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ON THE LATENCY OF NEGATIVE AFTER-IMAGES IN RELATION TO BRIGHTNESS OF STIMULUS

BY

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1. Introduction.

Working with white circular discs of $22'$ of visual angle as stimuli, *Creed* and *Granit* (1) measured the latent period of the negative after-images following 30 seconds fixation of these objects, exposed against a black background. The after-images were projected upon a white screen, lowered by means of a pulley at the end of the fixation period. The measurements were made at different distances from the fixation point, and from the results curves were plotted relating the latency of the after-image (ordinate) to the visual angle subtended by the distance from the fixation point (abscissa). It was found that the latent period was longest in the middle of the *fovea centralis*, and that, on passing out towards the periphery, it shortened on a hyperbolic curve to a point at about 2° of visual angle from the fixation point. Then there followed a rather sudden lengthening of the latency which reached a second maximum, the »hump«, at about $2^\circ 30'$ from the fixation point. On passing further out towards the periphery, it again, though more gradually, became shorter. (Figure 13 of this paper conveys a good idea of the type of curve met with.)

To find an adequate explanation of these results was difficult, but it seemed rather natural to seek for structural differences in the retina corresponding to the three significant parts of the curve: (i) the first hyperbolic fall, (ii) the »transitional area« with the hump, and (iii) the second fall towards the

periphery. The first part of the curve, as far as the retina is concerned, is exclusively a cone curve; further out, at its minimum, rods begin to appear within the area stimulated.*) In the transitional area rods come into play in much greater force than the cones. The hump, it was suggested, therefore indicated, as it were, that a new organ now took part in the reaction, causing some kind of interference phenomena.

In order to throw more light upon these problems we have investigated the influence of the intensity of the stimulus and the state of adaptation upon the latent period of the after-images. To that end an apparatus was constructed by means of which the intensity of the stimulating light could be altered independently of the general illumination of the room.

2. Method of experiment.

Into the dark-room of the physiological laboratory was brought a big blackened case ($200 \times 50 \times 50$ cm.), divided by a ground glass placed 50 cm. from the back and 150 cm. from a door in the front of the case, where the observer was seated. Through an opening in the door he had a view of the middle part of the ground glass, a circular area of about 25 cm. diameter. The rest of the glass was hidden by an opaque screen just in front of it. In back of the ground glass a black metal projection apparatus could be set to show circular light patches of $22'$ of visual angle on the glass. These appeared against a black background, since the case as well as the projection apparatus was lightproof and aberrant light from the opening in the front door was excluded by a big piece of black velvet cloth nailed to the sides of the opening. The light beam for the stimulus passed through an opening in the projection apparatus. On the right side of that opening a row of small holes could be opened and shut separately and adjusted so as to give the faint light spots required for the fixation points.

Between the ground glass and the screen in front of it a lamp was placed on the bottom of the case. This lamp together with the one of the projection apparatus was connected to a double switch by means of which the light of the stimulus could

*) For references, consult the paper by Creed and Granit (1).

be made to vanish at the moment the ground glass brightened. Thus the ground glass was also used as a projection background for the after-images. By screening the lamp in front of the glass carefully the strength of illumination on the glass was adjusted so as to allow a black thread cross just to become visible. Three vertical threads, 3 cm. apart, crossed a horizontal one, and when the projection background turned up the observer directed his gaze on to that cross which first came into sight. There was no need of placing one of the crosses exactly in front of the peripheral fixation point used for the time being, as the sudden exchange of the fields at the end of the fixation period always caused an involuntary displacement of the gaze. The dark-room was well illuminated, and the same lamps were used in all our series. The eye was given 20 minutes of rest before the experiments were begun.

The method of experiments was as follows: the experimenter gave a short warning, and 5 seconds later, at another signal, the observer shut his eyes, folded the velvet cloth around his head and rested his chin on the lower edge of the opening in the front of the case. Twenty seconds later, at another warning, the experimenter called out »Now«, and the subject directed his gaze on to the fixation point on the ground glass. Twenty-five seconds later the experimenter set a smoked drum in rotation the sound of which served as a warning to the observer. At 30 seconds the experimenter exchanged the fields, the projection background turned up, and the subject marked this moment with a Morse key, connected to a signal writing below a Jacquet time-marker on the drum. As soon as the after-image appeared he again pressed the key. All the latencies were measured afterwards from the records. The peripheral light spots followed in haphazard order known only to the experimenter (T. H. as a rule), who likewise served as one of the subjects.

3. The influence of varying the intensity of the stimulus.

The first series to be described consist of experiments in which the intensity of the test light was varied. The brightness of the patch on the black background was too high to be used in experiments involving long fixation times. By placing the

neutral tint glasses devised by Prof. Tscherning in the way of the rays, the intensity of the stimulus could be varied in steps of $1/10$. The light completely disappeared with the glass No. 6 when the eye was in the state of adaptation prevailing during the experiment. With the dark-adapted eye glasses Nos. 10 + 2 marked the limit.

Four series were taken, the intensities of which were determined by the glasses 1—4. They will be referred to as 1.0, 0.1, 0.01, and 0.001, respectively. One series consisted of a single value for each retinal point tested. The curves of figs. 1—12 are based on arithmetical means of three readings; the only exception to this rule being the curve of fig. 12 which gives the average of two values. The visual angle subtended by the distance between the centre of the test light and the fixation point is plotted as abscissa, and the latent period of the after-image as ordinate. The visual angle of the test light is $22'$. On the abscissa also is marked the distance from the fixation point in cm.

All of the curves show that the latent period shortens from a high value in the middle of the fovea towards a paracentral point. Then there follows a second maximum at about $1^{\circ}50'$ of visual angle. This is the »hump« in the curve, described by *Creed* and *Granit* (1), but here it is located about 1° nearer to the fovea. These authors found a renewed shortening of the latency towards the periphery. In our low-intensity curves the hump is followed by a shortening of the latency, more or less continuous towards the periphery, but in most of the high-intensity curves there is a renewed rise to be found in the periphery and the stronger the stimulus, the more pronounced the rise. The tendency of the low-intensity curves to sink towards the periphery is less marked with observer A. U. than with the other two, whose curves bear a great resemblance to those of *Creed* and *Granit*, when weak stimuli are employed.

Most curves show that the brightness of the test light doubtless has an influence upon the latent period of the negative after-images, although a difference of intensity, amounting to about 100 times a given one may be required in order to ascertain it. In the fovea the effect of the variation of the intensity is considerably smaller than in the other parts of the retina.

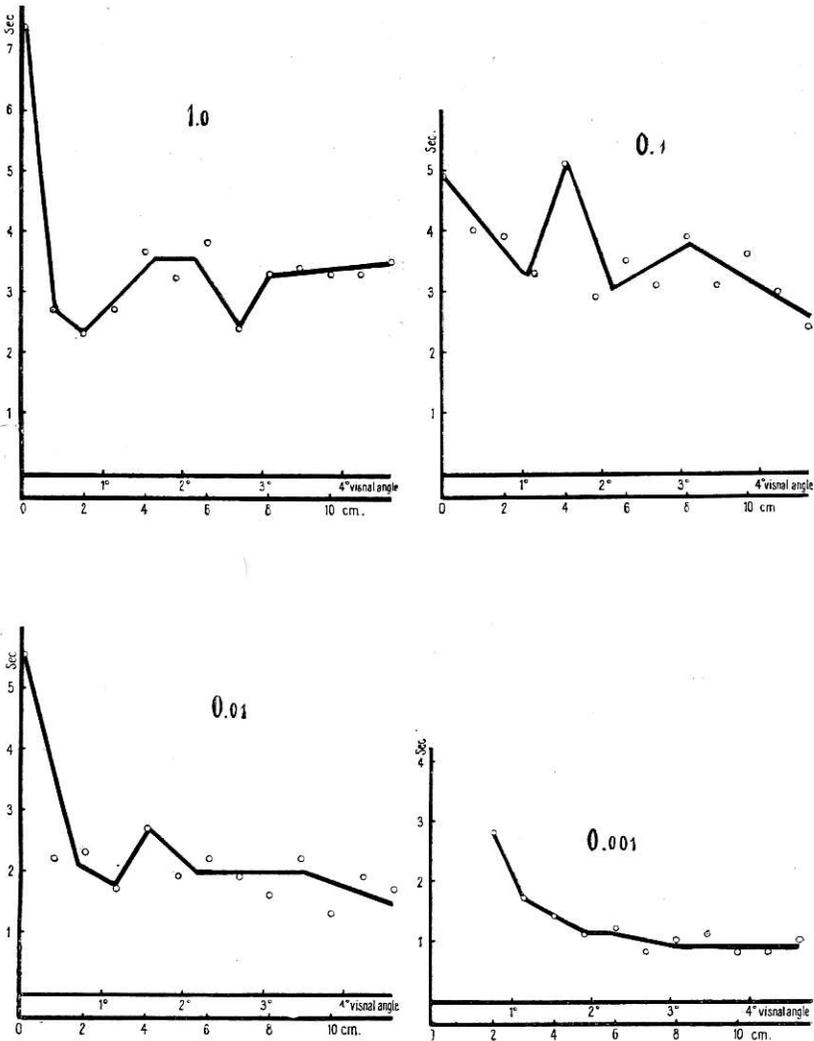


Fig. 1—4.

Results with observer H. The brightness of the stimulus is indicated on the diagram. For explanation, see text.

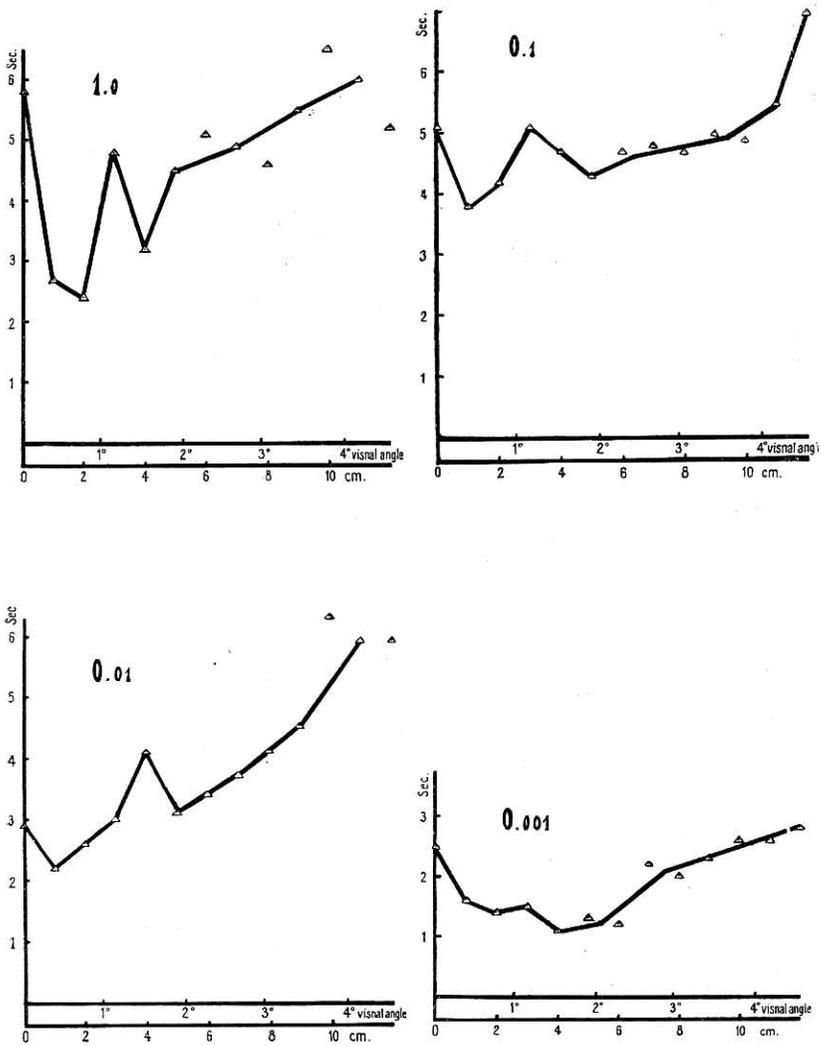


Fig. 5—8.

Results with observer U. The brightness of the stimulus is indicated on the diagram. For explanation, see text.

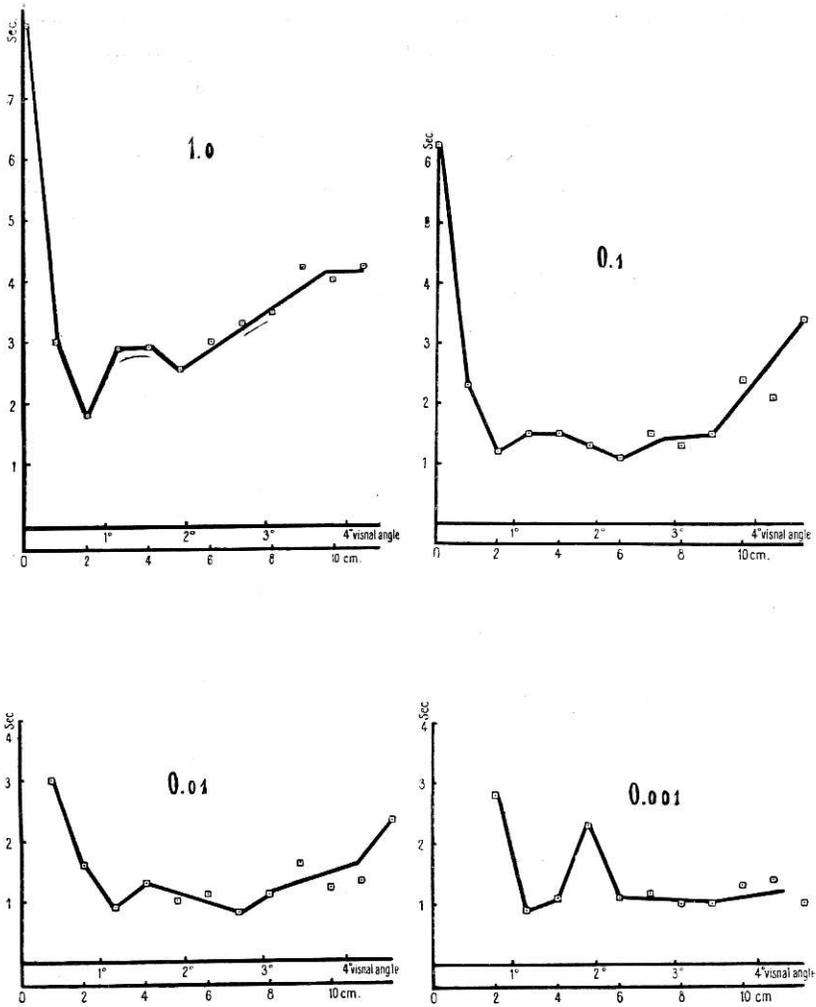


Fig. 9—12.

Results with observer G. The brightness of the stimulus is indicated on the diagram. For explanation, see text.

Working within too narrow limits of intensity and only with central fixation, *Juhasz* (2), as well as *Creed* and *Granit* failed to notice any effect of altering the intensity of the stimulus upon the latency. But from our experiments it follows that in any part of the retina, except *perhaps* at the edge of the fovea the latent period increases with the intensity of the stimulus. The greater the difference of intensity separating two series, the fewer the number of exceptions to this rule. Another effect of increasing the intensity of the stimulus is also shown by our curves; the size of the hump in the curve increases with the strength of the stimulus, *i. e.* the corresponding lengthening of the latency is greater in the transitional area than in the surrounding parts. With weaker stimuli even the existence of a hump is to be questioned. With stronger stimuli some indication of a displacement of this elevation in the curve towards the fovea is given by our results, but whether it is casual or not cannot be decided. The curves show other irregularities besides, but it is significant that »the hump« is always to be found in the same region whereas none of the other elevations are repeatable.

Great accuracy cannot be expected from work on subjective phenomena such as after-images; still we find the general outlines indicated clearly enough — though the influence of one possible source of error, inherent in the technique adopted, will have to be considered. A disadvantage of using a good diffusing surface such as a ground glass is that around the stimulus will appear a halo of scattered light, brighter the brighter the stimulus, and more accentuated in the periphery. This will be more visible if, as in our experiments, the background is black. Such a halo was in fact seen regularly with the stronger stimuli, though never very markedly in the centre. In the periphery it also became more extended. This halo, as was to be expected on account of our method, was equally apparent when the stimulus was viewed monocularly through the aperture of an artificial pupil with a diameter of 3 mm., nor did the latency of the after-images thereby undergo any alteration. In the series No. 0.1 the halo was found to be restricted to the periphery. In the fovea as well as in the paracentral area the stimulus was of normal size and limitation. In the

series No. 0.01 the halo had moved still further out into the periphery and with the weak stimulus of series No. 0.001 it was altogether absent.

This zone of scattered light formed a belt of decreasing intensity encircling a spot of great strength of illumination. If our results be accepted as far as the lengthening of the latency with the increase of the intensity of the stimulus is concerned, one consequence of our experimental conditions can be predicted: the weaker intensity prevailing along the edge of the stimulus must cause a faint extended after-image of short latency. Within this image there must appear a later intensification and contraction, due to the centre of the stimulus having a higher intensity and, accordingly, longer latency. This was, in fact, what happened, and so far our views are confirmed. The latency of the intensification and the simultaneous contraction of the larger greyish image to a size approximating that of the stimulus was the one signalled by our observes, as long as a definite two-phase rise occurred; i. e. approximately as long as there was the halo to be seen around the test patch. The early, extended greyish image had the short latency characteristic of the peripheral after-images following weaker stimuli. With this low intensity of the stimulus the peripheral images, like the central ones, rose above the threshold with a constant size and blackness. Only observer A. U. in series 0.001 still noticed the two-phased rise in the outer periphery. In series 1.0 and 0.1 he even had it in the fovea, differing in this respect from the two other observers, who never found this phenomenon very definite in the central part of the field of vision. In series 1.0 it became evident in the transitional area, and, with weaker stimuli, moved towards the periphery behaving in this respect like the halo above mentioned. In series 0.01 it was restricted to the extreme periphery. The influence of this factor upon our results will be reconsidered below.

The difference between centre and periphery, so well borne out by our curves, is less marked with observer A. U. than with the other two. His fovea is, as it were, reacting in a more peripheral manner. From the phenomenological point of view, as mentioned above, his foveal after-images also belong to a more peripheral type than those of R. G. and T. H. A com-

parison of his high-intensity curves with those of his fellow workers brings out the same difference in terms of measurable quantities. In spite of his curves having a very marked hump, the transition from foveal values to peripheral ones takes place more gradually. The typical steep fall of the curve from the centre towards the transitional area is to be found only in the series 1.0. In the other series the curve is flattened out. His humps are nearer to the centre than those of R. G. and T. H. and the rise in the periphery is far more accentuated. If the course taken by our curves be explained as dependent upon the distribution of cones and rods in the retina, it should be remembered that Abney and Watson (3), on functional grounds, have made it highly probable that there are individual variations in the distribution of these retinal elements, and that there even seems to be a small class of persons with rods scattered all over the macula.

In the course of our experiments it was noticed that stronger stimuli invariably caused a lengthening of the duration of the after-images. A similar finding we owe to *Juhasz* (2) for complementary negative after-images. These differences are considerable, the after-images of series 0.001 being fugitive so as to be difficult to detect for an untrained observer, those of series 1.0 lasting for half a minute and more. Yet the latency was found easier to measure than the duration, since eye movements complicate exact estimation of the latter.

4. Discussion.

The explanation given by *Creed* and *Granit* (1) to account for their findings was that the change in the latency from point to point on the retina is determined by the changing character of the receptors. As mentioned above, this was based on the correspondence between the significant parts of the curve and the distribution of cones and rods in the retina. Our curves, corresponding to weaker stimuli, are very similar to those of *Creed* and *Granit*, only that the hump is about 1° nearer to the fovea. Does this fact exclude an explanation along the same lines? In our curves the hump still is outside the fovea and anatomically corresponds to an area in which rods begin to appear, whereas, in the curves of the latter authors, it fell on

an area in which the rods should be expected to come into play in greater force than the cones. The relative activity of rods and cones in vision, to some extent, will alter with different experimental conditions. The dark room was very well illuminated in our experiments; *Creed* and *Granit* had a single lamp of about 80 c. p. in the middle of the room, we had about 200 c. p., shaded by white writing paper, just above the observer's end of the large black case. Another difference between our method and the one used by these authors may also account for the displacement of the hump; viz., the projection background, which was white in their experiments and faintly illuminated, greyish in ours. As recently pointed out by *Ebbecke* (4) the after-images are very much dependent upon the brightness of the field upon which they are developed, being grey or black against a white background, and bright if viewed with the eyelids shut.

When considering all this, and also that our technique allowed of a more rapid change from the stimulating luminous patch to the field used as projection background than the method by *Creed* and *Granit*, we find it probable that these factors might account for the displacement of the hump, and that this phenomenon, so prominent in our curves, is identical with the similar one described by the latter authors.

In order to account for the influence of the brightness of the stimulus upon the hump, it will be necessary to offer first an explanation of the effect of the intensity factor upon the latent period of the after-images in general. The lengthening of the latency, caused by the increase in the brightness of the test patch, seems to be best accounted for by assuming a similarly increasing duration of the *positive* after-effect following the stimulus. The truth of this assumption, which is both simple and in accordance with what is known about the positive after-effects of stimulation, is not invalidated by the fact that positive after-images were not seen in our experiments. It is well known that positive after-images are not seen unless the conditions are especially favourable. (See e. g. *Helmholtz* (5) p. 230, or *Parsons* (6) p. 113). *Ebbecke* (4) has recently shown that the physiological after-effect (*Nacherregung*) does not necessarily presuppose visibility of the after-image. The after-effect as

determined by the excitability is very resistant to extraneous influences whereas any intercurrent stimulus will make the after-image vanish. *Ebbecke* also finds that positive after-images can be shown to exist as long as negative ones, if the background is suitably chosen. His results support our assumption that the lengthening of the latency of the negative after-image following the increase in the brightness of the stimulus is due to a lengthening of the positive after effect in the area excited. The long duration of the negative after-images following strong stimuli then would show that both the negative and the positive processes behave similarly with respect to the brightness of the object, as on *Ebbecke's* results would be reasonable to expect.

The elaboration of a detailed hypothesis to account for the influence of the intensity of the stimulus upon the latency of the after-images is a matter of minor importance. Of greater interest seem to us the facts relating to the hump in the curve, but especially that increasing the brightness of a peripheral test patch has essentially the same effect upon the latency as moving the stimulating object to the centre. It is, as it were, identical in principle with making the peripheral retina behave more and more like the fovea. The central part of the curve is much less influenced by the increase in the intensity of the stimulus. As the intensity increases all the values relating to the fovea and its edge — except at abscissa 0 in the case of observer A. U. — are subject to smaller increments than the values relating to the peripheral part of the curve including the transitional area. The periphery thus seems to undergo a greater change of function when the intensity increases, than the centre, which needs a high intensity in order to give rise to any after-images at all, and which is also working near to its threshold for after-images. The compared values give a lengthening of the latency in the centre amounting to about 1.3 times as the intensity increases; the corresponding figure for the periphery is about 3 or 4 times. Observer A. U., as pointed out above, in this respect also is behaving somewhat differently, although the change along the curve is in the same direction as for his fellow workers.

It has been pointed out by *Parsons* (7) that the peripheral retina behaves like a central retina of diminished sensitivity.

But if the stimuli are strong enough this difference disappears: then even the fields of vision for colour extend to the extreme periphery. The explanation of this peculiar ambivalency of the peripheral receptors was given by *Granit* and *Harper* (8). Using the flicker method they found that *spatial summation* plays a much greater role in the periphery as, indeed, is to be expected on account of its structure. Increasing the size of the object was shown to raise the fusion frequency — as does an increase of the intensity of the stimulus — by a much greater amount in the periphery than in the centre. This was shown to be due to synaptic reactions (summation) in the ganglionic layers of the type described by *Sherrington* and coworkers in central structures. Summation also was shown by *Granit* (9) to take place in the periphery between four patches separated by an unstimulated area; which, indeed, shows the great importance of this factor in peripheral vision. If the intensity is low there is much less, if any, peripheral summation in the light adapted eye as shown by *Granit* (9) and also by the work of *Henius* (10) on thresholds of brightness. The great summative power of the periphery with stronger stimuli also might give the clue to an explanation of the fact that the peripheral retina with respect to the latency of the negative after-images with bright stimuli behaves like the fovea. Its lack of sensitivity is overcompensated for by spatial summation, which makes the effect of the increased intensity of the stimulus relatively more prominent in the periphery than in the centre. *Granit* and *Harper* in an unpublished investigation found the effect of summation to increase gradually when passing out from the fovea to the periphery. This will account for the displacement of the peripheral rise in the curve towards its end when the test light is getting weaker. If the stimulus is weak it will have to be moved further out in order to be influenced by summation. The identical behaviour of the halo around the test patch, as the intensity is diminished, suggests that its greater extension in the periphery, which at least partly is dependent upon the oblique angle of incidence, also is favoured by summation and certainly itself favours summation. *Granit's* (9) experiment with the four separated stimuli definitely proved the existence of a physiological irradiation of the

effect in the periphery. This source of error, being inherent in the eye itself is hardly to be overcome. But as far as the mode of function characterizing the periphery is concerned, our curves probably truly show what ordinarily takes place in the periphery when the intensity of the stimulus increases, namely an extension of the spatial effects. The peripheral retina, as it were, is adapted to the limitations set to it by the refractory system. It has little visual acuity and great summative power.

If the stimulus is weak, then the curves only show a decreasing latency of the after-images when the test patch is moved towards the periphery. If for the sake of the clearness of exposition this be taken as the »normal curve« the question arises as to what is measured by it. Hardly the general sensitivity of the retina to light since the sensitivity rises towards the paracentral area, as shown by *Heinz* and *Lippay* (11). Further out it again diminishes, if, as in these experiments, very small objects are used so that the greater spatial summation of the extended stimuli is not allowed to overcompensate for the lack of sensitivity in the periphery (8). It might be that the curve shows the sensitivity to successive contrast; the phenomena of contrast are said to become more marked towards the periphery. But such an assumption does not amount to more than stating in accordance with the experimental evidence that ours is a curve showing the variation of the specific sensitivity to negative after-images in different parts of the field of vision. The suggestion made by *Creed* and *Granit* (1) that the course of the curve should be accounted for on the basis of the distribution of the receptors on the retina still offers the best way of relating the findings to the structure of the organ employed. Hence it follows that each retinal point stimulated, because of its own particular receptor pattern, will be characterized by a certain value of the latent period of the negative after-image as long as the spatial effects from adjacent receptors can be disregarded. This has been done for the »normal curve« by using *small objects of low intensity*. Upon the »normal« low intensity curve relating the latency of the after-images to the distance from the fovea, the effects of an increased intensity of the stimuli should be superimposed.

As far as the general lengthening of the latency of the after-

images with the brighter stimuli is concerned this was accounted for by assuming a similarly increasing duration of the positive after-effect. The striking influence of the intensity of the stimulus upon the hump in the transitional area makes this complicated phenomenon but little easier to understand. Below it will be shown that dark adaptation does not influence a hump, caused by a comparatively weak stimulus, the weakest possible that still definitely gives this phenomenon. This result is well in accordance with the fact shown by our intensity series, that with weak stimuli no hump is to be seen. We, therefore, should be justified in drawing the conclusion that a state of adaptation and a strength of stimulus that favours scotopic vision has nothing whatever to do with the hump. Restated in terms of the duplicity theory: favouring pure rod vision does not favour the processes determining the lengthening of the latency in the transitional area. Yet, this does not exclude the suggestion of *Creed* and *Granit* that the hump is due to some kind of interaction between the rods and cones. It is hardly conceivable that a strong stimulus should not stimulate the rods, but, if this be so, then the hump certainly would be more of a cone phenomenon. More likely is the alternative explanation, that the rod function undergoes a change when the strength of the stimulus is increased. And this change of function, as was shown by *Granit* (9), at least involves an augmentation of the spatial effects. Strong stimuli break through the synapses and sum with one another, whereas weak stimuli do not, or sum to a lesser degree. This evidently means greater possibilities for interaction of any kind between stimuli of greater intensity, and is well in accordance with our finding that humps occur only if the stimulating light has been bright enough. Besides if the hump were not due to some kind of interaction between different receptors, it would be difficult to understand why it actually is of the nature of a hump in the curve, i. e. why the values on either side of it are lower. There is less reason to suppose that the receptors in this region should be altogether different from those on either side, the less so as the localization of the hump seems to be subject to variation with the experimental conditions. Still it seems always to be localized to what *Creed* and *Granit* termed the transitional area

where the change from an organ dominated by cones to one dominated by rods takes place. This tends to support the assumption that the hump is due to interaction between rods and cones. But whether this spatial effect actually is of the nature of an inhibition of the after-image remains doubtful. It may equally well be of the nature of a reinforcement of the positive after-effect, as suggested by our explanation of the effects of the increased intensity upon the stimulus.

As far as the hump is concerned the main outcome of these experiments is that it probably owes its appearance to some kind of interaction in the synaptic connections of the rods and cones. The evidence at hand, its localization to the transitional area, its dependence upon stimuli over a certain minimal intensity, the fact that strong stimuli are known to favour interaction, (8), that the periphery further out reacts in the same way to the increasing intensity, all tend to support this view originally put forth by *Creed* and *Granit* (1).

5. *Effect of dark-adaptation.*

With regard to the relation supposed to exist between the distribution of rods and cones on the retina and the latent period of the after-images it was deemed necessary to study the influence of dark adaptation upon these phenomena. A negative result like the one anticipated evidently does not exclude our explanation of the phenomena in the transitional area along the lines developed in this paper, whereas a positive one naturally would have shown that the hump had something to do with rod function as such. Besides, it was thought to be of some interest to compare the influence of the enormous physiological sensitization, involved in dark-adaptation, with the known effects of increasing the intensity of the stimulus.

We need not dwell long upon this subject. The experiments were made after 30 minutes of rest in darkness and the adjustment of the apparatus was completed in the very faint illumination given by a strongly absorbing, dark red lamp. In fig. 13 the filled circles represent the arithmetical means of three such scotopic series, compared with the corresponding series in photopic vision. The stimulus was given an intensity approximating that of No. 3 of the earlier series, as with a

stronger stimulus any influence of dark adaptation in the area excited would have been destroyed during the long fixation period. Such experiments were many times repeated, but we were never able to trace any influence of dark adaptation surpassing the variations set by the method and the experimental conditions in general.

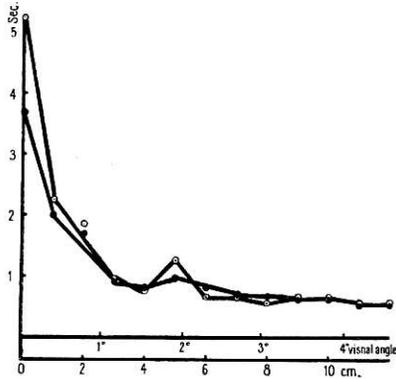


Fig. 13.

Dark adaptation and light adaptation compared. Results with observer H.

Summary.

The latent period of the negative after-images following stimulation with a circular test patch of 22' of visual angle of diameter has been measured under known conditions. The brightness of the test patch has been varied on an arbitrary scale in steps of 1/10 by means of Tscherning neutral tint glasses. For each intensity used the latency has been measured at different distances from the fovea and curves have been plotted relating the latent period of the after-images (ordinate) to the visual angle subtended by the distance from the centre of the stimulus to the fixation point (abscissa).

With weak intensities the latency shortens rapidly towards the edge of the fovea and then less rapidly towards a point situated about 5° out in the periphery. In the middle of the fovea no after-image can be elicited with very weak stimuli.

With strong stimuli the latent period of the after-images increases and between 1°30' and 2° there appears a hump in the curve showing that in this area the lengthening of the latency is relatively greater than in the surrounding parts. The latency may increase about 2 or 3 times in the periphery when it only increases about 1.3 times in the centre.

The lengthening of the latent period of the negative after-images with the strength of the stimulus is accounted for by assuming a similarly increasing duration of the immediate positive after-effects of excitation.

The much greater effect of increasing the brightness of the test patch in the periphery is explained on the basis of recent experiments showing that with strong stimuli the summative power of the periphery increases so as to overcompensate for its lack of sensitivity as compared with the centre.

The hump is assumed to be due to interaction in the synaptic connections between the two types of receptors.

Dark-adaptation does not influence the latency of the after-images nor does it influence the size and localization of the hump.

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