ON THE LATENCY OF NEGATIVE AFTER-IMAGES FOLLOWING STIMULATION OF DIFFERENT AREAS OF THE RETINA.

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INTRODUCTION.

ALTHOUGH the after-images following sudden flashes of light have been the subject of careful investigations and measurements, notably by von Kries (16), McDougall (19), and Fröhlich (6), quantitative data regarding the after-images following longer lasting fixation of white or coloured objects are few in number and of a non-systematic nature. The earlier literature on the subject is mostly concerned with their rather complex phenomenology and its bearing on that particular theory of colour vision which in each case has inspired the investigation. It is not surprising, therefore, that cautious physiologists have been shy of attempting in this way to procure information about vision, and have turned to processes where quantitative work is at least as easy to accomplish and is more amenable to interpretation. (Cf. for example, Parsons (22), p. 114.)

Yet some experiments by Juhász (15) indicate that the latent period preceding the development of such after-images can be estimated with an accuracy sufficient for analysis. We therefore undertook a preliminary study of the problem, and, relating it to comparatively well-known anatomical and physiological facts, measured the latency of the negative after-image of a white object in different parts of the field of vision. One of us (R. G.) had recently been making comparable experiments in which "after-images of movement" were studied with reference to the area of retina on which the primary image fell (8, 9).

Our investigation is confined to the ordinary persistent after-image (McDougall's "secondary image" (19), some other writers' quaternary image), which is readily seen when, after fixation of any well-defined object, the gaze is transferred to a point on a uniform background. Purkinje (23) first described the rhythmical disappearances and re-appearances of these images, and their periodicity has been more recently studied by Grünberg(10). Our earlier experiments were also directed to elucidate the factors influencing the periodicity, and it was only later that we were struck by certain features of the latency and determined to concentrate our attention on this latter problem. Our method of experiment was quite unsuitable for observing the much earlier momentary after-images following short flashes (McDougall's "recurrent images"), which, under the names of Hering's image, Purkinje's image (Bidwell's ghost), and the tertiary image, have been extensively studied by others. Some mention will however be made of them in connection with the interpretation of our results.

METHOD.

The experiments were carried out in a photographic dark-room in the laboratory, lighted by a single opal-glass electric lamp of about 80 candle-power at one end of the room. Before any observations were made, 20 to 30 minutes were allowed to elapse so that the observer's eyes might become adapted to the illumination. The condition of the eyes in this illumination may be described as one of moderate light-adaptation. Against the evenly black wall at the opposite end of the room from the lamp, white circular discs, provided with a fixation point, were observed binocularly. The discs were of paper coated with a mixture of zinc oxide and barium sulphate, and their illumination worked out at just over 5 metre-candles. The observer's eyes were 1·50 metres from the disc, and the time during which the disc was fixated was (in all experiments except where otherwise stated) 15 seconds. Before each fixation period the observer shut his eyes for 30 seconds in order to get rid of disturbing effects caused by after-images of the objects in the room.

The method of experiment was as follows. The experimenter was provided with a stop-watch, which he started while the observer sat on a stool with a chin rest in front of him. When the second hand reached 15 seconds the experimenter called out "Half a minute," and the observer closed his eyes. The experimenter gave a warning at 40 seconds, and at 45 seconds called out "On." The observer then opened his eyes and fixated the disc. At 60 seconds the experimenter lowered a screen (measuring 64 by 51 cm. and of the same white as the object) over a pulley, thereby covering the disc. The observer rapidly directed his gaze on to a fixation mark placed in the middle of the screen and so arranged as to be directly over the mark previously fixated on the disc. As soon as he saw the negative after-image appear, he said "On," and the experimenter noted the time. For the next observation, experimenter and observer changed places.

The lowering of the screen could be accomplished in half a second, a time short enough for most cases, as will be shown by the actual values of the latent periods measured. With practice on the part both of observer and experimenter, we believe that we have attained accuracy to within 0·2 second, but we are fully aware of the many technical improvements that could easily be introduced in these rather provisional arrangements. The early departure of one of us from England deterred us from embarking on a more ambitious programme.

RESULTS.

Experiments with discs of constant size.

When two discs, each of 6 cm. diameter and with their centres 11 cm. apart, are used as object with the fixation point at the centre of one of them, an untrained observer will notice at once that the negative after-images of the two discs do not appear on the screen simultaneously. After a latent period of 2 to 3 seconds, that of the peripherally situated disc suddenly appears, but nothing is to be seen of the central after-image until a further interval of 2 or more seconds has elapsed. The first phase of the periodic after-image also ends in the peripheral image some seconds before the disappearance of the central image. To study this phenomenon in detail it is advisable to use smaller discs, and for most of our experiments we have employed discs of 1 cm. diameter (22′ visual angle). The after-images are more difficult to observe than those of larger discs, and some practice is required before accurate records can be made.

Fig. 1 illustrates an experiment of this kind with 1 cm. discs at varying horizontal distances from the fixation point. The visual angle subtended by the distance between the centre of the disc and the fixation point is plotted as abscissa, and the latent period of the bluish-black[1] after-image as ordinate. Three discs at different distances from the central fixation point were used simultaneously as stimuli and their after-images timed. The disadvantage of this method is that the exact time relations of two images rising almost together cannot be accurately recorded, but on the other hand more values can be obtained under similar conditions without disturbing effects of fatigue entering in. Experience has taught us that results are unreliable if either observer

[1] The light has a yellow tinge.

attempts to make more than about fifteen separate observations at a single sitting. Each value plotted represents the arithmetical mean of at least three observations, and care was taken that the discs were not

Fig. 1.

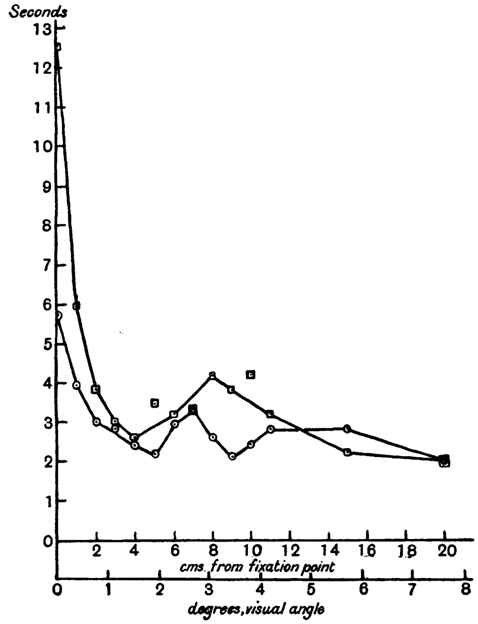

Fig. 2.

Fig. 1. Latency of negative after-images of 1 cm. (22′ visual angle) discs at varying distances from fixation point on horizontal meridian. Experiment of 21. v. 28; three discs used for each observation; each value plotted is the mean of three observations. Fixation period, 15 seconds. The upper curve is that of observer R. G.; the lower that of observer R. S. C.

Fig. 2. The same as Fig. 1. Experiment of 29. v. 28; two discs used for each observation. Fixation period, 30 seconds. Upper curve, observer R. G.; lower curve, observer R. S. C.

too close together. The smoothness of the curve drawn through the points bears witness to the reliability of the method. In the similar experiment shown in Fig. 2, only two discs at a time were used. (This series is one of the few in which we have fixated the object for 30 instead of the usual 15 seconds.) And in a third experiment of the same kind, a curve showing precisely the same features was obtained by observation of single discs.

Fig. 3 shows the same experiment for the vertical meridian. Each point represents the average of two measurements. The object in each observation was two 1 cm. discs, one with its centre either at 0 or at

1 cm. from the fixation point. The other was first moved progressively further out, and then back again towards zero. This set of observations was confirmed by another series taken a few days later. The dotted line

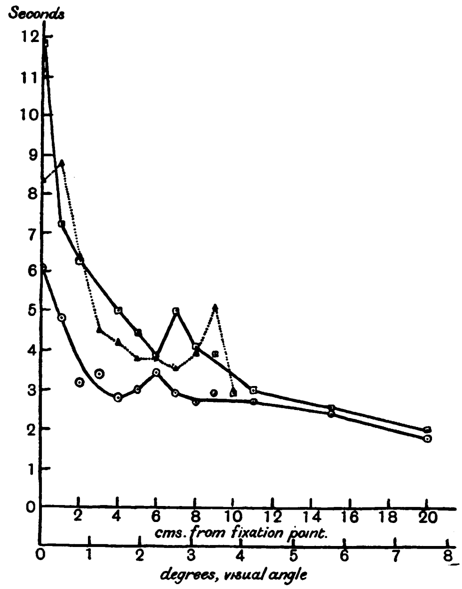

Fig. 3. Latency of negative after-images of 1 cm. (22′ visual angle) discs at varying distances from fixation point on vertical meridian. Experiment of 30. v. 28; two discs used for each observation; each value plotted is the mean of two observations. Fixation period, 15 seconds. Upper curve, observer R. G.; lower curve, observer R. S. C. Dotted line, untrained observer W. S. T. who was unable to maintain his fixation for discs more than 10 cm. from fixation point.

is the curve of a third untrained observer and is less regular than the others. He was in complete ignorance of the purpose of the experiment.

It will be seen that the latency of the after-image is longest in the fovea centralis, and that on passing out towards the periphery, it shortens on an almost perfect curve to a point at about 1° 50′ of visual angle. Then there is a rather sudden lengthening of the latency, which reaches a new maximum at about 2° 30′ from the fixation point. Passing further out towards the periphery, it again, though more gradually, becomes shorter. The second maximum, or "hump," was found with unfailing regularity in every experiment. Its position varied slightly from day to day, but was always between 2° and 3° from the fixation point. It was generally slightly more peripheral in observer R. G. than in observer R. S. C., and more peripheral still in a third subject W. S. T. Sometimes it occupied a relatively broad region of the curve; sometimes the rise in the latency was restricted to a single point. An exploration of the "transitional area" between 1° 30′ and 3° with single discs in the horizontal meridian, each observation repeated three times, confirmed this part of the curve.

Using bigger (2 cm.) discs subtending 45′ of visual angle, and measuring the latent periods of the after-images at a series of points on the horizontal meridian, all of the values for each of us in one experiment fitted well into a comparatively regular hyperbolic curve, with the exception of one which fell out higher. For R. S. C. this reading was with the centre of the disc 3° 25′ from the fixation point, and for R. G. 4° 10′. The hump is therefore probably rather further out with larger than with smaller discs and is less well marked. Our observations on discs of this size are however limited to only two early experiments, and the principal reason for mentioning them is that it was the plotting out of one of them that led to the discovery of the hump. At that time we had no reason to suspect its existence, although it seemed likely, for reasons to be mentioned later, that some change of shape of the curve might appear in that region. Lest it should be said that suggestion influenced our results, we were careful in later experiments to avoid looking at our own figures until the series was completed.

Although struck by the regularity of our findings and its apparent relation to what is known about structural and functional differences between the corresponding areas of the retina, we naturally first considered the possibility of having timed different phases of the after-image on passing out from the centre to the periphery. About the latencies of the images of which the centres were within 1° of the fixation point, there could be no doubt whatever. Until the negative after-image appeared, there was nothing to be seen on the screen except sometimes a bright positive after-image which gave way to the gradually intensifying dark negative image. The after-image of a 1 cm. disc with the fixation point at its centre differed from the others in being much fainter (as also was its primary image), and this sometimes led to its being timed too late or occasionally to its failing to appear at all. With discs more than 1° from the fixation point, R. G. sometimes noticed a bluish image on the screen just as it fell down, *i.e.* with a latency of less than 0·5 second. This image in most cases rapidly vanished, giving place to a short indefinite positive image followed by the ordinary black negative after-image (with a minimum latency of 1·8 seconds). On rare occasions this rapidly vanishing after-effect was also seen by R. S. C.

and W. S. T. There is some doubt as to its nature which will be discussed again in the account of the next experiments. But in the present connection, its nature is less important than the question whether it has interfered with our timing of the first negative phase. Apart from the fact that only one observer was certain about its appearance, it seems to be too early and momentary to be able to interfere with any images other than the most peripheral ones. Besides, it was so faint and rapid with 1 cm. discs as to be scarcely noticeable, whereas the ordinary negative after-image outside the fovea was so black that it could not get lost during the 4 seconds or more of its first phase. It is also significant that the latencies continue to get shorter for some distance outside the point at which the momentary image first appears; the position of the hump, in fact, cannot be exactly correlated with its appearance.

An adequate explanation of our findings can scarcely be attempted at present, but the lines along which it is to be sought for are certainly indicated by the structural differences between the retinal areas tested. The transitional area in our curves appears at a visual angle where, according to Hering(13) and others, the retina changes its structure from that of an organ dominated by cones to a rod organ. The wholly rod-free area is smaller—perhaps restricted to the fovea, *i.e.* about 1° of visual angle (Parsons(22), p. 13), or somewhat bigger (about 2° horizontally) according to functional tests by von Kries and Nagel(17) and by Fröhlich and Vogelsang(7). The careful experiments of Abney and Watson(1) make it highly probable on functional grounds that individual variations in the extent of the rod-free area are to be found, and apparently there is even a small class of persons with rods scattered throughout the macula. But outside an area subtending about 4° of visual angle (corresponding to 2° of the abscissa in our curves, since we are only taking account of the radius), the rods suddenly come into play in greater force than the cones. If this be so, the sudden rise in our curves probably indicates that, as it were, a new organ is now reacting to the stimulus, and that either the latency of the after-image of an object whose primary image falls on rods in this area is longer than that of one falling on cones, or there is some more complicated interaction between the two structures leading to a lengthening of the latent period. Evidence that interaction does occur will be adduced in the next section.

That the hump varies slightly in its position, in its steepness, and in its extent, from day to day seems to be well accounted for by the varying condition of the observers' eyes. Although time was always allowed for adaptation to the illumination of the room at the beginning of each experiment, the conditions were probably not really identical on dull days and on days of brilliant sunshine. Burch((3), esp. p. 212) has shown that the after-effects of bright light last much longer than is generally supposed. The intensity of the primary stimulus may also have varied slightly from day to day, as the ordinary town supply of electricity was used to feed the lamp. That the hump should be less sharp with larger than with smaller discs is also consistent with the explanation outlined above, for the transition from cone organ to rod organ (or mixed organ) will be less abrupt in the former than in the latter case.

Even if the rod-free area is confined to the fovea, at least the first three points plotted in Figs. 1, 2 and 3, *i.e.* those of 1 cm. discs with centres at 0, 1 cm., and 2 cm. from the fixation point, are values for after-images corresponding to primary images falling wholly on cones. The initial steep fall is therefore exclusively a cone curve, and is indicative of functional differences between the cones in the centre of the fovea and those further out. Other evidence pointing in the same direction has been brought forward by French (5) and by Heinz and Lippay (11), who state that the threshold of difference of brightness is higher in the centre than at the edge of the fovea. It is tempting to imagine that to the right of the hump the cone curve is replaced by a rod curve of similar hyperbolic shape.

Finally a few remarks must be made about the phenomenology of these images. The appearance of momentary negative images of extremely short latency, and of positive images preceding the first phase of the ordinary negative image, has already been described. Both the primary image and the after-image of a disc in the centre of the field of vision differ from all others in that they are fainter, and the after-image has fewer phases. This is no doubt due to the inferior sensitivity to light of the fovea as compared with the rest of the retina. On the other hand the contour of a peripheral after-image is naturally less distinct than that of a central one. Black negative images always tend to be surrounded by a bright halo. Phases after the first are progressively fainter and have less distinct contours. The development of the first negative phase shows interesting alterations—perhaps best observed with a 2 cm. (45′) disc—on passing out from the centre of the field of vision. Images close to the fixation point rise very gradually to a maximum of blackness; those in the "transitional area" begin in a similar gradual way, but then a sudden intensification occurs and the plateau is reached at once; further out still no slow rise is found, but the image suddenly appears in its maximum intensity[1]. In every case the disappearance of the first phase is equally sudden. It is always interesting to compare the sensations evoked in consciousness by appropriate stimuli with the mechanical responses of the muscles of an unconscious animal in purely reflex action. The slow rise of the central after-images (? cone response) may be regarded as analogous to what Liddell and Sherrington (18) have called "recruitment" in reflex action; while the sudden rise (? rod response) is reminiscent of the "*d'emblée*" type of reflex.

With 1 cm. discs, the primary image at points more than 2° from the fixation point frequently pops in and out during the 15 seconds' observation period. This fact was studied by Aubert (12) and by Holth (14), and is probably essentially the same as that described by Dunlap (4). In one observation at 7° 30′ from the centre of the field of vision, one of us estimated that the primary image disappeared in this way for more than half of the 15 seconds' fixation period. The after-image was, however, as intense and distinct as ever, and appeared with the usual latency. It therefore seems that the after-image is not dependent on the perception in consciousness of the primary object, but is conditioned merely by previous excitation of some part of the retino-neural apparatus.

Experiments with discs of varying size in the centre of the field of vision.

The observations detailed above suggest many further simple problems, but the time at our disposal has not allowed us to tackle systematically more than one. This was to investigate the relation between latent period of after-image and size of disc, other conditions being kept constant. Juhász (15) gives a few figures showing that the complementary after-image of a red object appears after a shorter latency with large objects than with small. Our findings confirm and amplify his.

In making these observations, we were going back to a type of experiment which, at the beginning of our work, we repeated many times for the sake of practice, but which we did not, at that time, think simple enough to continue. When reconsidering the first complete series of these preliminary observations, in which the fixation point was always

[1] Since the above was written, a communication by Walther (25) has come to our notice. He too records the same difference between the development of a central after-image and that of a peripheral one, and mentions the fact that the former are less intense in colour.

at the centre of the disc, it was found that by plotting the visual angle subtended by the *radius* of a disc as abscissa and the latency of its after-image as ordinate, a curve similar to the one for small discs at different degrees of eccentricity was clearly indicated. The first falling part of the curve flattened out at about the same visual angle and was followed by a rise, but as we had not used discs big enough to cover the whole range corresponding to the curve for small discs, we were not in possession of the requisite data for deciding whether the resemblance was complete, *i.e.* whether a renewed shortening of the latent period occurred beyond 3° from the fixation point. We therefore decided to repeat the experiments with discs up to 22 cm. in diameter. Here again, as shown in Fig. 4, which gives the arithmetical means of three series, we met with higher values for the latencies in a "transitional area" between 2° and 3° of visual angle subtended by the radius of the disc. Beyond this point the latencies became shorter. Six separate experiments all supported these findings, and the height of the hump was frequently (as in Fig. 5) more than 1 second. By taking averages of a number of experiments a smoother curve is obtained, but the hump tends to be flattened out since its size, position, and extent vary slightly from time to time just as they do with the small objects. It is immaterial whether the observations are made with series of increasing size, or of decreasing size, or whether the discs are taken in haphazard order. Two experiments in which the visual angle was altered by varying the distance of the observer's eyes from discs of constant size, were less satisfactory but still showed evidence of the hump.

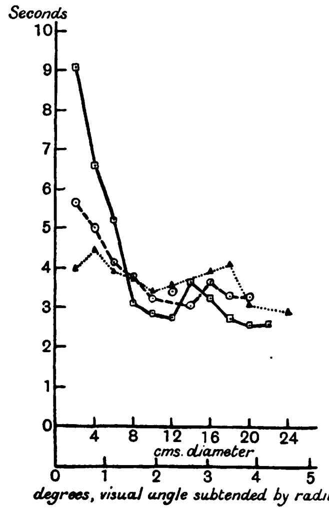

Fig. 4. Latency of negative after-images of discs of varying diameter with the fixation point at their centres. Continuous line, observer R. G.; broken line, observer R.S.C. Each value plotted is the mean of three to five observations from the experiments of 8. vi. 28, 11. vi. 28 and 12. vi. 28. Fixation period, 15 seconds. Dotted line, untrained observer W. S. T. Means of two to four observations from experiments of 6. vi. 28 and 13. vi. 28.

Suggestion can, we believe, be eliminated as a factor in our records by three considerations. (*a*) When attention is concentrated on seeing the first sign of the after-image, it is impossible to judge time accurately, and the observer was afterwards often surprised to find how mistaken he had been in his estimate of the relative lengths of some of his periods. (*b*) We were careful not to look at our own records until each experiment was completed. (*c*) Fig. 4 shows two experiments in which a third untrained observer, who was quite ignorant of the results we were expecting, took part. His curve bears a certain resemblance to his other curve with the small discs (Fig. 3), and is unlike both of our own. The peak of his hump occurred with the 18 cm. disc in each of the three experiments of the present type at which he made observations.

A number of interesting deductions can be drawn from these findings. If we take the curve drawn as a continuous line in Fig. 4 as paradigm, the behaviour of the after-image of the 12 cm. disc (2° 17′ radius) is worthy of attention. The whole image invariably appears at the same moment, although the steep descent of the curve from 2 cm. to 8 cm. might lead one to expect that the latency of its central part would be considerably longer than that of its edge. The process of development of the after-image does not seem to need more than a start from the periphery in order at once to be set going all over the area previously stimulated. Since the central area can be regarded functionally as a blind spot in this experiment, the phenomenon is exactly comparable with that filling up of the blind spot corresponding to the optic disc, which, in normal vision, has led to so much investigation and discussion. The facts may be expressed as a general law by saying that the latency of the after-image of the disc as a whole is that corresponding to the region of retina on which the image of its edge falls.

A further important application of this rule is seen in the case of discs of 14 cm. and 16 cm. diameter. Their edges fall in what we have termed the transitional area, where the latent period is longer than that in areas more central and more peripheral. One might anticipate therefore that the after-image would first appear as a ring of about 12 cm. diameter and then, either gradually, or perhaps at once, spread inwards and outwards until the disc was complete. In practice nothing of the kind occurs. There is no sign of a negative after-image at the end of the latent period characteristic of a 12 cm. disc. Not until 1 second or so later does the after-image appear, and it is seen from the first as a complete dark disc. The edge seems to be the determining factor, and the after-effects in consciousness of previous stimulation of areas of retina within that edge seem to be inhibited for about 1 second. Whatever the explanation may be—whether psychological or physiological, if such a distinction be of any value—the finding as such illustrates the great importance of contours in vision, and also sheds light on the means employed to overcome the difficulty of possessing in the retina two structures (rods and cones) of different sensitivity and functions, and to combine them in use as a single sensory organ. For if we were right in our previous argument in interpreting the hump as due to the excitation of rods, we have here in the transitional area the rod mechanism coming into action in overwhelming force and actively inhibiting the after-effects which would otherwise have followed stimulation of cones. Such an assumption is not altogether new. It has been adopted by P. von Liebermann and by Müller (20, 21) to account for some experiments on the foveal scotoma in scotopic vision, and one of us (8, 9) has used it to explain some observations on the after-effect of seen movement.

It has been seen that, so far as their latent periods are concerned, the behaviour of the after-images of discs of varying size bears a close resemblance to that of after-images of small discs at varying angular distances from the fixation point, and that the visual angle subtended by the radius of the former can be correlated with the degree of eccentricity of the latter. The same is true also of their phenomenology, which is very much easier to observe with these large discs than with small. Positive images were frequently (but not invariably) seen both before the first negative phase, and between later negative phases, with all sizes of disc. Large discs gave after-images with more phases and a longer total duration than did small (cf. Juhász (15)), but their contours were less sharp. Phases after the first were always less black and less well defined. Frequently they were also patchy, but it is noteworthy that the dark patch invariably included a considerable length of edge and was never in the middle of the field previously occupied by the disc. In the third and later periods it was rather unusual for the image of the whole disc to be visible throughout, but some part of the edge was always the first portion to appear and the last to disappear.

Observer R. G. saw the early momentary image or ghost (described in the last section) with great regularity in these experiments. It was not present with small discs, but appeared as soon as the radius reached a visual angle of 1° 30′, and then became darker and clearer with further increase in size of the disc. It was therefore seen central to the transitional area, and persisted throughout this region and beyond it. With the larger discs employed, the image actually timed was separated from the ghost by a much shorter interval than when observations were made in the transitional area. Sometimes with very large discs the two almost appeared to overlap. It is clear then that the hump on our curves cannot be dependent on timing the ghost in some cases and the ordinary negative image in others. Even if, for purposes of argument, we count the ghost as R. G.'s first period, the second period now shows the hump, which, as we believe, ought rightly to be ascribed to the first. Other observers occasionally saw the ghost with big discs. As to its nature, there is every reason to believe it to be a characteristic of rod vision—perhaps Purkinje's image, which, as Fröhlich and Vogelsang(7) have lately shown, always jumps the fovea. So soon as the primary image falls on a sufficient number of rods, it is seen; but this number is less than that required for the renewed lengthening of the latent period in the transitional area.

Discs of less than 8 cm. diameter show the slow development of maximum intensity in the first phase of the negative after-image that was described as characteristic of areas dominated by cones; while those of more than about 16 cm. diameter give a *réaction d'emblée.* In the transitional area a stepped rise was noticed—at first a gradual process of development, terminated by a sudden jump to the full intensity. The preliminary slow rise was cut short by the second intensification earlier with larger than with smaller discs. This is a matter which requires a few words since it leads to complications in timing the first appearance of the after-image. The surprisingly long latencies which one of us recorded on some days for the smaller discs, we are inclined to ascribe to a relative insensitivity to the feeble early part of the stepped rise. We have made attempts in a few experiments to record at the same time both the beginning of the rise and the point when full intensity is reached. Fig. 5 shows one of these. The intervals given are probably too long for the discs of nearly 14 cm. diameter, where the stepped rise was replaced by a simple abrupt beginning. It is difficult to call out and to record the second point when it follows close on the first, so that the upper of the two curves probably ought to be rather lower. But the hump is quite definite in both. In some of the other experiments R. G. attempted always to time the very first sign of the after-image, and R. S. C. the point at which maximum intensity was reached. The general features of the two curves were always the same.

Experiments with discs of varying size in the periphery of the field of vision.

When experiments of the kind described in the last section were made with the centre of each disc 11 cm. (4° 12′) to one side of the fixation point, the results, as shown in Fig. 5, were entirely different. The latent periods for discs of all sizes were the same, within 0·4 second for one observer, and 0·2 second for the other. In an earlier series, although this remarkable constancy was not attained, there could be no doubt that the interpretation was the same.

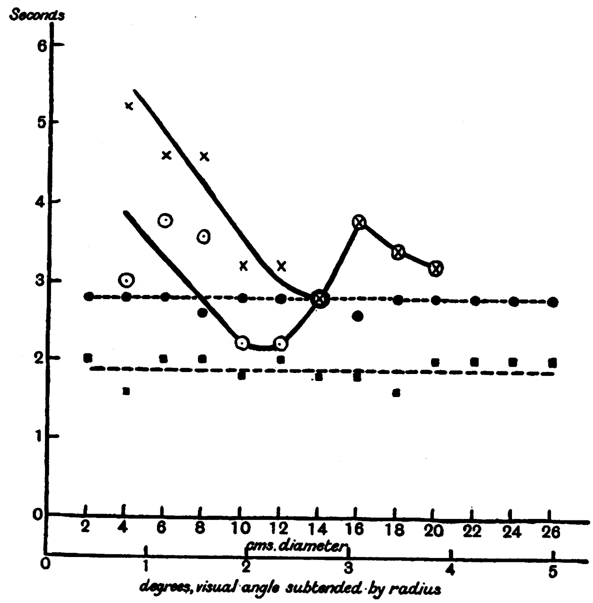

Fig. 5. Continuous line, discs of increasing size in centre of field of vision. Experiment of 8. vi. 28; observer R. S. C. Circles, latencies of first appearance of after-image; crosses, attainment of maximum blackness. Single values. Full description in text.
Broken lines, discs of decreasing size with centres 11 cm. (4° 12′) from fixation point. Single values from experiment of 13. vi. 28. Circles, observer R. S. C.; squares, observer R. G.

The conclusion that the after-images were all essentially alike was further supported by their appearances. R. G. saw a "ghost" before all of them, but it was more distinct and lasted longer with the larger objects. On one of the days R. S. C. saw it consistently too, and it made the timing difficult because it seemed to run into the first phase of the ordinary after-image. The development of all the images was equally sudden. The total duration of big ones was longer than that of small, and their contour was better defined. The 2 cm. ones had such indefinite boundaries that they were difficult to observe accurately and appeared merely as dark smudges. One of us noted that the after-images of small discs were blacker than those of large. This may have been an effect of contrast.

In these experiments the images of discs of 20 cm. and more in diameter must have fallen partly on the fovea, and when the diameter was more than 22 cm. they overlapped the fixation point. The facts that the latency was not then lengthened and that the after-image was seen as a complete whole from the moment of its first appearance, afford further evidence (*a*) of the filling in of a contour across a functional blind spot, and (*b*) of the rods being the controlling power when a large number of rods and a small number of cones are stimulated together. If the conditions were reversed, it might perhaps be possible to obtain evidence of an extensive stimulation of cones inhibiting the after-effects of a restricted stimulation of rods, but we have no evidence on this point.

Discussion.

Two important principles in the physiology and psychology of vision are well illustrated in the experiments described above. One is the importance of form, exemplified (*a*) by the filling in of areas and contours in a blind region of the field of vision, and (*b*) by the observation that the length of the latent period preceding the development of a negative after-image is dependent on the region of retina on which the edge of the primary image falls, and is independent of the position of other parts of the image. An experiment of a slightly different kind is also of interest in this connection. It was mentioned earlier that when the centre of a 6 cm. disc is used as fixation point and a second similar disc is put with its centre 11 cm. to one side, the after-image of the latter appears at least 2 seconds before that of the former, and the periodicities of the two images are independent. If the two discs are now combined into a single figure by filling the intervening space with a white strip 6 cm. broad and the observation is repeated, the appearance of the negative after-image varies with different observers. R. G. sees at first only the dark image of the peripheral end of the object; the blackness then sweeps across like a shutter until the whole figure is complete; but at the conclusion of the first phase both ends disappear together. R. S. C. sees the outline of the whole figure from the moment the image becomes visible, but the periphery is at first darker than the end fixated; both ends fade simultaneously. Two other observers reported that at the very beginning of the first phase they saw the complete figure of uniform blackness and with sharp outline, but that it faded from the distal end inwards. As is only natural, the existence of a contour uniting the two discs therefore modified in each case the appearance and time relations of the after-images evoked by central and peripheral stimulation, and to a greater or less extent synchronised them. An interesting series of rather similar observations has been reported by Rothschild(24).

The second principle is the interaction which occurs between the various receptors stimulated by a primary image. In our experiments this manifested itself as inhibition of the cone mechanism by the rod mechanism. We have no information as to the anatomical site of the process, but in view of the recently published work of Adrian and Matthews(2) on interaction of neurones in the conger eel's eye, it may well take place in the retina.

On the factors other than the area of retina stimulated, which influence the length of the latent period, our evidence is for the most part of a negative kind. Juhász(15) found that the latency shortens as the size of the disc increases. Our experiments show that this is approximately true when the centre of the disc is the fixation point, but that when the centre of the image is outside the macula, the areal extent of the primary image is devoid of influence. In other words, the *number* of receptors stimulated is of no significance (at any rate with discs subtending more than 22′) provided the edge of the image falls predominantly on receptors outside our "transitional area." The changes in latency with discs in the centre of the field of vision are due, not to any effect of spatial summation, but to the fact that the edges are falling successively on receptors of changing character.

Juhász also says that within wide limits the latent period is not dependent on the intensity of the primary image, and that for short durations of the primary stimulus the latent period shortens as that duration is lengthened. With both of these statements our findings are in complete agreement. A comparison of Figs. 1 and 2 shows that for the cone part of the curve the latencies after 30 seconds' fixation are consistently shorter than those after 15 seconds' fixation. On two occasions we have measured the latent periods with various discs under the usual and under greatly increased illumination. On one occasion the illumination of the object was increased tenfold by using a second lamp. The experimenter interposed his shadow between this lamp and the screen at the end of the fixation period, so that the field on which the after-image was projected remained constant. The latencies of the after-images of five discs, the smallest 2 cm. and the largest 18 cm. in diameter, were not sensibly affected, though, as between the various discs, they ranged from 2 seconds to 9 seconds. The actual figures are given below, those in brackets being for the strong illumination. Their standard of accuracy is probably not as high as usual owing to the disturbing conditions of experiment for observer and experimenter.

	2	4	8	14	18 cm. diam.
R. G.	8·0 (6·0)	4·6 (4·6)	2·0 (1·8)	2·8 (2·8)	2·8 (3·0) seconds
R. S. C.	5·4 (6·2)	(2·4)	2·2 (2·2)	2·4 (3·0)	2·6 (2·4) seconds

On the other occasion, the illumination of both object and screen was increased threefold by bringing the lamp nearer. Unfortunately only two discs were observed, but the result was as follows:

	2	4 cm. diam.
R. G.	9·0 (7·6)	7·0 (7·0) seconds
R. S. C.	6·0 (6·0)	4·0 (4·2) seconds

These rather fragmentary observations (strongly supported however by Juhász) are mentioned because they make it highly improbable that variations in the size of the pupil influence the latency of after-images. In any case such variations in the pupil in response to light cannot, of course, explain the hump in any of our curves, nor indeed any part of the curve in Figs. 1, 2, and 3.

SUMMARY.

1. The latent periods preceding the development of the negative after-images of white circular discs have been measured under known experimental conditions. Using small discs of constant size at varying distances from the fixation point, the latent period is longest in the centre of the field of vision, shortens rapidly to a point about 2° from the fixation point, then increases to a new maximum between 2° and 3° from the fixation point, and thereafter again shortens.

2. The second maximum or "hump" in the curve is interpreted as being due to the rods replacing the cones as the dominant receptor organs in and beyond this area. Changes in the appearance of the after-image lend support to this idea.

3. The after-images of discs of varying size in the centre of the field of vision were next investigated, and it was found that a precisely similar curve was obtained by plotting the visual angle subtended by the radius of the disc as abscissa and the latent period as ordinate. The latency of the after-image of the disc as a whole is that corresponding to the region of retina on which the image of its edge falls.

4. This finding is a striking illustration of the importance of contours in vision, and also affords evidence of inhibition of the cone mechanism by the rod mechanism. Observations on the phenomenology of the images amplify and confirm the argument.

5. The latent periods of the after-images of discs with their centres in the periphery of the field of vision are (within wide limits) independent of their size.

6. The factors which influence the length of the latent period are briefly discussed.

Mr W. S. Tegner, Scholar of New College, kindly acted as observer in a number of these experiments.

REFERENCES.

1. Abney, W. de W. and Watson, W. Phil. Trans. A, 216. pp. 91–128. 1916.
2. Adrian, E. D. and Matthews, R. This Journ. 65. pp. 273–98. 1928.
3. Burch, G. J. Proc. Roy. Soc. B, 76. pp. 199–216. 1905.
4. Dunlap, K. Amer. Journ. of Physiol. 55. pp. 201–11. 1921.
5. French, J. W. Trans. Opt. Soc. Lond. 21. pp. 1–33. 1920.
6. Fröhlich, F. W. Grundzüge einer Lehre vom Licht- und Farbensinn. pp. 38–45. Jena, 1921; Zeitschr. f. Sinnesphysiol. 52. pp. 60–88. 1921.
7. Fröhlich, F. W. and Vogelsang, K. Pflüg. Arch. 207. pp. 110–16. 1925.
8. Granit, R. Zeitschr. f. Sinnesphysiol. 58. pp. 95–110. 1927.
9. Granit, R. Brit. Journ. of Psychol. 19. In the press.
10. Grünberg, K. Zeitschr. f. Biol. 61. pp. 73–92. 1913.
11. Heinz, M. and Lippay, F. Pflüg. Arch. 218. pp. 437–47. 1927.
12. Aubert, H. Physiologie der Netzhaut, pp. 97–105. Breslau, 1865.
13. Hering, E. Pflüg. Arch. 61. pp. 106–12. 1895.
14. Holth, S. Det normale synsorgans indirekte stirreblindhed. Norsk Mag. for Laegsvidenskaben. Kristiania. Tillaeggshefte, July, 1896.
15. Juhász, A. Zeitschr. f. Sinnesphysiol. 51. pp. 233–63. 1920.
16. von Kries, J. Zeitschr. f. Psychol. u. Physiol. d. Sinnesorg. 12. pp. 81–101. 1896; 29. pp. 81–98. 1902.
17. von Kries, J. and Nagel, W. A. Zeitschr. f. Psychol. u. Physiol. d. Sinnesorg. 23. pp. 161–86. 1900.
18. Liddell, E. G. T. and Sherrington, C. S. Proc. Roy. Soc. B, 95. pp. 299–339 and 407–12. 1923.
19. McDougall, W. Brit. Journ. of Psychol. 1. pp. 78–113. 1904.
20. Müller, G. E. Darstellung und Erklärung der verschiedenen Typen der Farbenblindheit, pp. 141 et seq. Göttingen, 1924.
21. Müller, G. E. Nachrichten v. d. Gesellsch. d. Wissensch. zu Göttingen. Math.-Phys. Kl. pp. 225–8. 1924.
22. Parsons, J. H. An Introduction to the Study of Colour Vision. 2nd ed. Cambridge, 1924.
23. Purkinje, J. E. Beobachtungen zur Physiologie der Sinne, 1. p. 105. 1823.
24. Rothschild, H. Arch. für Ophthalm. 112. pp. 1–28. 1923.
25. Walther, A. Pflüg. Arch. 77. pp. 53–69. 1899.