Photochemical laws and visual phenomena

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By measuring the course of recovery of visual sensitivity in the dark, after exposure to light, it has been demonstrated that all the phenomena of recovery can be explained—qualitatively—by the known fundamental principles of photochemistry. In particular, the reciprocity law, which is widely valid in photographic processes, only holds under certain limited circumstances for visual phenomena. In the case of foveal vision the reciprocity law does not hold, owing to the rapid recovery process, except for very brief periods of exposure. In the case of parafoveal vision the recovery process for the scotopic mechanism is sufficiently slow to allow validity of the reciprocity law over a wide range of exposure periods, although the law still breaks down for the parafoveal photopic mechanism. This circumscribed validity of the reciprocity law is of practical service in that the effect of many experimental conditions can be predicted from a very limited set of suitably chosen experimental data. It may be noted that it has not been found necessary to introduce any postulate involving recovery of the nervous transmission system as part of the recovery process.

1. INTRODUCTION

It is generally accepted that a visual sensation is produced by a photochemical reaction in the retina, the secondary effects of this being transmitted by nervous action to the brain. It follows that the recovery of the state of dark adaptation after exposure of the eye to light may be due to a reverse reaction after the photochemical decomposition, to replacement of the supply of photosensitive substance from an ancillary reservoir or to a recovery process in the nervous transmission system, or to a mixture of some or all of these processes. The type of mixture will depend upon the relative velocities of the various processes. In the work to be described some results have been obtained which throw a little light on this problem.

Briefly, the state of the retina, after exposure to light, is measured by the course of recovery of its sensitivity after the stimulus has been discontinued. This mode of test reveals differences which are not easily or certainly detected while the eye is still exposed to the stimulus, possibly because it is a test more simply connected with the state of the retina than are tests carried out during the exposure of the light stimulus.
A few theoretical considerations may be introduced here in order to lead up to the subsequent discussion of the experimental results. The fact that the sensitivity of the eye is reduced by exposure to light and recovers in the dark shows that the photochemical decomposition by light of retinal substances is accompanied by a reverse reaction. No direct method is at present available to determine the nature and kinetics of the reverse reaction, except in very general terms, but a qualitative description of the phenomena to be expected can be deduced by assuming, for instance, that the reverse reaction is mono-molecular. Similar conclusions are reached by assuming other types of reverse reaction, but the mathematics is simplest for the monomolecular case. It should be emphasized that the theoretical treatment below is purely illustrative and is given for the purpose of crystallizing ideas on the subject. From the researches of Lythgoe, Goodeve and others on visual purple it appears probable that the reverse reaction of the photo-process in the retina is complicated, possibly a chain reaction, and representation by a mono-molecular reaction formula is only useful for qualitative illustration.

If $n$ is the concentration of molecules of the photosensitive substance at time $t$, $N$ is the equilibrium concentration in the dark and $I$ is the intensity of light falling on the retina, the equation representing the kinetics of the reaction during exposure of the eye to light is

$$\frac{dn}{dt} = KIn - L(N - n),$$

where $K$ and $L$ are constants of the forward and reverse reactions. Integrating this, and putting $n = N$ when $t = 0$ (initial state of dark adaptation),

$$n = \frac{N}{KI + L} (KI e^{-(KI + L)t} + L).$$

When the light is cut off the reverse reaction will proceed alone according to the equation

$$\frac{dn}{dt} = L(N - n),$$

which, on integration, gives

$$N - n = (N - n_0) e^{-Lt},$$

where $n_0$ is the value of $n$ at the moment of cutting off the light.

It remains to make some assumption which will connect concentration of photosensitive substance $n$ with the threshold brightness sensitivity $I_T$ of the eye. The simplest assumption is probably that a certain minimum
message must be sent to the brain in order that the test field may be perceived. It is also assumed that the equation relating to perception of the test field is of the simplified form

$$\frac{dn}{dt} = KI_T n,$$

and that the message sent to the brain is a function of $dn/dt$. At the threshold, then, $dn/dt$ is a constant and $I_T$ is inversely proportional to $n$.

It is of particular interest to see what happens when the product $It$ is constant, that is, when the eye is given a constant exposure in the photographic sense, the individual quantities $I$ and $t$ having various values. If the reverse reaction were absent or even very slow in comparison with the forward reaction, then it is obvious that the reciprocity law would be obeyed. If, however, the reverse reaction is comparable in speed with the

![Diagram](http://rspb.royalsocietypublishing.org/)

**Figure 1.** Theoretical recovery curves.

forward reaction, the state of affairs will be very different, and the curves of figure 1 have been calculated to exemplify what happens. $K$ and $L$ have each been taken equal to $10^{-2}$, the product $It$ to 3000, and $N$ to unity. These values of $K$ and $L$ were chosen to give curves as similar as possible to the experimental curves.

The result, shown by the full-line curves in figure 1, is a family of curves in a fan-like formation, each curve starting at a different initial value and tending to the same final value at infinite time. It may also be noted that for small values of time of exposure ($p$) the curves tend to coalesce.

Another point of interest is what occurs if the value of $L$ decreases when $p$ becomes large. It is possible that the primary photochemical decomposition is followed by secondary chemical reactions of relatively slow speed. When $p$ is large these secondary reactions might produce appreciable effects and the result would be represented approximately by a decrease
in the value of \( L \). The dotted curve in figure 1 exhibits one case of the effect of a decrease in \( L \); a characteristic crossing over now occurs in the family of curves.

2. Plan of experiments

The experiments were mainly directed towards finding within what limits the reciprocity law holds for retinal photo-processes, as a step in the attempt to describe the behaviour of the eye by a limited number of general physical laws. The experiments were therefore grouped so as to bring together all those relating to a given total exposure, and each group carried through in as short a time as possible: a single day sufficed in most cases. An individual experiment was carried out by first giving the eye a period of dark adaptation, half an hour for foveal, an hour for parafoveal observations. The mode of experiment then varied according to whether foveal or parafoveal vision was used.

For foveal vision the eye was exposed to the primary conditioning stimulus for the requisite period and the time interval determined between cutting off the conditioning stimulus and first seeing the test field. This process was repeated for a series of intensities of the test field, giving a series of times, increasing as the test-field intensity decreased, from which the complete recovery curve could be plotted. The number of repetitions required for a complete curve could, in practice, be reduced to a half or a third by arranging a filter to be dropped into the test-field beam as soon as the test field was sighted, thus preparing for a longer time of recovery without the necessity for a fresh conditioning exposure.

In the case of parafoveal vision a single exposure to the primary conditioning stimulus was made and threshold measurements made thereafter, at first as quickly as possible, making use of the dropping filter technique if necessary, then at greater leisure as time proceeded. In this way a fairly complete recovery curve was obtained with a single conditioning exposure. The detail of the earlier parts of the curve is not so well shown as by the foveal method, but this is not of great importance, as the main interest for present purposes lies in the intermediate and final portions of the curve.

3. Apparatus

The apparatus is shown in diagrammatic plan in figure 2. Both conditioning and test fields are seen by Maxwellian view, so that the effects of variation in pupil size may be avoided. The conditioning field beam is concentrated to a focus twice before reaching the eye in order to form
suitable points for the insertion of shutters, $S_1$ and $S_2$. $S_1$ is a rapid-acting electromagnetic shutter working on the principle of the string galvanometer, the shutter blade being attached to the centre of the string; this serves for the control of all periods of exposure down to 0.03 sec. For shorter exposures, in order to obtain a reasonably high shutter efficiency, a dropping shutter $S_2$ is used, periods being calculated from distance of fall and width of opening. Neutral filters $F_1$ and $F_2$ are placed near the light source $I$, which is mounted in a light tight box, and neutral wedges $W_1$ and $W_2$ near points where the light beams are brought to a focus. For this reason the test-field beam is also concentrated to a focus once before reaching the eye. Auxiliary neutral filters in an automatic dropping mechanism are placed at $F_3$. The shutter $S_3$ in the test-field beam is hand operated, and is used for parafoveal work to give exposures of approximately a second; the exact value is not at all critical when it is as long as this.

![Diagram](image)

**FIGURE 2.** Diagrammatic plan of apparatus. $I$, lamp with small V-filament; $B$, light tight box; $L_1$, $L_2$, $L_3$, $L_4$, $L_5$, lenses; $F_1$, $F_2$, $F_3$, neutral filters; $W_1$, $W_2$, neutral wedges; $S_1$, rapid acting electromagnetic shutter; $S_2$, drop shutter; $S_3$, hand operated shutter; $P_1$, $P_2$, reflecting prisms; $D$, test-field diaphragm; $M$, pellicle mirror; $E$, eye of subject.

The test field is limited in size to a diameter of 0.5° by the diaphragm $D$. For the conditioning field the full aperture of the lens is used, giving a field diameter of 12°. The semi-reflecting mirror $M$, which enables the eye to see the test field superposed on the conditioning field, is a thin film of celluloid cemented to a framework of brass; when dry the shrinkage produces sufficient tension to make the film flat.

Field intensities are assessed by measuring the candle-power of the final image at the eye. This is done by comparison with a small lamp of known candle-power mounted beside the image at the same distance from the
photometer. The latter is an illuminometer with Maxwellian view of the external field. An image of the light source to be measured is formed in the eye ring of the instrument, so that the photometer field is seen full of light. In order to avoid errors due to the pupil efficiency effect the eye ring of the photometer is not larger than 0.5 mm. diameter. The apparent brightness of the visual field will be equal to the candle-power of the image at the eye divided by the area of the pupil in square feet. A pupil diameter of 3 mm. has been chosen as a convenient value.

4. Results

Results have been obtained for both foveal and parafoveal vision over a wide range of intensities and times of exposure. All relate to the author's right eye and were obtained for white light in both conditioning and test fields, the colour temperature being approximately that of the gas-filled lamp. Positions in the visual field are specified by reference to the external field as seen from the observing position.

4.1 Results for a foveal test area

To investigate the foveal area of the retina the test field was centrally fixated as accurately as possible, and as it subtended an angle of 0.5° at the eye it fell completely within the retinal area usually accepted as foveal. The results are shown in figures 3–10, each figure containing a group of recovery curves for which the product of brightness of conditioning field (B) and period of exposure (p) is constant. The logarithm of the brightness threshold is plotted against the logarithm of the time after cutting off the conditioning stimulus, and the curves are labelled with their individual values of B and p.

These groups of curves can be compared with the theoretical curves of figure 1. Take, for instance, the curves of figure 7, for which the product Bp is nearly the same as for the theoretical curves. It is obvious that a numerical fit has not been obtained and hence, as expected, the assumptions made regarding types of reactions, etc., are too simple. Nevertheless, there is a definite family resemblance between the curves of figure 1 and those of figure 7. The points of resemblance may be enumerated: (a) the different starting points corresponding to different times of exposure; (b) the final convergence to a common value; (c) the tendency to coalesce for small values of p; (d) the crossing over of curves for large values of p, pointing to some sort of secondary chemical reaction, or, possibly, diffusion of the end-products of the initial reaction. All these points of resemblance
may be observed also in figures 4–6. In figure 3 the crossing over of curves is absent, presumably because none of the times of exposure is very long. In figures 8–10 cross-over is also absent, but the explanation is probably different. It seems more likely that in these cases the total exposure, and hence the amount of photochemical decomposition, is so large that the tendency towards crossing over has merely brought the curves together over their lower ranges.

![Graphs showing log threshold vs log time for different values of pB.](http://rspb.royalsocietypublishing.org/)

**Figure 3.** $pB = 28$.  **Figure 4.** $pB = 95$.  

![Graphs showing log threshold vs log time for different values of pB.](http://rspb.royalsocietypublishing.org/)

**Figure 5.** $pB = 280$.  **Figure 6.** $pB = 950$.  

**Figures 3–6.** Variation of threshold with time.

### 4.2. Results for a parafoveal test area

Results for a parafoveal test area $8^\circ$ to the nasal side of the fixation point are shown in figures 11–18. They are arranged in groups on the same plan as the foveal results.
In the parafovea there are, according to ideas now universally accepted, two main types of visual mechanism, photopic and scotopic, the former being present alone in the fovea in most subjects. It is to be expected, therefore, that the parafoveal recovery curves will show evidence of these two mechanisms. On looking through the parafoveal curves it will be seen that in all groups, apart from one or two special curves, there is an initial period in which the curves are in the fan formation already noted in the fovea, followed by a period of coincidence lasting until dark adaptation is complete. It is reasonable to assume that the initial period is showing the
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Figure 15

Figure 16
Figure 17

Figure 18
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phenomena of photopic vision, the later period those of scotopic vision. The coincidence of curves in the later period is interpreted as showing that the reverse reaction is so slow compared with the forward reaction that the reciprocity law holds over a wide range of conditions to a fairly high degree of precision.

It may next be noted that in figures 13–16 the curve in each group corresponding to the longest periods of exposure of the conditioning field crosses over the other curves. The presumption is that here, as in the fovea, a secondary reaction is making itself felt. In figures 17 and 18 the crossover effect is very small, not much greater than the probable error of the measurements. The explanation of this, as in the foveal case, is probably that the amount of photochemical decomposition is so high that the secondary reaction has very little effect in displacing the end point.

Finally, the curves of figures 17 and 18 exhibit a feature not clearly present in any of the other curves, namely, an apparent splitting-up into two portions, one above and the other below a value of log threshold of approximately 3.2. This again looks like a separation of the photopic and scotopic mechanisms. Such separation evidently requires a large total conditioning exposure and is favoured by a high intensity of conditioning stimulus.

5. General inferences

The most important practical result obtained is that within certain limits the parafoveal visual process obeys the reciprocity law, enabling behaviour under large numbers of conditions to be predicted on the basis of relatively few experimental data. Explicitly, the predictable behaviour includes recovery of dark adaptation in fovea or parafovea when the initial conditioning stimulus is of short duration (under 1 sec. approximately), and the middle and later stages of recovery in the parafovea when the initial conditioning stimulus does not exceed 100 sec. in duration.

On the theoretical side it has been found that the phenomena of changing state of adaptation of the retina may be completely explained, in a qualitative way, by the fundamental principles of photochemistry, including a simple assumption of some type of secondary reaction following the main photochemical change. It may be noted that it has not so far been found necessary to introduce any component of recovery due to the nervous transmission to the brain. The quantitative explanation depends largely on the theory of the kinetics of chemical reactions, a subject in which theoretical finality does not appear to have been reached, so that finality in the visual problem is likewise unattained.