THE NATURE OF FOVEAL DARK ADAPTATION.*

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I.

In a previous paper (Hecht, 1919-20, c) on the dark adaptation of the human eye, I attempted an analysis of the existing data on peripheral dark adaptation for the purpose of securing some hint of the physicochemical basis of visual reception. Early in the course of that analysis it became apparent that, aside from the deficiencies in the data themselves, there were lacking some rather elementary concepts on which to rest an objective treatment of the data. For example, there existed no notion of the relation between the intensity of the stimulating light and its photochemical effect in the retina. Moreover, it had apparently never been deemed necessary to entertain any ideas with regard to a mechanism with which to link up the variations in the sensitivity of the retina at different times.

Clear concepts of at least these two matters lie at the foundation of any attempt toward a rationally objective interpretation of the sensory behavior of the eye. It became necessary, therefore, to supply these defects in terms of what had fortunately been found in the studies of the photosensory responses of certain invertebrates (Hecht, 1921, e). As a result of these assumptions it was possible to analyze the data of dark adaptation of the eye, and to account for the phenomenon in terms of a comparatively simple photochemical mechanism.

The analysis was made on the best available data. These data were concerned with the periphery of the eye only. This condition

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proved to be of advantage, because it opened the possibility of connecting the findings with what is known of the properties of visual purple. Moreover, the conclusions which were secured pointed to certain crucial experiments to be made with visual purple, thus suggesting a new mode of attack in this line of work (Hecht, 1920-21, d).

However, as far as the eye as a whole is concerned, the analysis was incomplete, because it did not include the properties of the fovea. Although the fovea is essentially an instrument for bright vision, and general dark adaptation, a phenomenon of dim vision, it still seems desirable to find out what occurs in the fovea during a stay in the dark. A study of the published data\(^1\) shows that they are to a large extent insufficient and inconsistent, and that they involve some fundamental sources of error. It has therefore become necessary to investigate the matter from the beginning from a new point of view and with a new type of apparatus. I have done this, and the results show in a gratifying fashion that it was worth while. Not only has it been possible to find the facts and regularities, but it has been possible to account for the discrepancies of the results of other workers.

II.

1. There are three major and several minor sources of error which enter into a study of dark adaptation. With but few exceptions previous work on foveal adaptation has been done without much consideration of the major sources, and with but scant attention to the minor ones. It is necessary to consider these possibilities of error carefully.

Measurements of the course of dark adaptation presume an original condition of light adaptation. It would seem obvious that this must be kept constant if the measurements are to have any significance. Still, this necessary starting point has been consistently disregarded, even when its significance has been recognized. We find that light adaptation is secured by such irregular means as reading in a room (cf. Dittler and Koike, 1912) or walking in the street (cf. Nagel and Schaefer, 1904). In some cases it is noted whether the day is cloudy or bright, but no account is taken of the circumstance.

\(^1\)A review of the literature will be found in the papers by Tschermak (1902), Wölfflin (1910), and Dittler and Koike (1912).
A second source of error involves the change from light adaptation to darkness. It is again almost obvious that this change must be clean cut and accurately timed. In almost all of the previously published data this transition has involved the walking or running of the subject from the light-adapting location to the dark room. It follows that no measurements can be made during the variable interval of running or walking. Even if such measurements were possible, they would be of little significance for a study of the process, because one could not tell when dark adaptation actually began.

The third source of error involves the movements of the iris. At least two distinct things happen when a light-adapted eye is removed to darkness: the pupil dilates and the retina increases in sensitivity. In order that the data may be made to mean something, it is necessary to isolate the separate effects of these two factors.

The means which I used to study foveal adaptation have taken into account all these three sources of error. In addition I have considered certain precautions to limit the measurements to the foveal region. The entire procedure takes place in a large dark room. A constant condition of light adaptation is secured by having the subject look from a fixed distance at a brightly illuminated screen for a given interval. The change from bright illumination to complete darkness is made by shutting off the artificial source of illumination. The result is a clean cut transition. Simultaneously with this change, the subject is not even required to leave his seat. He merely raises his head 5 cm. when the lights are turned off, and is at once ready for measurement.

In the preliminary experiments I attempted to take care of the changes in the iris by the use of an artificial pupil. For several reasons I abandoned this method. First, it was rather clumsy, and proved to be a stumbling block in the accomplishment of a rapid change from the position of light adaptation to that in which the measurements were made. Second, the recent excellent experiments of Reeves (1918) made it possible to correct for pupil variation. And third, in consequence of the feasibility of this correction, it seemed desirable to secure the gross results. This would enable one to make comparisons with previous investigations, and would also give a correct notion of the total change in the eye as a whole, which is itself of some interest.
In order to confine the experiments to central vision, I utilized its characteristic perception of form and color. The object to be looked at was a red cross. The form was secured by a cross-shaped opening of such size that when looked at directly its image fell well within the rod-free area of the macula. The color was secured by a red filter. The measurements were determinations of the minimum illumination at which the subject could clearly see the object both as a cross and as a red one.

2. The essential parts of the assembled apparatus are given in Fig. 1, which shows three views of the arrangements. The screen for light adaptation is marked $N$. It is a closely woven linen screen similar to those used for white window shades. It is illuminated from behind by two Mazda lamps, $L$, 150 watts and 115 volts, backed by polished reflectors, and set 60 cm. from the screen. The switch for turning the lights on and off is in the hands of the experimenter. The subject looks at the region of the screen lying between the two lights; that is, between the two dashed circles in the front view of Fig. 1. The brightness of this field is 90 millilamberts, which is equivalent to an illumination of 0.028 candles per square centimeter of screen.

The construction of the apparatus for measuring the minimum intensity at which the red cross becomes visible is shown in partial section in the side view of Fig. 1. At $C$ there is a sheet of opal glass. In contact with it, on the side facing the observer, is a Wratten Filter No. 70. This limits the transmission to the rays beyond 650 μm, and thus insures the participation of the cones only. In front of the filter there is the opening already referred to. It is a cross-shaped opening in an opaque piece of cardboard. It is 24 mm. in diameter, each arm of the cross being 8 × 8 mm. The area of the cross is thus 320 sq.mm. The observer's eyes are placed next to the opening in the viewing box, above $P$. The appearance of this opening is seen in the front view. The distance from the eye to the cross is 55 cm. The cross therefore gives an image 0.65 mm. in diameter, which is about two-thirds the diameter of the rod-free area.

The illumination of the red cross is secured by means of a small microscope lamp situated in a lamp house, and properly surrounded by black screens. It is a 15 watt, 115 volt, concentrated filament, Mazda lamp, and may be considered as a point source for our purposes.
It rests on a movable carriage which rides freely along the bottom of the long rectangular blackened box shown in the figure. The carriage is only slightly narrower than the box, so that a proper and continuous centering of the lamp is insured. The light from the lamp falls on the opal glass, which diffuses it. It then passes through the filter,

and goes to the eye. The illumination through the red cross may be varied by changing the distance of the lamp from the diffusing plate of opal glass. The intensity of the illumination emitted by the red cross is measured for a given position of the lamp, and the intensity at any other position calculated on the inverse square law. In these
experiments the lamp was always farther than 30 cm. from the opal glass; in this way a uniform illumination of the cross was assured.

The wires for the lamp run through a brass tube. This is rigidly set in the lamp carriage, and projects through a slit in the upper wall of the blackened box. The brass tube then turns a sharp right angle, and lies about a millimeter above the top of the box perpendicular to the long axis of the box, as shown in the top view of Fig. 1. Because of the rigidity of the construction, the lamp carriage can be easily moved by pushing on the outside arm of the brass tube. Moreover, the location of the lamp is in this way indicated by the position of the horizontal brass arm. An exact record of this position is made in the dark by running a pencil along the edge of the arm, and making a mark on the long strip of paper \( R \) which is stretched along the top of the box beneath the brass arm. The position of the brass arm indicative of a given location of the lamp is carefully measured. Its subsequent locations may then be read off with a meter stick from the established zero point.

The lamp is controlled by the experimenter by means of a noiseless switch \( W \) attached to the edge of the protruding brass arm.

III.

The actual manner of making a series of measurements deserves some attention. With each subject I spent a preliminary period of about 30 minutes explaining the nature of the experiments and the construction of the apparatus. Aside from putting the subject into an interested frame of mind, this preliminary period serves as an experimental precaution. It allows time for the effects of the outside light, which is variable, to disappear. The starting point is therefore the same for all the experiments.

The subject is seated in a comfortable chair, the height of which is so adjusted that the eyes of the particular subject can look comfortably into the opening of the viewing box \( B \). He then lowers his head, rests his forehead against the edge \( P \) of the box, and looks at the light-adapting screen. The subject keeps himself in a relaxed condition. To facilitate this, the chair is so placed as to give full support to the subject's back. Also, the edges of the viewing box are padded with black felt. 5 minutes are allowed for light
adaptation. Measurements made with regard to this point show that the process is accomplished in much less time (cf. Lohmann, 1906), but this interval is chosen to cover all contingencies. Near the end of the time the subject is given notice, and at the proper moment, the experimenter turns out the bright lights. The subject raises his head at once, and looks into the viewing box.

A few preliminary experiments showed at once that the rate of dark adaptation of the fovea is exceedingly rapid during the first minute of darkness. To make frequent and rapid measurements during this short interval is out of the question. Aside from the technical difficulties, there is the fact that repeated tests of the visual threshold must disturb the process of adaptation. The failure to appreciate this source of error has vitiated many of the experiments of Piper (1903) on peripheral adaptation, and nearly all of the results of Wölflin (1910) on foveal adaptation. An ideal method would be to make but one reading following each light adaptation. This however would weary the subject, even if it did not fatigue the eye, which is not at all certain. The method finally adopted is a compromise between these two extremes.

Only one eye is used at a time in making the measurements. The eye to be used is under the control of the experimenter, who determines it by moving a slide \( D \) near the ocular end of the viewing box (Fig. 1). The subject acts as if he were looking with both eyes. Indeed, many of the subjects were unaware of which eye they were using, or that they were using only one eye; a few were able to distinguish them easily.

Before the bright lights are turned off, the small lamp is set at a given distance from the opal glass. When the lights are turned off, the subject looks in and announces the moment he sees the red cross. The time is taken by the experimenter with a stop-watch. The bright lights are turned on, the subject becomes light-adapted again, and the process is repeated with the other eye; this time the light has been placed nearer or farther depending upon the time it took the subject to see the cross. In this way after three or four trials the distance is determined at which the subject can see the red cross almost as soon as he looks into the box, immediately after the room has been darkened. The rate of dark adaptation at the beginning is so rapid
that it is impossible to measure this point accurately. The difficulty lies not so much with the determination of the intensity, as with the measurement of the exact time of dark adaptation. Half a second makes an enormous difference in the threshold, as will presently be apparent. However, a rough idea of the order of magnitude of the threshold after about 2 seconds dark adaptation can be secured in this way, and as such it is valuable.

All this time the subject has gained practice in locating the red cross. The experiment then begins in earnest. After the subject has again been light-adapted, the measuring lamp is set at such a place that the subject will see it after about 5 seconds in the dark. The slide is set for observation with the left eye, and the subject looks in as usual and announces when the red cross appears. The time is taken with a stop watch, the measuring lamp is turned out, and the position of the lamp marked on the strip of paper. The subject withdraws his head from the viewing box, and sits comfortably in the dark.

Readings of the stop-watch and observations of the time in the dark are made by a very dim light which is carefully screened from the subject. This dim light is turned on momentarily when it is needed by means of a spring contact controlled by the experimenter's foot. Repeated tests on this point have never revealed an instance when the subject was able to notice this illumination.

The slide in the viewing box is now adjusted for the right eye. The lamp is moved far back in the long box, and 2 minutes after the beginning of dark adaptation, the subject is requested to look into the viewing box. The measuring lamp is then turned on and brought nearer and nearer the cross opening at a rate of about 3 cm. per second. The subject then announces the moment he sees the red cross. The time is taken with a stop-watch which was started exactly 2 minutes after dark adaptation had begun. The lamp is turned off, its position is marked and numbered on the recording paper, and the subject is told to sit back comfortably in the dark. 6 minutes after the beginning of dark adaptation, the slide is set for the left eye, and a measurement made as in the last instance. The process is then repeated after 10 minutes of dark adaptation, this time with the slide set for the right eye. 15 minutes after the beginning of dark adaptation, a reading is made with the left eye again; and after 20 minutes adaptation,
with the right eye. It will be seen that observations with the same eye are made never less than 6 minutes apart. In the other three instances the interval is greater than that, being 8, 9, and 10 minutes, respectively.

After the last observation the bright lights are turned on, and the subject again becomes light-adapted for 5 minutes. The entire process described in the last three paragraphs is then repeated, except that the first observation is made with the right eye, the others following in alternating order. In this way an independent set of determinations is secured for each eye, reaching from the beginning to the end of dark adaptation. These six pairs of duplicate points are, however, not sufficient to map out accurately the entire course of dark adaptation. Therefore intermediate points are secured in the following way.

The subject is again light-adapted. The lights are turned off, and a determination is made with the left eye after about 30 seconds dark adaptation. The lamp is brought closer and closer in the usual manner until the subject announces the appearance of the red cross. The time is taken and the distance recorded. The subject rests in the dark, and after 3 minutes in the dark a measurement is made, this time with the slide set for the right eye. The bright lights are then turned on, the subject becomes light-adapted, and the 2 measurements are repeated, this time first with right eye for 30 seconds adaptation, and then with the left eye after 3 minutes dark adaptation.

It is not necessary to detail the method any further. Suffice it to say that two sets of ten determinations are secured, a set for each eye. The whole procedure may be shown in Table I, which gives the details of a single experiment. The table shows first, the order in which the observations are made; second, the period extending from the time when the bright lights were turned off, to the time when adaptation was announced; and third, the distance which the measuring lamp had to be brought before the subject announced that she saw a red cross. Each horizontal line in the body of the table indicates 5 minutes light adaptation. Thus, between two horizontal lines are the readings made during a single period of dark adaptation. An entire experiment takes about an hour and a half.
An observation is never verified immediately. Once the subject has announced that he sees the red cross, the lamp is at once turned off. If an observation is questioned either by the subject or by the experimenter, it is repeated later after a fresh light adaptation, and the subject is unaware of its repetition. The practice of verifying a reading within a second or so involves a number of fresh sources of error such as retinal fatigue and refractory period which are bound to influence the final result (cf. Cobb, 1919, p. 437). I, therefore, consistently avoided such a method.

### IV.

1. After several preliminary experiments, I made a final set of measurements with fifteen subjects. Of these, eight were men and seven women. Their ages varied between 28 and 35 years. They were all of more than ordinary intelligence, all but one having been

### TABLE I.

*Record of a Single Experiment on Dark Adaptation of Fovea.*

*Subject, M. G. 9*

<table>
<thead>
<tr>
<th>Order No.</th>
<th>Duration of adaptation.</th>
<th>Distance.</th>
<th>Order No.</th>
<th>Duration of adaptation.</th>
<th>Distance.</th>
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<td>mm.</td>
<td>Right eye.</td>
<td>min. : sec.</td>
<td>mm.</td>
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<td>1410</td>
<td>4</td>
<td>10:15</td>
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<td>1345</td>
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<td>20:10</td>
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<td>1100</td>
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<td>:05</td>
<td>352</td>
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<td>1355</td>
<td>9</td>
<td>6:12</td>
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<td>805</td>
<td>19</td>
<td>:17</td>
<td>495</td>
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</table>

Horizontal lines between measurements indicate a period of 5 minutes light adaptation.
university trained. Most of them were teachers; the rest were professional people acquainted with scientific matters. They were all interested in the experiments, and did all they could to follow instructions in the method of making observations.

The nature of the data which I secured with these people is well illustrated in Fig. 2, which gives the results of two experiments on the same subject made four days apart. Each point represents a single reading with one eye in the manner described. The ordinates record the illumination emitted by the red cross when it just becomes visible. The data are not corrected for changes in the pupil area. The figure shows very clearly that the experiments were conducted under conditions that give reproducible results. I made a number of these duplicate sets on several individuals, and all show the same degree of coincidence in the position of the points.

In the results as a whole there is a certain amount of variation from individual to individual. One subject may be consistently

Fig. 2. Results of two experiments made 4 days apart with the same subject. The points are single readings as explained in the insert.
less or more sensitive than another. However, the shape of the curve of dark adaptation remains the same, and the degree of variation is not much more than would be expected from inspection of the points in Fig. 2. To show this, I have plotted in Fig. 3 the results of the first five subjects. The other ten subjects give exactly the same kind of data. Each point in Fig. 3 is the average of two readings, one for the left eye and one for the right. It is apparent

FIG. 3. Data for the first five subjects. Each point is the average of two readings, one for the left, and one for the right eye.

that the experiments are reproducible not only in a given individual, but in a group of individuals as well. In presenting the complete data I have therefore combined the measurements of the fifteen subjects, thus getting an average of thirty determinations of each of the ten points on the curve of dark adaptation. These average results are given in Fig. 4. It will be seen that the shape of the curve and the location of the average points are similar to those shown for the single points in Figs. 2 and 3.
2. One thing stands out prominently in all these figures. It is that the dark adaptation of the eye, as measured by foveal vision, begins immediately, and proceeds at a precipitous rate for the first 30 seconds. The data in Figs. 2, 3, and 4 begin to record the events which happen after the first 7 seconds in the dark. This is because things happen too fast for accurate measurement before the first 7 seconds. As noted in a previous section, however, I have made some observations of the threshold after 2 seconds of dark adaptation for the purpose of securing an idea of the order of its magnitude. An average of twenty measurements gives this threshold a value of $140 \times 10^{-4}$ millilamberts. From Fig. 4 it can be seen that the threshold after 7 seconds of dark adaptation is about $40 \times 10^{-4}$ml. After 30 seconds in the dark the threshold drops to about $12 \times 10^{-4}$ml. Because of the nature of the curve of dark adaptation, as described in a later section, it is possible to extrapolate backwards and find what the value of the threshold is at zero seconds dark adaptation. This turns out to be
454 \times 10^{-4} \text{ml.} The threshold thus drops in the first 30 \text{seconds} to about 3 \text{per cent of its initial value.}

During the next 20 \text{minutes} the threshold further decreases, but only to about 3 \times 10^{-4} \text{ml.}, and remains there. It is therefore clear that the change which takes place after the first 30 seconds is comparatively insignificant in the light of the first rush of events. There is, however, no sudden point at which the process of adaptation begins to slow down. It slows down from the moment it begins, and as can be seen from the figures presented so far, its course is continuous and smooth.

v.

1. The precipitous course of foveal adaptation during the first few seconds is at the bottom of the curious results obtained by previous workers. It will not be irrelevant to consider in some detail the better and more recent of these investigations. Inouye and Oinuma (1911) studied foveal adaptation by the following method. A double tube was constructed through which the two eyes could look simultaneously at different fields. The brightness of the two fields could be separately controlled by a rotating sector of black and white cardboard. The idea was to keep one eye light-adapted, and the other dark-adapted, and then to vary the illumination in one tube until both eyes saw equally bright fields.

The actual procedure calls for a preliminary light adaptation of both eyes by reading in the laboratory near the dark room. One eye is then dark-adapted with a black bandage. After the proper interval the subject rushes into the dark room, tears the bandage from his eye, and looks through the two tubes. The sector wheel has been set, and the subject compares the brightness of the two fields. After repeated trials for the same amount of dark adaptation, the position of the sector is found which results in apparent equality of the two fields. The entire process is then repeated for different amounts of dark adaptation. These experiments were repeated by Dittler and Koike (1912), who used smoked glasses instead of a sector wheel with which to reduce the illumination of the dark-adapted eye.

The results secured by these two sets of investigators show a leisurely kind of dark adaptation for the fovea, Dittler and Koike's
data showing much the slower rate. For example, after 3 minutes adaptation the eye requires 22.5 per cent of the illumination of the light-adapted eye in order that both see the same brightness. After 30 minutes adaptation the ratio of light to dark-adapted eye is as 100 to 8. This represents total dark adaptation.

The explanation for this leisurely adaptation lies in the extreme rapidity with which adaptation actually proceeds during the first few seconds. Consider Dittler and Koike's method. One eye is light-adapted while the other is dark-adapted, and the standard of measurement is the light-adapted one. To get into the dark room takes a few seconds; to get to the apparatus takes a few more seconds; to remove the bandage, to accommodate, and to make a judgment also take a few seconds. During part of this time the light-adapted eye is in the dark, and as Fig. 4 shows, it is very rapidly becoming dark-adapted. When the comparison is being made, the light-adapted eye is no longer light-adapted. Its threshold is much lower than it was a few seconds ago. As a standard of comparison it is entirely too low, the situation being the same as if the measurement of dark adaptation were begun after the first few seconds have elapsed. This, together with the fact that the degree of light adaptation is low to begin with, could make the course of adaptation correspond with that portion of the curve in Fig. 4 which lies below, say, the middle of the scale of ordinates. This condition accounts for the apparent slowness of the process and for its small extent, both of which are characteristic of these and of the older investigations.

2. Considered from this point of view, these older results constitute a significant check on the validity of the experiments presented in the present paper. My measurements were made with red light, and it might perhaps be thought that the course of dark adaptation would be different if the experiments had been conducted with white light.

To meet this criticism I made a few experiments on my own eyes, using red light at one time and white light at another. Although the actual threshold illumination is not the same in the two cases, the rate of adaptation is the same. This matter has already been considered by Nagel and Schaefer (1904, p. 283), who came to the same conclusion. They used red, blue, and green lights and found that the same order of change is secured with all three colors. In other words, the Purkinje phenomenon does not exist in the fovea.
Moreover, the experiments which I have just reviewed, though differing in accuracy from mine, are indeed roughly comparable to them when properly evaluated, as I have pointed out above. They show, for example, that foveal adaptation practically ceases after 10 minutes in the dark. In addition, if the value of the light-adapted eye as a standard be tripled or quadrupled, as it must at least be because of the initial speed of adaptation, the final degree of dark adaptation represents about 1 per cent of the condition of the light-adapted eye. This is practically the same value which is found in the present experiments. Calling the initial threshold $454 \times 10^{-4}$ ml., the final threshold of $3.4 \times 10^{-4}$ ml. represents a drop to 0.8 per cent. Therefore the results with red light show the same course of adaptation as experiments with any other light. A careful analysis of our present data will thus be of significance for the general problem of adaptation and foveal vision.

VI.

The data as they stand include the results of two phenomena: the movement of the iris, and the change in the fovea. In order to isolate the effects due to the foveal changes alone, it will be necessary to correct the data for variation in the pupil size. If the pupil area did not vary, the energy received by the retina would depend on the intensity of the illumination. On the other hand, if the intensity were to remain constant, the energy transmitted to the retina would be directly proportional to the varying area of the pupil. It then follows that since both intensity and pupil area vary, the energy received by the retina is proportional to the product of the intensity and the area.

We have measured the intensities; it is therefore necessary to introduce the data for the area of the pupil. These can be supplied from the experiments made by Reeves (1918). The experimental situations in the two cases are comparable. Reeves determined the changes in the pupillary diameter in darkness following adaptation to artificial illumination of about 100 ml. In my experiments the light adaptation field had a brightness of 90 ml. These illuminations result in practically the maximum effect in constricting the pupil.
In Fig. 5 are given the results calculated from the diameter values in Table IV of Reeves' paper. From the smoothed curve it is simple to find the pupil areas corresponding to the points plotted in Fig. 4. It is not necessary to correct for the effect of the cornea on the apparent size of the pupil, because we are interested in the relative variation in the pupil area. Calling unity the area of the pupil after 7.1 seconds dark adaptation, the first point in Fig. 4, I have computed the relative areas of the pupil for the different points in Fig. 4. These values are given in Table II.

![Graph](image)

**Fig. 5.** Change in the area of the pupil during dark adaptation. The data are computed from the diameters given in Table IV of Reeves' (1918) paper.

In the last column of the same table are given the values of the products of the measured intensity into the relative area of the pupil. These numbers represent the intensity thresholds at different times in the dark on the assumption that the pupil area has maintained a constant area equal to its value at 7.1 seconds. This point is chosen arbitrarily because it is the first accurately measured point in these experiments. Any other point would have done just as well, because all that we are concerned with are the relative changes at constant
TABLE II.

Relation between Apparent Illumination, Area of Pupil, and Corrected Illumination.

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<thead>
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<th></th>
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<td>1.63</td>
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</tr>
<tr>
<td>1217.0</td>
<td>3.37</td>
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</table>

Fig. 6. Dark adaptation of fovea independent of pupil changes. The points are those in Fig. 4 corrected in terms of Fig. 5. They represent the illumination necessary to stimulate the fovea assuming a constant pupil whose area is 27.1 square millimeters. This is the area at 7.1 seconds dark adaptation, and corresponds to the first point in Figs. 4 and 6.
pupil diameter. These results are plotted graphically in Fig. 6, and their values are indicative of the changes which take place in the fovea independent of the movements of the iris. It is to the interpretation of these data that we shall now turn our attention.

VII.

In considering the action of light in vision, it is hardly an assumption to suppose that the first effect of the light is the photochemical decomposition of a sensitive substance. Our measurements represent this effect in terms of the minimum intensity of illumination required to produce a visual sensation at different times in the dark. What is the relation between the intensity of the stimulating light and its objective photochemical effect? In the analysis of peripheral adaptation (Hecht, 1919-20, b) I assumed that the photochemical effect is proportional to the logarithm of the intensity. The reasons for this assumption were first, that such a relationship had been found in the clam, Mya; and second, that the gamut of change undergone during peripheral adaptation was so enormous that a logarithmic relation is the only one that would bring the data into a form amenable to ordinary comprehension and analysis. These reasons are not imperative. They derive their final justification on the pragmatic ground that the assumption of a logarithmic relation results in the formulation of a simple chemical picture which accounts for the data satisfactorily.

The range of dark adaptation in the fovea is not a tithe of the extent encountered in the periphery. The older data indicate a change from 10,000 to 1 in the minimum intensity necessary for a peripheral effect. Cobb's (1919) more recent experiments, as well as my own unpublished ones, indicate even a greater change than this. The older measurements were faulty in a number of ways, particularly in their neglect of the first few seconds of adaptation. Compared to these changes, those presented here for the fovea are really small in extent. When corrected for constant pupil diameter, the necessary minimum for a response after 2 seconds of foveal adaptation is about \(70 \times 10^{-4}\, \text{ml}\). The extrapolated value at zero becomes, after pupil correction, \(103 \times 10^{-4}\, \text{ml}\). After 20 minutes the intensity as given in Fig. 6 is about \(6 \times 10^{-4}\, \text{ml}\). This range of change represents noth-
ing startling, it being the kind ordinarily encountered in chemical processes. In treating the data further I have therefore assumed that the photochemical action of the light is directly proportional to the intensity. This is a common enough situation in photochemical reactions, and in addition, obtains in the photic sensitivity of *Ciona* (Hecht, 1918–19, a).

It follows from Fig. 6 that the quantity of sensitive material decomposed in order to produce a threshold effect in the fovea gradually but consistently decreases during dark adaptation. What is the basis for this variation? In other words, with what chemical or physical entity or process in the fovea can this gradual decrease be associated? I have previously outlined a possible hypothesis to account for this, and because of its success in the study of the responses of *Ciona* and *Mya* as well as of the periphery of the human eye (Hecht, 1921, e), I venture to suggest its application in the present circumstance.

Let us consider what might conceivably happen in the fovea. We have accepted the existence of a photosensitive substance. During light adaptation this substance must be decomposed to a considerable extent. Associated with this is a decided increase in the threshold of stimulation. During the succeeding period of dark adaptation there is produced a characteristic decrease in the threshold which proceeds according to a definite pattern. During this time it seems reasonable to suppose that the sensitive material is in some way being formed again, and that its concentration in the sense cells is increasing.

The continuously decreasing threshold cannot be directly associated with this increase in sensitive material. One reason for this is the fact that they vary in the opposite sense. A more cogent reason is the nature of the sensitive material itself. In its essence it must be an inert material so far as the sensory process is concerned. Otherwise it would continually be initiating visual effects. It is only after it has been changed into something else by the light, that it produces its characteristic reaction.

Indeed, it is to this decomposition product that we must look for some objective visualization of the process of dark adaptation. This decomposition product undoubtedly enters into some secondary reaction. I have elsewhere suggested that in *Mya* and *Ciona* it serves to catalyze a second reaction, the end-products of which constitute
the “inner stimulus” for the nerve endings. It is not necessary at present to be specific on this point. It is enough to accept the general idea that the decomposition product is the active agent in the early stage of the formation of the visual impulse. Its effects, catalytic or otherwise, will undoubtedly be a function of its concentration in the sense organ. An increase in this concentration will cause an increase in its effect. It would, therefore, seem a reasonable assumption to make that the increase in concentration necessary to produce a perceptible effect in the secondary reaction is directly proportional to the concentration already present. This is the “compound interest law” which is at the bottom of so many physical and chemical phenomena.

The assumption then is that in order to produce a photosensory effect, the light must cause an increase in photolytic products proportional in extent to the concentration already present in the sense organ. Such an assumption has served successfully in the analysis of the photosensory process in Mya and Ciona and in the periphery of the human eye. Moreover, in the case of Ciona it was possible to put the matter to a critical experimental test, the results of which completely vindicated the assumption (Hecht, 1918-19 a, p. 162).

VIII.

In the case of the present data as given in Fig. 6, this assumption plus the one relating intensity and photochemical effect lead to this. The ordinates, representing the intensity of the threshold, are directly proportional to the amount of photolytic products formed by the light. These values are in turn directly proportional to the concentration of photolytic products already present in the sense organ. The curve of dark adaptation of the fovea therefore represents the changes which take place in the concentration of the photochemical decomposition products in the sensory mechanism.

It is apparent that this concentration is decreasing steadily. This decrease can represent one of two possible processes: either the products are diffusing out of the sensory cells, or they are reacting chemically in the formation of some other substance. The nature of the curve in Fig. 6 will be of some aid in deciding between these alternatives.
The relation between the intensity \( I \) and the photochemical effect \( E \) is linear, and is represented by the equation of a straight line

\[
E = k I + b
\]

The constant \( k \) will depend on the units employed; it may therefore be made equal to unity by changing the units. The constant term \( b \) represents the intercept on the \( y \) axis. In the present case, omitting the factor \( 10^{-4} \), it turns out to have a value of \(-6.0\).

It is then necessary to find what the relation is between the photochemical effect \( E \), representing the concentration of photolytic products, and the time \( t \) during which the eye has been in the dark. Calculation shows this relation to be that of a bimolecular chemical reaction

\[
k = \frac{1}{a t} \times \frac{z}{a - z}
\]

in which \( k \) has a value of \( 0.00271 \).

In the calculation of the data according to the bimolecular isotherm, \( a \) is taken as the value of the first point in Fig. 6. This makes \( a \) equal to \( 39.3 - 6.0 \), or \( 33.3 \) units. Correspondingly, \( t \) is taken as zero at 7.1 seconds, and the other values of \( t \) are computed accordingly. This avoids the use of any highly uncertain values of the threshold at the first movement of dark adaptation. Once the constant \( k \) has been determined in this way, it is possible to calculate the real value of \( a \) at \( t = 0 \). This extrapolation from the experimental results and the above equation gives \( a \) a value of \( 103.2 \) units. It should be noted that the curve in Fig. 6 is drawn from values calculated from the equation of a bimolecular reaction in which \( k \) has the value already given.

Several things follow from the fact that the curve is that of a bimolecular reaction. One is that the gradual disappearance of the decomposition products is not a process of diffusion. Under certain conditions the rate of diffusion may be a linear function of time. More normally it is a function of concentration. In the latter event its course is represented by an equation similar to that of a monomolecular reaction. A bimolecular reaction isotherm represents not a process of diffusion, but one of chemical reaction only.
Granting the chemical nature of the process, it is obvious that there exist two products of decomposition which are disappearing from the reaction mixture by combining to form something else. Concomitant with this, in the same sense cells, there is being produced an increasing concentration of photosensitive material. What more reasonable step is there than to assume that it is being formed by the combination of the decomposition products that are disappearing?

We are therefore led to the conclusion that in the photosensory mechanism of the fovea there exists the following arrangement of materials. There is a photosensitive substance $S$ whose rate of photolysis at threshold intensities is a linear function of the intensity. The photolysis of this material results in the formation of two products of decomposition $P$ and $A$. The concentration of these decomposition products at any moment determines the sensitivity of the sensory mechanism, in that the amount of photolytic action necessary for a threshold, visual effect is directly proportional to the concentration of photolytic products already present. Finally, these decomposition products constantly recombine to form fresh sensitive material, their combination proceeding according to the kinetics of a bimolecular reaction. We have thus the familiar reversible reaction

$$
\text{light} \\
S \rightleftharpoons P + A \\
\text{"dark"}
$$

in which the products of decomposition serve as the precursors of the sensitive material.

IX.

It is not necessary at this time to dilate on the simplicity with which such a reversible system accounts for the observed facts (cf. Hecht, 1919-20, c, p. 514). It will suffice to point out that the "dark" reaction obviously accounts for dark adaptation; that the stationary state, in which the "dark" and light reactions are balanced, takes care of the condition of sensory equilibrium in which the eye has become adapted to a given light intensity; and that the process of light adaptation represents merely the displacement of the stationary state of the reaction to the right, due to the increased action of the light.
It is worth drawing attention to the fidelity with which the calculated curve of Fig. 6 adheres to the observed facts of dark adaptation. For further testimony Table III is presented showing this agreement in the usual manner. Considering all the things which enter into the experiments and into the calculations, the agreement seems striking.

This agreement, however, need not be considered an infallible experimentum crucis. It is possible that some other formula might fit the facts just as well. However, the significance which attaches to the agreement is that it follows from a reasoned construction of what may take place in the cone cell of the fovea. The circumstance that a similar type of photochemical mechanism differing in local detail of application serves to account for the photosensitive behavior of Mafa, and for that of the peripheral retina, heightens the plausibility of the general picture.

With regard to these local differences in the treatment of the general idea there are several interesting points to be considered. I shall indicate just one of these. For the periphery (rods) of the eye the application of the principle of a reversible reaction depends on the assumption of a logarithmic relation between intensity and photo-

<table>
<thead>
<tr>
<th>Duration of adaptation.</th>
<th>Threshold intensity.</th>
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<tbody>
<tr>
<td></td>
<td>Observed.</td>
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<tr>
<td>sec.</td>
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<tr>
<td>7.1</td>
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</table>
chemical effect. For the fovea (cones), however, a similar interpretation depends on a linear relation between intensity and photochemical effect. What constitutes the basis of this difference between rod and cone will be a nice point if it is ever established. I have already suggested (Hecht, 1919-20, b) that the logarithmic relation may hinge on some absorption phenomenon associated with the sensory mechanism. However, a detailed treatment of this and other possibilities is not appropriate at this juncture, and will be reserved for a later occasion.

The general idea which I have suggested as underlying all these phenomena of photic sensitivity has an immediate use. In the case of *Mya* it has served as a means of suggesting fresh and crucial experiments that have already contributed materially to its support. In venturing to suggest a similar mechanism for the eye, I hope that it may help to point the direction in which further work may be done. It would seem that by such a method progress may be made in the rather chaotic field of visual physiology. A concrete picture, though it limits itself to the initial events in vision, should serve better than the vague, sweeping theories of which there are already far too many.

**SUMMARY.**

1. After a discussion of the sources of error involved in the study of dark adaptation, an apparatus and a procedure are described which avoid these errors. The method includes a control of the initial light adaptation, a record of the exact beginning of dark adaptation, and an accurate means of measuring the threshold of the fovea after different intervals in the dark.

2. The results show that dark adaptation of the eye as measured by foveal vision proceeds at a very precipitous rate during the first few seconds, that most of the adaptation takes place during the first 30 seconds, and that the process practically ceases after 10 minutes. These findings explain much of the irregularity of the older data.

3. The changes which correspond to those in the fovea alone are secured by correcting the above results in terms of the movements of the pupil during dark adaptation.

4. On the assumption that the photochemical effect of the light is a linear function of the intensity, it is shown that the dark adaptation
of the fovea itself follows the course of a bimolecular reaction. This is interpreted to mean that there are two photolytic products in the fovea; that they are disappearing because they are recombining to form anew the photosensitive substance of the fovea; and that the concentration of these products of photolysis in the sense cell must be increased by a definite fraction in order to produce a visual effect.

5. It is then suggested that the basis of the initial event in foveal light perception is some mechanism that involves a reversible photochemical reaction of which the "dark" reaction is bimolecular. Dark adaptation follows the "dark" reaction; sensory equilibrium is represented by the stationary state; and light adaptation by the shifting of the stationary state to a fresh point of equilibrium toward the "dark" side of the reaction.

Dr. W. E. Forsythe of the Nela Research Laboratories was kind enough to calibrate the illumination emitted by the red cross and by the light-adapting screen. I take pleasure in thanking him for his courtesy and help in this connection.

I also wish to express my appreciation of the graciously cooperation of my various friends who served as subjects in what must have been a tedious performance. I feel particularly indebted to those who were sufficiently interested and kind to serve as subjects for duplicate and triplicate experiments.

BIBLIOGRAPHY.
Hecht, S., (a) The photic sensitivity of *Ciona intestinalis*, *J. Gen. Physiol.*, 1918-19, i, 147; (b) Intensity and the process of photoreception, 1919-20, ii, 337; (c) The dark adaptation of the human eye, 499; (d) Photochemistry of visual purple, 1920-21, iii, 1; (e) The photochemistry of the sensitivity of animals to light, *Science, N. S.*, 1921, liii, 347.
Reeves, P., Rate of pupillary dilatation and contraction, *Psychol. Rev.*, 1918, xxv, 330.