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THE NERVOUS SYSTEM IN VISUAL ADAPTATION*

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DURING the course of the day the light intensity varies widely, and the human visual mechanism is able to alter its sensitivity to light to suit the prevailing conditions. At night the eye may be as much as 10,000 times more sensitive to light than it is during the day.

Opinion as to the nature of this adaptation mechanism is divided into two main groups:—

1. That which asserts with Hecht (1920, etc.) and his pupils that adaptation is entirely a photochemical phenomenon; the sensitivity changes being wholly explained by the bleaching and regeneration of light sensitive pigments.

2. That which maintains that there is, as well as the photochemical adaptation, some change in the sensitivity of the nervous apparatus.

Broadly, the photochemical idea is that during light adaptation

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visual purple and other visual pigments are bleached with the formation of products which are not sensitive to light. Bleaching lowers the concentration of sensitive material in the retina, and, in consequence, the sensitivity of the mechanism to light. The recovery of sensitivity in the dark is due to the resynthesis of the sensitive material from its photo-products. The absolute threshold light energy as measured during dark adaptation is some simple function of the concentration of this sensitive material in the retina.

Hecht and his pupils do not admit any change in the sensitivity of the nervous apparatus during adaptation; receptors, retinal synapses, optic nerve fibres, lateral geniculate bodies, etc., are merely the means by which the state of affairs in the photochemical system is relayed to the brain.

It is, of course, admitted that the state of the nervous system can influence the value obtained for the threshold energy during dark adaptation. The subject may be under the influence of drugs, or inattentive, or breathing air deficient in oxygen, so that in each case the light energy required to evoke a threshold sensation will probably differ from normal. What is not admitted is that sensitivity changes in the nervous system can occur in response to alterations in the light stimulus at the eye.

Mandelbaum (1941) states the "photochemical" point of view as follows: "Dark adaptation according to classic photochemical concepts reflects simply the regeneration of the photo-sensitive pigments in the rod and cone cells; it is purely a retinal phenomenon and is confined to the sentient cells. This view is not universally accepted to-day. Although the bleaching and regeneration of visual purple are so easily demonstrated and so obviously a part of the visual mechanism, some assign it to a secondary position; others supplement this mechanism with various hypothetical nerve mechanisms, all of which are vague and for which there is no evidence."

Crawford (1946) also states: "... 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 ..."

The "photochemical" explanation has somewhat eclipsed any other view and an attempt is made to present below some of the evidence in favour of a nervous component to adaptation.

"Photochemical" Theories of Visual Adaptation.—It is sometimes argued that a "photochemical" theory of adaptation (Hecht, 1929 and 1937, for instance) leaves no room for nervous adaptational changes (Mandelbaum, 1941) and it is essential to see how far this may be true.

Hecht's theory can be stated qualitatively in symbols thus :—

This means that when light strikes the retina, a photochemical substance, S, is split into two photo-products, P and A. Freshly formed P and A, indicated by $\parallel \text{P} + \text{A} \parallel$, catalyses a further non-light sensitive reaction ($\text{L} \rightarrow \text{T}$) which results in the formation from the inactive substance (L) of an active substance (T) which initiates the nerve impulse. In addition, P and A combine in the dark to reform the sensitive material, S. This reaction, together with the photochemical breakdown, forms the basis of the sensitivity changes during light and dark adaptation.

The theory is based firstly upon experimental work with various invertebrates, such as the clam *Mya Arenaria*, which are sensitive to light and react by a motor response, the contraction of the syphon; secondly, upon the application of a knowledge of the kinetical behaviour of simple chemical reactions to the experimental results of both human and invertebrate experiments.

When *Mya* is illuminated continuously, it at first reacts by a strong contraction of its syphon, then as light adaptation proceeds, the syphon relaxes and the animal is less sensitive to light. In darkness the animal recovers its sensitivity, which recovery may be measured by determining the reaction of time to a dim test light of constant intensity.

In his final analysis for *Mya*, Hecht assumes that at all stages of dark adaptation a constant quantity of the photoproducts, P and A, freshly formed during stimulation by the test light, is required to produce a reaction in the syphon; and states that the velocity with which P and A are produced during this test light stimulation is proportional to the concentration of the sensitive material, S, present in the retina at that moment.

Hecht's theory may be illustrated graphically (Fig. 1, overleaf). In this diagram the time taken by the test light to produce P and A is represented on the abscissa, the quantity of photoproduct formed is on the ordinate, and the constant amount of P and A required at all stages of dark adaptation to stimulate the receptors is represented by the line XY. Early in dark adaptation this line is reached slowly, via OY, which results in the period, t_1 , which together with a latent period of constant duration makes up the reaction time. Later, when the sensitive material has been allowed to accumulate, the line XY is reached more rapidly, via OZ when the test light is applied, which results in the shorter period, t_2 , and a shorter reaction time.

FIG. 1.—Diagram to illustrate Hecht's "photochemical" explanation of adaptation in the visual mechanism.

Thus the values of the periods, t_1 and t_2 , and the values of the whole reaction time, should yield information about the way in which the sensitive material, S , regenerates in the retina, and Hecht finds that a hyperbola, which also describes the course of a bimolecular chemical reaction, can be constructed and fitted to the experimental determinations of the reaction time. Since this curve fitted the data within the experimental error, Hecht concluded that two substances, P and A , were recombining during dark adaptation to form the sensitive material, S , a conclusion which is not entirely justified.

Now it is clear that although the rate of photochemical decomposition may vary with the concentration of the photosensitive pigment, i.e., the slope of the line OY may alter, the variation may be insufficient to account for the whole of the sensitivity change during dark adaptation. The amount of freshly formed products required to stimulate the receptors may also vary during dark adaptation, this amount being larger at the beginning and smaller towards the end. This would mean that the sensitivity change is partly due to a change in behaviour of the receptors, and

that, in Fig. 1, the long period, t_1 , results from the need for the test light to form the larger quantity of photoproducts, OP, before impulses are generated in the receptors. In the shorter period, t_2 , which is found in the later stages of dark adaptation, only the amount OX, is required to stimulate the receptors, because they are then more sensitive to freshly formed photoproducts. The dark adaptation measurements should now describe to some extent the recovery of the sensitivity of the receptor part of the nervous apparatus.

Indeed, Hecht's hypothesis is merely one of many which might have been chosen. Hecht was aware of the difficulty of choosing between "photochemical" hypotheses on the basis of the above dark adaptation measurements alone (1923), and he makes his choice between the first of those stated above and yet another hypothesis, by consulting the behaviour of *Mya* when the animal is brought to various steady states of light adaptation.

The difficulty is further emphasised when the data from human subjective experiments is considered. Here Hecht (1920; 1921; 1929) has had to make a further assumption (as Houstoun, 1930, has pointed out) to relate the concentration of the photo-sensitive substances to the measurements, because the ordinates are now no longer reaction time, but the logarithm of the threshold energy required to produce a minimum sensation. The assumption made is that the concentration of sensitive material present in the retina at any moment during dark adaptation is inversely proportional to the logarithm of the threshold energy necessary to evoke the minimum sensation of light. Once again a "bimolecular" curve was derived and was found to fit the data if the rod and cone portions of the results were treated separately. On the other hand the data could easily be explained as for *Mya*, by assuming that the amount of photoproduct required to stimulate the receptors was not a constant, and that the threshold curve describes the recovery of sensitivity of the receptors. Such an explanation might be the better if it proved to be supported by other evidence.

Hecht's theory does not, therefore, exclude a nervous explanation for adaptation. Indeed, such a theory which rests merely upon the goodness-of-fit between certain derived curves and the experimental results, could hardly be conclusive without some further support. The fact that a hyperbola describes both a bimolecular chemical reaction and the behaviour of the reaction time during the dark adaptation of *Mya* does not entitle one to link these two phenomena as cause and effect. They may only be phenomena which are describable in the same mathematical language and require other evidence to forge the link

between them. It is a matter of some doubt as to whether the evidence from other visual measurements is adequate to support Hecht's theory as a whole.

Lythgoe's Discrepancy.—Numerous objections have been raised to Hecht's entirely photochemical explanation of visual adaptation (see, for instance, Lythgoe, 1940; Granit, 1947; Elsberg and Spotnitz, 1938).

Lythgoe (1940) pointed out that there is a large discrepancy between the magnitude of the change in concentration of photosensitive material and the change in the sensitivity of the visual mechanism during dark adaptation. On the basis of Hecht's views, if the concentration of the photosensitive material was to increase in the retina by a factor of two, the sensitivity of the visual mechanism should also be doubled. Actually, as Lythgoe points out, this does not fit the facts. If one assumes that Granit's figures for visual purple accumulation in the cat's retina apply to man, and then considers the rod section only of the human dark adaptation threshold curve, the visual purple approximately doubles its concentration between the 7th and 30th min. of dark adaptation. This is associated with a 1,000-fold increase in sensitivity and the visual purple increase is thus not nearly enough to account for the sensitivity increase.

One explanation for this discrepancy might well be that during the course of dark adaptation the receptors become 500-fold more sensitive to the products of the photochemical mechanism. If this were so, visual adaptation would be largely a nervous phenomenon.

Lythgoe was impressed, too, by the gradual reduction in the ability of the eye to perform the finer visual judgments as the sensitivity increased in the dark, and to harmonize these two effects he postulates that in the dark adapted eye there is a greater amount of nervous intercommunication in the synaptic layers of the retina.

Such a synaptic "switching" would account quite well for the discrepancy between visual purple accumulation and sensitivity increase.

The Shape of the Recovery Curves.—A further objection which has been raised by a number of authors (Winsor and Clark, 1936; Lythgoe, 1940; Wright, 1946) is that dark adaptation recovery curves following various degrees of light adaptation do not retrace one another's paths.

Consider two experiments, 1 and 2, where the light adaptation in 1 is greater than in 2. On the basis of Hecht's idea, $S \rightleftharpoons P + A$, the retinal concentration of the photosensitive material, S , at the moment of change-over from light to dark adaptation would be least in experiment 1 with the greater light adaptation.

Following the greater light adaptation, the concentration of photo-sensitive material, at first low, would rise when the subject was placed in the dark, until it was equal to the concentration existing in the retina at the moment of change-over in experiment 2. According to Hecht, the log of the threshold energy in the two cases should now be equal, because the concentrations of photo-sensitive material are alike. The only difference between the two experiments is that this equal threshold energy is reached at a later time in experiment 1.

From this point onward the rate of accumulation of the sensitive material should be the same in both experiments. Thus the shape of the log. threshold energy-time curves should also be the same and it should be possible to superimpose two curves following different degrees of light adaptation merely by shifting them parallel to the time axis.

This one cannot do in measurements obtained from human subjective experiments, because the curves are of different shape. Thus the simple scheme $S \rightleftharpoons P + A$ cannot be the whole truth.

The recovery of sensitivity is slower the longer the time of light adaptation, *i.e.*, the curves become more gentle in slope.

FIG. 2.—(After Crawford). Recovery curves of foveal sensitivity. The product of p , the light adaptation time, and b , the light adaptation brightness, is 283 for the left and 945 for the right diagram.

Crawford's very complete investigation (1946) illustrates this point (Fig. 2). For the results in this figure, the product of the light adaptation brightness and the time of its application was the same for all the curves in each diagram, so that the amount of light energy applied was similar for each member of the family of curves. To some extent the light adaptation time and brightness are interchangeable because the resulting dark adaptation curves are similar in shape, but if the time is prolonged for a matter of minutes (and the brightness appropriately reduced to maintain the quantity of light constant) a delay of recovery sets in which gives the curves the appearance of being crossed over each other. This "cross over" effect is only shown when the time of light adaptation is of several minutes' duration.

Wald's results also show the "cross over" of the curves, and Elsberg and Spotnitz (1938) have shown that increase of time is more effective than increase of brightness in delaying the recovery of the sensitivity of the fovea.

Haig (1941) could not demonstrate this effect, but when his results are compared with the more complete ones of Crawford (1946) it appears that his choice of the quantities for the time and brightness was unfortunate in that the particular values used do not demonstrate the effect.

In Wright's results (1946), the shape of the curve describing the recovery of foveal sensitivity to red light depends upon the duration of light adaptation. These results have been obtained by a binocular matching method instead of the more usual threshold energy measurement. Wright points out that for any given sensitivity, the rate of recovery at that point in the curve depends upon the preceding light adaptation. His curves following different light adaptation times certainly could not be superimposed upon each other by a simple shift of the curves parallel to the time axis.

Thus it appears that in those experiments where the light adaptation time is of the order of minutes, changes have been set up in the visual mechanism which result in a delay of recovery during the subsequent dark adaptation. It seems that time is required for the light to bring into play sensitivity changes which are not rapidly reversed and which are not brought into play to the same extent by increases in the brightness of the light adaptation source. The explanation of this delay in recovery, given by each author, is broadly similar. Wald and Clark (1937), for instance, have utilized the effect as confirmation of the former's views on the nature of the photochemical process.

According to Wald and Clark the events in the photochemical system may be represented thus :—

The breakdown of visual purple to retinene + protein is accomplished by light, and a further thermal conversion of retinene to vitamin A occurs. The visual purple may then be resynthesized either from retinene and protein or from vitamin A and protein, and the speed of the former reaction is postulated as greater than that of the latter.

Thus after a short exposure to a high brightness retinene would be the main photoproduct, there being little time to produce vitamin A. Recovery in the dark would then be rapid since it would rely on the fast reaction, retinene-visual purple. On the other hand, a longer exposure to a low brightness would allow vitamin A to be formed during light adaptation, so that the recovery would be more dependent on the vitamin A-visual purple process and therefore slower. A combination of these two processes could result, according to Wald, in a family of dark adaptation curves of differing slope.

Hecht, Haig, and Chase (1936) have followed Wald's explanation, and Wright (1946) has also come to the conclusion that regeneration of the sensitive substances may take place in two ways; one directly from photoproducts and the other, more slowly, from some reservoir of material the outflow from which is restricted. Crawford (1946) merely states that the effect could be explained by "... some sort of secondary reaction, or, possibly, diffusion of the end products of the initial reaction."

A different explanation has recently been given by Dartnall (1948). He postulates that the reduction of sensitivity in the light-adapted eye is due to the accumulation of large quantities of indicator yellow. Thus, after prolonged light adaptation, not only must the sensitive pigment visual purple be resynthesized, but also the indicator yellow must be destroyed, processes which would together lead to a long time of recovery. After short light adaptation times, only small amounts of indicator yellow have been formed. The recovery would then depend mainly on the fast resynthesis of the visual purple.

No author suggests, however, that variations in light adaptation

may have succeeded in separating to some extent the nervous and photochemical contributions to visual adaptation. The "cross-over" of Crawford's curves may be due to the initiation by long continued light adaptation of sensitivity changes in the nervous apparatus which are slow to develop and are only slowly reversed.

The Work of Hartline.—Recently, Hartline and McDonald (1947) have published a most complete investigation into the behaviour of a single visual cell of the eye of *Limulus*. They have recorded the action potentials from this cell, which are similar to those found in the optic nerve of other animals, and with this record have followed the dark adaptation of the cell after light adaptation for varying times to sources of various brightnesses. They found that for a considerable range of time and intensity, increases of either had a similar effect upon dark adaptation, but if the time of light adaptation was prolonged the "cross-over" effect noted above in the results from subjective experiments was observed. Hartline and McDonald follow Wald's explanation of this delay in recovery, but the effect may equally well be due to the appearance of a nervous component of visual adaptation. Hartline and McDonald's work would suggest that a nervous component in adaptation in man is confined to the visual receptors themselves. They might alter their sensitivity to the products of the photochemical reaction.

Indirect Adaptation.—Some of the strongest evidence in favour of a nervous component in adaptation is derived from experiments in which the adapting light is viewed indirectly. Using the binocular matching technique developed by Wright (1934), Schouten and Ornstein (1939) have studied the effect upon the foveal sensitivity of stimulation of a small area of the peripheral retina by a glare source of light. The left eye was used as a reference eye and was maintained in the dark-adapted state. The right, or test eye, could view a test stimulus with the fovea, together with the image of the glare source which did not fall on the fovea. A comparison between the test stimulus seen at the fovea of the eye stimulated by the glare and another stimulus seen with the fovea of the dark-adapted reference eye could be made by means of a binocular match.

With this apparatus Schouten and Ornstein found that there was a rapid reduction in foveal sensitivity of the test eye when the glare source was applied; a reduction which was complete in 0.1 sec., and they refer to this effect as α -adaptation.

If the glare source was extinguished within a few seconds, the foveal sensitivity made a rapid, but not immediate, recovery. If light adaptation was continued for a few minutes, however, recovery was much slower and several minutes would elapse before

it was complete. This the authors call β -adaptation and point out that this adaptation has no noticeable effect upon the foveal sensitivity during the period of light adaptation. It is only observed as a delay in recovery during the subsequent dark adaptation.

Since the glare-source stimulus is not applied to the fovea, and since there is a rapid depression of sensitivity in that region, Hecht's simple photochemical explanation of adaptation is quite inadequate, and Schouten and Ornstein have considered two main alternatives. First, that the adaptation is due to scattered light illuminating the fovea and causing light adaptation in the ordinary way, and second, that some "electrical effect" is set up in the retina by the image of the glare source and that the foveal sensitivity is depressed by such an effect being transmitted over the retina.

From the results of an experiment employing trans-scleral illumination, they come to the conclusion that α -adaptation is an "electrical" phenomena not due to the effect on the fovea of the scattered light in the globe of the eye. Their precise idea as to the nature of the "electrical" effect is a little difficult to discover from their paper. They also believe that β -adaptation, which more closely resembles the recovery of sensitivity as measured in threshold experiments, is due to "... the electrical processes in the retina."

Wright (1946) has repeated some of Schouten and Ornstein's experiments and confirms their results. He, too, thinks that scattered light is unlikely to have played a major part in the effect and follows Schouten and Ornstein in considering that the α -process is due to "... the electrical inhibitory action ..." of the large response from the retina stimulated by the glare source upon the response from the foveal retina stimulated by the much less intense test light. Wright prefers to explain the β -process at the fovea by postulating that there is in that region a diminution of the concentration of photo-sensitive material by a process of "photochemical drainage" towards the region of the retina stimulated by the glare source.

Crawford (1937) also measured the recovery of sensitivity in the retina after adaptation to a glare source and reported his results prior to those given by Schouten and Ornstein (1939). In his experiment the dark adaptation of both the fovea and parafovea (14° from the fixation point) were followed by threshold energy measurements following light adaptation either to a glare source situated 2.9° above the fovea or to a uniform background brightness, the image of which included and surrounded the fovea. This latter experiment was similar in every way to the usual measurements of dark adaptation. The two light adaptation sources were

equivalent, in that for each source the same amount of energy had to be applied to the test area during light adaptation to elicit a threshold response.

From Crawford's results it is clear that light adaptation produced by the glare source is similar in every way to that from the uniform background brightness so far as the subsequent dark adaptation is concerned.

Thus, in the indirect adaptation experiments, an effect has been achieved at the fovea by the image of a glare source not at the fovea, and it is difficult to see how a simple photochemical theory such as Hecht's could explain this effect, unless one postulates that scattered light is the cause of the foveal sensitivity change. Since this is unlikely a "photochemical" theory must explain how it is that alterations in the concentrations of the foveal photosensitive materials can be produced by stimulating another portion of the retina.

Wright's "photochemical drainage" explanation of the β -adaptation process requires an actual movement of sensitive material in the retina. It is generally held, however, that the pigment visual purple is intimately associated with the structure of the rod cells (Schmidt, 1938). If this is so, visual purple is unlikely to move about in the retina as suggested by Wright, and although it is possible that the β -process has a photochemical explanation, there is no real evidence for Wright's idea.

From Crawford's experiment (1937) it seems that a glare source may delay recovery of sensitivity for a time equal to that found in experiments in which a uniform light adaptation source is used, and it may well be that the usual threshold measurements follow the recovery of a β -adaptation process.

In view of the difficulties of explaining them by a "photochemical" theory, the results from indirect adaptation experiments point to the existence in the visual mechanism of components to adaptation other than photochemical ones. Such processes may well be nervous in origin.

The Effect of Light Adaptation of One Eye upon the Sensitivity of the Other.—In Hecht's photochemical theory of visual adaptation the nervous system behaves merely as a signalling apparatus so that the photochemical events may be relayed to the brain. Thus if it could be shown that light adaptation of one eye had an appreciable effect upon the light sensitivity of the other, it would suggest strongly that there was, in addition to change in concentration of photochemical substances, some change in the sensitivity of the nervous system, because it is difficult to see how stimulation of the nerves of one eye could cause alterations in the concentrations of the photosensitive materials in the other.

Unfortunately, opinion as to the experimental facts is not unanimous. Of the authors mentioned by Dorothy Adams (1929) some regard the two eyes as independent, whereas others ascribe to light adaptation of one eye various effects upon the sensitivity of the other. Helmholtz (1924) held that the two eyes are independent.

Of later workers, Crawford (1940) could find no change in the value of the threshold energy of a fully dark-adapted eye, when the light adaptation of its fellow was changed.

Mandelbaum (1941) has also measured the dark adaptation in one eye whilst applying a bright light to its fellow. No difference could be detected between one curve obtained in the normal way after light adaptation and another during which the opposite eye was subjected to a brightness of 6000 ml. through a 2 mm. pupil for several periods during the measurements.

Wright (1934) has devised a method for studying the adaptation of the eye, which relies upon a large measure of independence between the two eyes. In his method one eye is maintained in the dark-adapted state and is used as a reference eye. The other is brought to various levels of adaptation and its response to various stimuli compared with that of the reference eye by a binocular match between two fields, one of which is seen with each eye. The method assumes that light adaptation of the test eye has only a very small effect upon the dark-adapted reference eye. Wright (1946) says of his method, "The validity of the binocular method depends on the assumption that the sensitivity of the left eye is constant throughout the experiment and can, therefore, be used as a reference standard against which changes in the right eye can be recorded. This assumption is not strictly correct, since adaptation of the right eye undoubtedly induces minor changes in the left. At the same time tests by the threshold method . . . show quite definitely that any effect which is produced on the left eye is of a second order magnitude, and in no sense comparable to the much greater changes produced in the right eye. Such effects can, therefore, be neglected."

Schouten and Ornstein (1939) and Craik (1939) have also used Wright's binocular method for the study of adaptation, and have made similar assumptions concerning binocular interactions.

On the other hand, Elsberg and Spotnitz (1938) have marshalled evidence to show that adaptation of one eye does affect the sensitivity of the other and in their own experiments their results cannot be said to show only "minor changes" in the second eye. Dunlap (1921) also finds sensitivity changes in one eye due to stimulation of its fellow.

Helmholtz (1924) reminds us, however, that it is not easy to bandage one eye so that all light is excluded, and Crawford (1940)

suggests that in experimental systems which do not employ Maxwellian view, some leakage from the light adaptation system may occur to the dark-adapted eye and that this might account for any sensitivity changes found.

It is true that those authors who find central adaptation effects are those who do not use Maxwellian view and such a simple explanation may be correct.

Thus, unfortunately for those who hold that adaptation has a central nervous component, the balance of evidence is in favour of the independence of the two eyes. This would suggest that the site of the adaptation process, whether nervous or photochemical, is within the eye itself.

Craik and Vernon's Blinding Experiment.—Further support for the peripheral nature of visual adaptation was obtained by Craik and Vernon (1941). These authors were able to produce temporary blindness in an eye by applying pressure to the sclera. Then with a dark-adapted eye in a blinded state, light adaptation for a 3-minute period to a brightness of 12,000 e.f.c. through a 2 mm. pupil was undertaken. At the end of the light adaptation the eye was allowed to recover rapidly from the effect of the pressure and the subsequent dark adaptation curve was measured. This curve was found to be no different from a curve obtained after similar light adaptation of a normally functioning eye, if a slight delay in the initial stages of dark adaptation due to the recovery from the pressure may be neglected. The authors conclude, "The normality of the dark adaptation curve obtained with an eye which has been blinded during the bright adaptation period shows that light adaptation, both of rods and of cones, is a retinal reduction of sensitivity and not a cortical one, since the primary stimulation never reached the higher centres."

Some Fallacies.—Protagonists of a nervous theory of adaptation are apt to include certain evidence which is not valid. Visual adaptation is a change in light sensitivity, which is initiated by the presence or absence of a light stimulus. Before an effect can be considered as part of the normal visual adaptation mechanism it must be shown firstly, that light is the stimulus which causes the reaction, and secondly, that a change in the sensitivity to light is involved.

It is possible for light to have effects upon the nervous system, such as the alteration of electrical rhythms in the cerebrum, which, because a change in light sensitivity is not involved, cannot be part of the adaptation process. Again, light may alter the sensitivity of the visual mechanism to electrical stimulation (Bouman, 1935), but here too the effect cannot be called visual adaptation.

Sensitivity changes may occur in response to stimuli other than

light, such as sound (Kravkov, 1934), and stimuli applied to the autonomic system (Kekcheev, 1942), but here again these effects do not support a nervous theory of visual adaptation even though their site of action is clearly within the central nervous system, because no alteration in the light sensitivity of the mechanism is involved.

The Work of Granit.—If visual adaptation be entirely a photochemical phenomenon, it should be possible, in animals, to

FIG. 3. (After Granit and others).—A comparison between the recovery of the b-wave of the frog's electroretinogram and the accumulation of visual purple during dark adaptation.

● Recovery of sensitivity to test light of low intensity. ● Recovery to light of higher brightness. ○ Visual purple accumulation.

measure the increase in concentration of visual purple during dark adaptation and to record the sensitivity of the eye to light under similar conditions. If Hecht's views are correct, the sensitivity increase should run parallel to the increase in the visual purple concentration. Granit, Munsterhjelm, and Zewi (1939) have performed such an experiment on frogs and some of their results are shown in Fig. 3.

Here the progress of the sensitivity increase is followed by measuring the size of the b-wave of the electroretinogram, which

wave is considered to be the part of the trace most closely associated with the discharge in the optic nerve. The visual purple concentrations, which are determined by killing the animals at suitable moments during dark adaptation and extracting the pigment from the retina, are expressed as a percentage of the maximum concentration achieved in the dark. Granit points out that the mechanism did not recover at once from the depression of sensitivity created by light adaptation, whereas regeneration of visual purple began as soon as the animal was transferred to the dark. There was clearly no simple correspondence between concentration and sensitivity as is suggested by Hecht's theory. It appeared from these experiments that the sensitivity only recovered when the visual purple had accumulated to some 50-60 per cent. of its dark concentration.

Superficially, it would seem that here too a slowly reversible nervous component to visual adaptation could be delaying the recovery of sensitivity. Actually one must beware of accepting such a suggestion in this case.

Firstly, as Peskin (1942) has pointed out, Granit has used the size of the b-wave as the measure of sensitivity and not, as is the case in human experiments, the quantity of light energy required to produce a constant response (in this case a constant size of b-wave). Granit's technique might lead to a measured delay in recovery where none, in fact, existed.

This criticism is certainly important because, as may be seen from Granit's other experiments with the microelectrode technique in which the energy required to produce a constant response in frog's optic nerve fibres is measured, recovery of sensitivity begins much earlier.

Secondly, Mandelbaum (1941) has maintained that Granit and others (1939) failed to take proper precautions against visual purple regeneration. Peskin (1942) claims to have shown that visual purple regeneration in the living frog's eye is delayed for 10 minutes or so when bright sources are used for light adaptation. If these points are valid, it may be that the non-correlation is in some way incorrect.

On the other hand, another experiment (Granit, Holmberg, and Zewi, 1938) supports the failure to obtain a simple correlation. By applying to living frog's eyes small quantities of monochromatic light, these authors found that the b-wave could be completely suppressed, *i.e.* the sensitivity of the visual mechanism greatly reduced, without there being any detectable diminution in the amount of visual purple that could be extracted from the retina after similar monochromatic illumination. That this is due to failure to destroy the visual purple with monochromatic light, and

not to regeneration during extraction, is shown by the observation that the same amount of monochromatic light would only produce a diminution of about 2 per cent. in the concentration of a visual purple solution. In such a solution regeneration of 98 per cent, of the visual purple would be most unlikely.

Thus there is evidence here also which does not fit easily into a photochemical explanation of adaptation.

A Pupillary Experiment.—Recently the author (Thomson, 1949) has performed some experiments which strengthen the belief that there is a nervous component to adaptation.

Two series of dark adaptation measurements were made following a standard 15-minute period of light adaptation. The pre-light adaptation treatment in the first series was a period during which the eyes were in darkness, and in the second, in a bright outdoor light. A difference was detectable in measurements of pupillary diameter made during the subsequent dark adaptation, larger diameters being found after the period in darkness.

After considering several possibilities, it appeared improbable that the photochemical system could influence the nervous mechanism when the eyes were in the dark. Thus the pupillary differences found were most likely maintained by nervous messages other than those initiated by a light sensitive substance, for example, the discharges found by Granit (1947) in dark-adapted and unstimulated single fibre preparations.

These discharges could signal to the pupillary muscles whilst the eyes are in the dark sensitivity differences produced in the nervous mechanism by the pre-light adaptation treatment.

Summary

The idea presented in this article is that the sensory receptor cells in the retina, which are in contact with the photochemical system of the eye, play a part in visual adaptation. It is proposed that these cells alter their sensitivity to the end-products of the photochemical reactions and that this sensitivity change is in addition to any which may be attributed to the photochemical mechanism.

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