our values and those computed in terms of the inverse square ratio. Each point is the average of ten readings. The data are plotted on a logarithmic grid the better to show the errors at low illuminations.

VI

Measurements with Constant Adaptation Secured in a Variety of Ways

For the first series of measurements we used an adapting intensity of 55 meter candles. From our calibrations we computed for each sector disc the distance from the 400 watt lamp at which the clam must be placed on the table in order for the disc and the light to furnish this illumination. The combination of distances and sectors are to be found in Table I. This set-up now enables us to place an animal in such a position with each sector that the illumination on it is constant even though secured by different intensities and different ratios of light and dark exposures. To accomplish such a procedure easily and securely we fixed a series of wooden blocks on the edge of the table, so arranged that the movable board containing the stimulating light and the animal fitted against them by means of an overhang of the board which slid along the edge of the table. In this way the board could be repeatedly placed accurately in any position in a few seconds.

The procedure in this series of measurements was of the following nature. The board was placed in a given position, the corresponding sector disc was attached to the motor and the motor started. The adapting light was turned on and an animal placed in the proper spot on the board. The animal remained exposed to this adapting illu-

mination for 5 minutes. At 5 minute intervals its reaction time was measured three times to the stimulating light which had an intensity of 2250 meter candles. The animal was then placed in the dark for half an hour. After this it was exposed to the same adapting illumination as before, but secured by a different combination of distance and sector disc. It was given 5 minutes adaptation and three more readings of its reaction time to the same stimulating light as before were made.

TABLE I

Reaction time of ten animals to a stimulating light of 2250 meter candles after adaptation to 55 meter candles obtained either by continuous illumination or by intermittent illumination furnished by seven different combinations of rotating sector openings and distances from the light.

Sectored disc	Calibrated transmission of sector	Distance of animal from lamp	Relative reaction time										
			Animal No.										Average
			I-1	I-3	I-5	I-8	I-9	I-10	I-11	I-12	I-13	I-14	
	per cent	*cm.*											
I	2.19	51.5	1.00	1.06	1.01	0.96	1.10	0.98	0.96	1.01	1.01	0.94	1.00
II	4.38	72.8	1.00	0.96	1.03	1.04	0.96	1.05	1.09	1.03	0.97	1.04	1.02
III	10.69	113.7	0.98	1.00	1.01	1.06	0.91	0.91	0.96	0.98	0.93	0.98	0.97
IV	19.83	154.8	1.02	1.05	0.92	0.99	0.91	0.95	1.04	1.07	0.99	0.90	0.98
V	25.00	173.8	1.02	1.01	0.94	1.01	0.98	1.05	0.98	1.01	1.01	1.03	1.00
VI	51.80	250.2	1.00	0.96	1.03	0.99	1.00	1.00	0.98	0.98	1.05	0.97	1.00
VII	76.54	304.2	1.00	1.03	1.03	1.01	1.05	1.02	1.01	0.98	0.99	1.03	1.02
No disc	100.00	347.7	1.00	0.92	1.05	0.94	1.10	1.05	1.01	0.98	1.05	1.00	1.01
Actual average reaction time in seconds...			1.30	1.98	1.88	1.35	1.43	1.50	1.56	1.19	1.75	1.67	

Our experience has shown us that 5 minutes light adaptation is adequate. The adapting light was kept on, of course, all the time during and between the measurements of the reaction time, so that when the last reaction time was measured for each combination of disc and distance the animal had been adapting for 15 minutes. No difference in reaction time was found between the first and the last readings.

Continuing in this way, the seven combinations of distance and sector disc were run through with an individual animal. Somewhere in the series we also adapted the animal to continuous light of the

same brightness and measured the reaction time three times at 5 minute intervals. To make these eight sets of measurements with a single animal required a day.

We measured ten animals in this way. The data secured are given in Table I. For simplicity in presenting the data we give at the bottom of the table for each animal its average reaction time for all the measurements; that is the average of twenty-four readings. This value is then put at 1.00, and for each combination of disc and intensity the corresponding reaction time (average of three readings) is given as a fraction of the average value. In this way all the animals are immediately comparable.

Since the reaction time depends upon the adapting intensity, then, if Talbot's law holds, the reaction time to these eight adapting combinations of sector and distance should be identical. If not, they should show some systematic variation relating them to the size of the sector opening or to the impinging intensity. Table I shows that for each animal the reaction time varies in no specific way; and that its general variation is of the order expected in these measurements.

This can be seen by comparing the measurements for a given animal in a vertical column with the measurements for the different animals in a horizontal column. The averages of the ten animals for each combination of sector and intensity never differ more than 3 per cent from the mean of all the readings, and most of them differ by less. The average difference from the mean is 1.2 per cent, which is well below our photometric error using the present apparatus. Therefore, this series of experiments indicates that for the clam Talbot's law is valid, and that the clam does not distinguish between a continuous and an intermittent illumination of the same brightness.

VII

Measurements with Different Adaptation Intensities

After completing the measurements just recorded, we considered it too precarious to rest a conclusion on a single intensity, even though it was secured in eight different ways. Our previous work (Hecht, 1923) has shown that the relation between adapting intensity and reaction time is sigmoid, and possesses a fairly flat portion in which the

reaction time changes very slowly with the adapting intensity. It seemed possible that the particular intensity which we investigated might lie in this region,—in which case measurements of the reaction time are not delicate enough to show up slight differences in intensity. This, in fact, is precisely the case, as Fig. 4 shows. However, the relation between adapting intensity and the reaction time to a constant stimulating light also has two very steep portions. In these portions

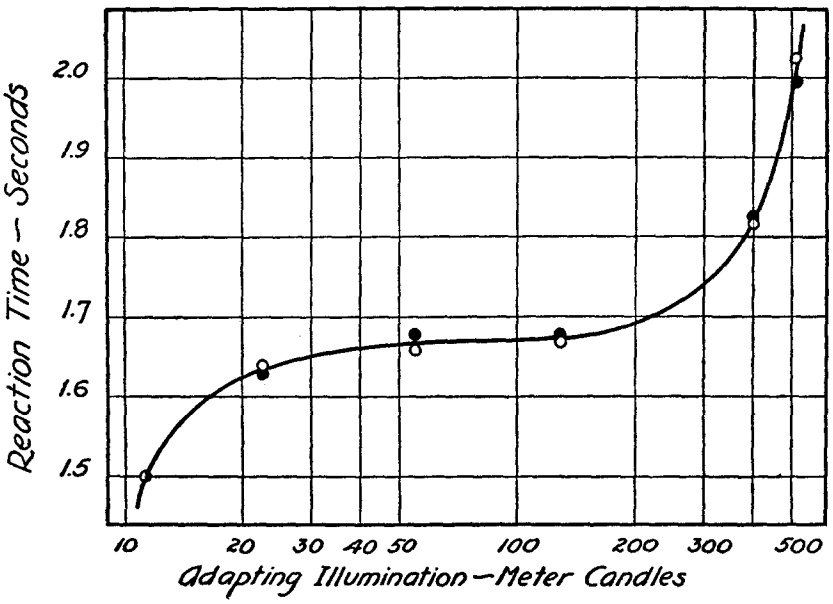

FIG. 4. Relation between adapting intensity and reaction time to a constant stimulating light. The open circles are for adaptation to continuous light, whereas the solid circles are for adaptation to intermittent light. The two produce the same results.

the reaction time is a very delicate measure of the intensity. We therefore decided to investigate the relationship over a sufficiently wide range of adapting intensities to bring out the phenomenon as a whole, including the two very steep, and for our purposes, critically valid sections.

The second series of measurements was made with a variety of adapting intensities. Each adapting intensity was secured in two

ways—by continuous illumination and by intermittent illumination—and the reaction time to a constant stimulating light measured for each. We used the same discs as before, but instead of a 400 watt lamp, we used a 100 watt lamp for the adapting source; the stimulating light remained the same, and gave an illumination of 2250 meter candles.

The measurements were made as follows. For intermittent light the board was always in one position, at 51.5 cm. from the light. A sector disc was placed on the motor and the motor put in action. An

TABLE II

Reaction time of six animals to a stimulating light of 2250 meter candles after adaptation to a series of illumination intensities secured by continuous light and by intermittent light. (I = intermittent; C = continuous).

Intensity in meter candles	Reaction time in seconds													
	Animal No.												Average	
	II-3		II-4		II-5		II-6		II-7		II-8			
	I	C	I	C	I	C	I	C	I	C	I	C	I	C
11.29	1.60	1.57	1.50	1.43	1.57	1.57	1.53	1.60	1.53	1.53	1.27	1.30	1.50	1.50
22.58	1.73	1.70	1.57	1.77	1.77	1.70	1.67	1.63	1.70	1.67	1.33	1.37	1.63	1.64
55.11	1.80	1.80	1.77	1.70	1.70	1.67	1.70	1.67	1.67	1.67	1.47	1.43	1.68	1.66
128.9	1.90	1.87	1.77	1.73			1.67	1.67	1.67	1.63	1.40	1.43	1.68	1.67
394.6	1.97	2.00	1.87	1.83	1.83	1.87	1.80	1.87	1.93	1.83	1.60	1.50	1.83	1.82
515.5	2.00	2.23	1.97	2.00	2.17	2.20	1.97	1.90	2.00	2.03	1.87	1.83	2.00	2.03

animal was then exposed to the resulting illumination for 5 minutes adaptation, and its reaction time taken three times at 5 minute intervals as before. It was then given 15 minutes in the dark. After this, the board was moved to such a distance from the light that the animal would receive the same illumination with continuous light as it had previously had with intermittent. It was given 5 minutes adaptation, and its reaction time to the same stimulating light as before was measured three times at 5 minute intervals. It was then given 15 minutes in the dark. The board was then replaced in its previous position, a new disc placed on the motor, and the animal exposed for adaptation to the light from a new disc and 100 watt

lamp for 5 minutes. Its reaction time was then measured three times as before. Continuing in this way the animal was adapted to a series of different intensities, each paired so as to be continuous or intermittent. In each case its reaction time was measured in the usual way, three times at 5 minute intervals.

For this series of measurements, we used only six discs so that with each animal there were made twelve groups of three reaction time measurements. It was possible in this way to do one animal a day.

The results are in Table II which gives the average reaction time for each of six animals to light of 2250 meter candles when the animal has been adapted to a series of five intensities produced by intermittent light and by continuous light. For the highest illumination, we measured the reaction time of the animal adapted to continuous light two times: once with the motor running as in the case of intermittent illumination but with no sector disc attached, and once with the motor quiet as was usual with continuous light. This served as a check on the adequacy of the measurements. It is apparent from comparison of the reaction time of the animals after adaptation to intermittent illumination and after adaptation to continuous illumination that there is no difference in the reaction time of the animals under the two conditions. This is brought out by the average of the six animals shown in the last two columns of the table. The largest difference happens to be between the readings made under the identical condition of adaptation to continuous illumination except that the motor was running in one series and not running in the other.

The results are shown graphically in Fig. 4, and it is apparent that the reaction time in the two cases follows exactly the same relationship to the adapting intensity regardless of whether it is an intermittent or a continuous illumination. This is particularly the case in the two rapidly changing portions of the curve, where any slight difference between the two would at once become evident.

We may then conclude from these two series of measurements that as predicted from purely theoretical considerations of its dark and light adaptation, *Mya* cannot distinguish between intermittent and continuous illumination of the same visual brightness. It is therefore shown to obey Talbot's law within the limits of error of these measurements.

SUMMARY

On the basis of previous knowledge of the photosensory behavior of *Mya* it is shown that Talbot's law for the effectiveness of stimulation by intermittent illumination should be valid. Two series of measurements are reported in which the photosensory effects of intermittent and continuous illuminations are compared. The results demonstrate the validity of Talbot's law for *Mya*.

BIBLIOGRAPHY

Aubert, H., Physiologie der Netzhaut, Breslau, E. Morgenstern, 1865.

Brücke, E., Über den Nutzeffect intermittirender Netzhautreizungen, *Sitzungsber. k. Akad. Wissensch., Math.-naturw. Cl., Wien, Abt. 2*, 1864, **49**, 128.

Dolley, W. L., Jr., The relative stimulating efficiency of continuous and intermittent light in the tachina fly, *Archytas aterrima*, *Am. J. Physiol.*, 1923, **64**, 364.

Ewald, W. F., The applicability of the photochemical energy-law to light reactions in animals, *Science*, 1913, **38**, 236.

Ewald, W. F., Versuche zur Analyse der Licht- und Farbenreaktionen eines Wirbellosen (*Daphnia pulex*), *Z. Sinnesphysiol.*, 1913–14, **48**, 285.

Exner, S., Bemerkungen über intermittirende Netzhautreizung. *Arch. ges. Physiol.*, 1870, **3**, 214.

Ferry, E. S., The use of the rotating sectored disc in photometry, *Phys. Rev.*, 1893, **1**, 338.

Fick, A., Ueber den zeitlichen Verlauf der Erregung in der Netzhaut, *Arch. Anat. u. Physiol.*, 1863, 739.

Grünbaum, O. F. F., On intermittent stimulation of the retina. Part II, *J. Physiol.*, 1897–98, **22**, 433.

Hecht, S., Sensory adaptation and the stationary state, *J. Gen. Physiol.*, 1923, **5**, 555.

Hecht, S., Photochemistry of visual purple. III. The relation between the intensity of light and the rate of bleaching of visual purple, *J. Gen. Physiol.*, 1924, **6**, 84.

Hecht, S., Die physikalische Chemie und die Physiologie des Sehaktes, *Ergebn. Physiol.*, 1931, **31**, 243.

Helmholtz, H., Handbuch der physiologischen Optik, Hamburg and Leipsic, Leopold Voss, 1865.

Hyde, E. P., Talbot's law as applied to the rotating sectored disc, *Bull. Bureau Standards*, 1906, **2**, 1.

Kleiner, A., Physiologisch-optische Beobachtungen, *Arch. ges. Physiol.*, 1878, **18**, 542.

Kohlrausch, A., Tagessehen, Dämmersehen, Adaptation, in Bethe, A., von Bergman, G., Embden, G., Ellinger, A., Handbuch der normalen und pathologischen Physiologie, Berlin, Julius Springer, 1931, **12,** pt. 2, 1499.

Loeb, J., and Northrop, J. H., Heliotropic animals as photometers on the basis of the validity of the Bunsen-Roscoe law for heliotropic reactions, *Proc. Nat. Acad. Sci.*, 1917, **3,** 539.

Lummer, O., and Brodhun, E., Photometrische Untersuchungen. VI. Verwendung des Talbot'schen Gesetzes in der Photometrie, *Z. Instrumentkunde*, 1896, **16,** 299.

Mast, S. O., and Dolley, W. L., Jr., The relation between the stimulating efficiency of intermittent light and the length of the light and the dark periods, *Am. J. Physiol.*, 1924, **71,** 163.

Northrop, J. H., and Loeb, J., The photochemical basis of animal heliotropism, *J. Gen. Physiol.*, 1923, **5,** 581.

Parker, G. H., and Patten, B. M., The physiological effect of intermittent and of continuous lights of equal intensities, *Am. J. Physiol.*, 1912, **31,** 22.

Patten, B. M., A quantitative determination of the orienting reaction of the blowfly larva (*Calliphora erythrocephala* Meigen). *J. Exp. Zool.*, 1914, **17,** 213.

Plateau, J., Sur un principe de photometrie, *Bull. Acad. roy. sci.* (*Belgique*), 1835, **2,** 52.

Talbot, H. F., Experiments on light, *Phil. Mag.*, [3], 1834, **5,** 321.

Wiedemann, E., and Messerschmidt, J. B., Ueber Fluorescenz und Phosphorescenz. II. Abhandlung. Gültigkeit des Talbot'schen Gesetzes, *Ann. Phys. u. Chem.*, 1888, **34,** 463.