ON INHIBITION IN THE AFTER-EFFECT OF SEEN MOVEMENT

BY

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1. Criteria of the duration of the after-effect.

Different authors (1, 2, 8, 14) have measured the duration of the peculiar after-effect of seen movement, which, as is well known, consists of an illusion of movement in a direction opposite to the one presented, so that the possibility of getting quantitative relations for these after-effects under varying conditions must be regarded as within reach. Nevertheless, in measuring the duration of such a subjective impression as the one in question, there are certain difficulties to be encountered, which different observers might solve in different ways, thereby invalidating comparisons otherwise justified. Even the same observer, if not used to the method, might adopt different criteria at different trials when timing his after-effects of movements. This, however, for the average subject can be overcome by practice. The ordinary precautions to be taken in visual experiments involving fixation of an object left aside, the special difficulties here to be met with seem to arise from the retina being a double organ, partly dominated by cone-vision, partly by rod-vision. As is well known the peripheral retina is extremely sensitive to movement, and phenomenologically also peripheral impressions of movement are somewhat different from those of the central retina.

In the after-effect of movement these differences are exaggerated. Easiest to measure is the after-effect of a purely central movement, for this is steady, of a comparatively constant and slow speed (after a first sudden rush), and at the end rapidly runs down to a full stop. The illusion, if projected on an object in the field of vision, nearly always produces an apparent movement, not only within the projection of the area stimulated, but also of the thing itself if it be of a size not much exceeding this area. The purely peripheral movement evokes a most peculiar impression of an extremely rapid 'cloud' passing *over* the objects in the peripheral field of vision. Sometimes the objects in the periphery seem to move too, or rather to fall, but a concentration of the attention on the peripheral movement always reveals its peculiar character of being restricted to an outer molecular layer, the 'cloud,' derived in colour from the objects seen, but not influencing their steady position in space. A curve plotted on its speed as ordinate and duration as abscissa would show a higher position than a corresponding curve of a central after-effect, owing to its greater velocity, but it would finish less abruptly. This introduces a difficulty in measuring the duration of the after-effect, a difficulty which is enhanced by the trouble which most observers find in attending to happenings in the peripheral field of vision. The use of different criteria in timing the after-effects of movement is especially troublesome when the observers have to compare after-effects of the same object, at one distance from the eye falling upon a large retinal area including both rods and cones, at another distance forming a purely foveal image. In the former case there must arise a struggle between two phenomenologically different impressions, in the latter we have a distinct purely central after-effect, easy both to observe and to time. In the former case there is a very gradual disappearance of the illusion; sometimes it may stop moving for a fraction of a second and then start again. Only practice can teach an observer to apply the criterion, adopted in this and in an earlier (5) work: to time the definite disappearance of the illusion in both cases, not *e.g.* the first rapid phase and the beginning of the slower phase, when the retinal area stimulated is large, and the *whole* duration of the after-effect of an image restricted to the fovea. In the paper above referred to will be found figures (p. 110) showing the mean variation of observations under conditions similar to those to be described below.

2. RECOGNIZED FACTORS DETERMINING THE DURATION OF THE AFTER-EFFECT.

In earlier measurements of the duration of the after-effect of movement made by Basler (1), Kinoshita (8) and Wohlgemuth (14) there seems to be general agreement as to the effect of increasing two factors, *i.e.* size of object and velocity of stimulating movement. Both, within limits, lengthen the duration of the illusion following. The alteration of size (Basler), however, was not brought about by increasing the distance from the eye to the object, but by actually using objects of different size. These findings, both of which were confirmed in my previous contribution to the subject (*loc. cit.*), if re-stated in terms of retinal stimulation, mean simply, that the greater, within limits, the retinal area affected by the primary movement in its own direction and the greater its retinal velocity up to a value just short of the flicker point[1], the longer the duration of the after-effect.

Again, making the physical definitions of retinal size and velocity our starting-point, let us consider how an increase in the observation distance should influence the duration of the after-effect of movement. Evidently a lengthening of the distance from the eye to the moving object must produce not only a diminution of the retinal area stimulated but also a decrease in the retinal velocity of the moving object. Accordingly, the duration of the after-effect should become shorter, the above-mentioned factors both influencing the after-effect in the same way. The actual experiment has been carried out (5) and a quite different relation was found from the one theoretically to be expected.

3. EXPERIMENTAL TEST OF THESE FACTORS.

The apparatus used consisted of a drum covered with alternating black and white stripes, each of a width of 1 cm. This was observed through a square opening in a screen (in some experiments directly observed) for a rotation time of 30 seconds, and steady fixation of a central mark was continued until the after-effect had totally ceased. The speed of the movement was at the rate of about 10 cm. per sec. The duration of the after-effect was measured by means of a stop-watch. The whole

[1] There seems to be some difference of opinion as to the relation between the velocity of the primary movement and the maximal duration of the after-effect. Wohlgemuth (*loc. cit.* p. 50) finds that the duration increases with the velocity up to a velocity of about 10 cm./sec., which is the maximal speed used in our experiments, whereas other observers have noted increased durations with still higher speeds.

procedure was carried out in a well-illuminated room and precaution was taken to avoid fatigue, variations in adaptation, fixation, etc.

Briefly stated, the result without exception was that the after-effect lasted only for a moment (3–6 seconds), when the drum (15 × 15 cm. in most of the experiments) was viewed from a distance of about 25–50 cm.; on increasing the distance the duration of the after-effect became longer, reaching a maximum of about 10–15 seconds (somewhat varying with different observers) at a visual angle of about 2–4°. The dotted lines in Figs. 1–3 represent similar observations, the ordinates being duration in seconds plotted against visual angle on the abscissa. Theoretically the curves would be expected to have their maxima removed further out on the abscissa. The optima should, according to the laws above mentioned, be at a big visual angle corresponding to a short observation distance, even making due allowance for disturbances of fixation and shading, which do not enter into account at a distance of 25 cm., more than at longer distances, but might influence the results from about 15 cm. upwards. At these last distances also the reaction to the shape of the drum as a figural unit, a factor, the importance of which recent psychological work has emphasized (4, 12), might play a rôle, since the contour of the drum is difficult to perceive when facing it from very near. But this factor is a purely phenomenological one and cannot be estimated as to its influence from any other point of view. As we got the same results with smaller moving objects, and as from about 20 cm. further out no distinct alteration in the impression of the figure takes place, we should be justified in looking for an explanation along other lines.

4. Possible influence of the rods in diminishing the duration of the after-effect.

Some possibilities of explaining the phenomenon found have been discussed in the previous paper and some have been experimentally excluded (*loc. cit.*). The most probable line of reasoning, which the experiments recorded in the present paper also test, relates the experimental results to structural differences between centre and periphery of the retina. The optimum duration effect lies with different observers between 2 and 4° of visual angle. Now, the rod-free area measures about 2° 20′ of visual angle (3), but very few rods are to be found within an area subtending about 4° of visual angle (3), and their specific influence cannot in a well-illuminated room be considerable. It therefore seemed a highly probable assumption that the after-effect of movement in the rods exerts a restraining influence upon the development of the illusion of movement in the cones, which normally should predominate our perceptions by central fixation. The explanation is here given in the somewhat schematic way, customary when distinguishing between rod- and cone-vision, *i.e.* by relating the perceptions to the end-organ, where an anatomical basis for the differences between peripheral and central vision is to be found. Nothing is thereby hypothecated as to the real nature and localization of the process. One might perhaps think that the phenomenological differences between the central and the peripheral after-effect of move-

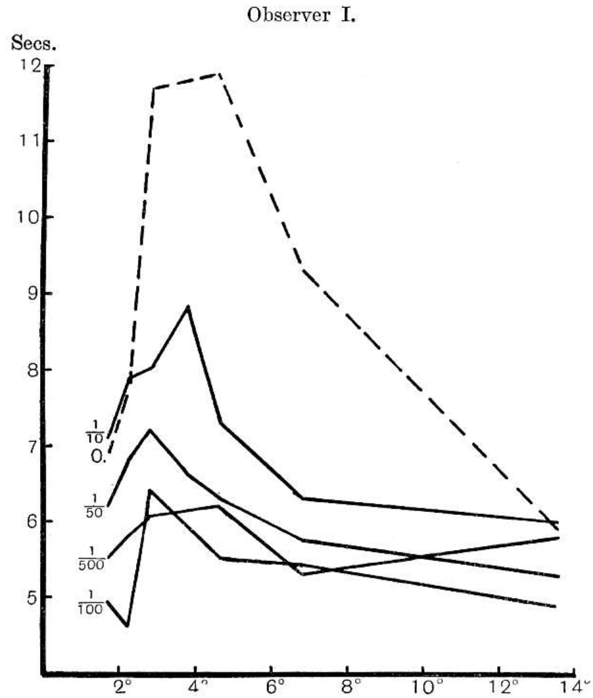

Fig. 1.

ment would suffice to explain the shortening in the duration of the illusion at large visual angles, the whole problem thereby assuming a purely psychological aspect, being referred to as a case of interaction or struggle between two rival impressions. That such an explanation does not seem likely will be shown later (pp. 155–6). Let us therefore examine a corollary of the hypothesis set forth above.

5. DARK-ADAPTATION AND THE DURATION OF THE AFTER-EFFECT.

The question to be investigated is the influence of dark-adaptation upon the course of the curve relating duration of after-effect to visual angle or distance. The mutual relations between rods and cones will be altered, the part played by the rods in vision being increased. For this purpose the Tscherning photometric glasses[1] were used, which allow of measurable constant degrees of scotopic vision, being graded so that

Observer II.

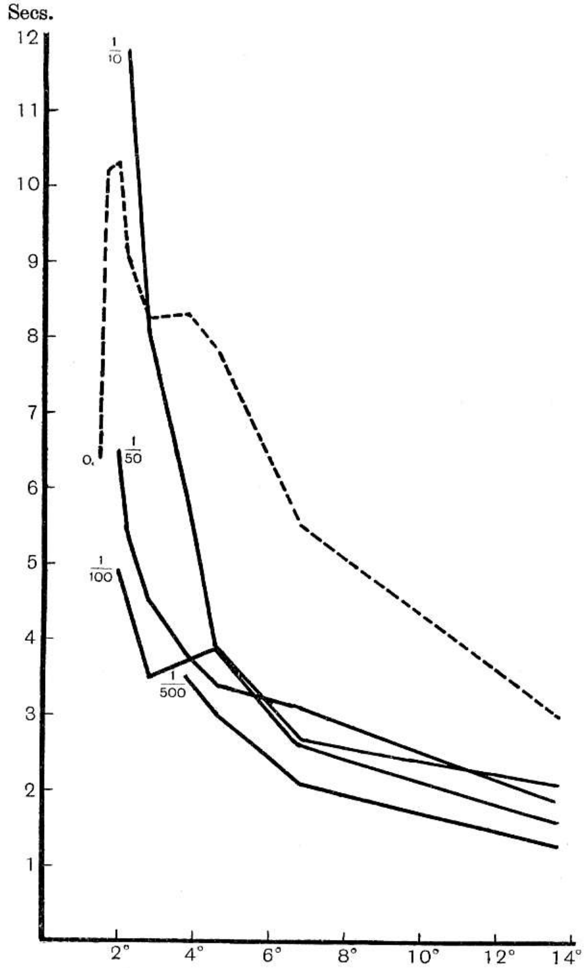

Fig. 2.

glass No. 1 lets 1/10 of the total light through, glass No. 2 $1/10^2$ or 1/100, etc. The glasses are neutral grey and fit to a dark rim, shutting out any passage of disturbing light into the eye. After half an hour's adaptation

[1] The photometric glasses, devised by Prof. M. Tscherning, are obtainable from N. Fischer, 32 Aaboulevarden, Copenhagen, and were kindly lent to us by Prof. Groenholm, University Ophthalmological Hospital.

the experiments were begun. Monocular vision was adopted. The arrangement was the one mentioned above, a screen restricting the diameter of the image to 12 × 12 cm. One experiment consisted of three readings at each distance used for a given degree of dark-adaptation. The experiments corresponding to the different curves reproduced were, for obvious reasons, conducted on different days.

It seemed important to have a standard for the normal durations of the after-effect at different distances, for comparison with the figures obtained in dark-adaptation. These are represented by the

Observer III.

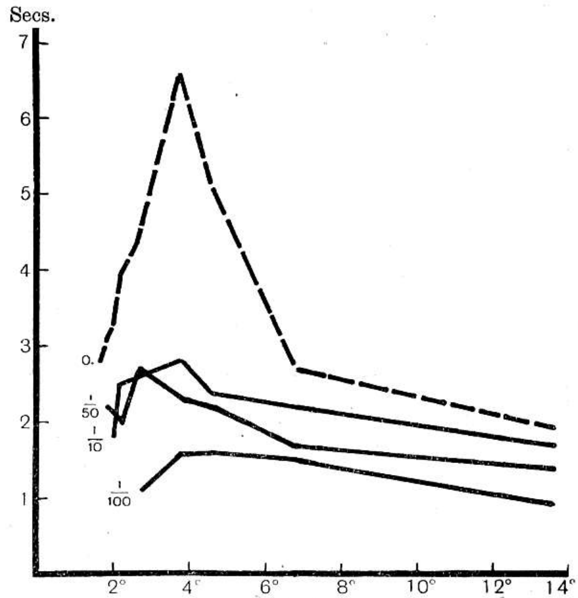

Fig. 3.

dotted lines in the diagrams (Figs. 1, 2 and 3). The distance was varied at intervals of 50 cm., the single values being in each case the averages of the three measurements taken. Reading the diagram from the right to the left, *i.e.* following the variation of the duration with an increasing observation distance, the gradual rising of the 'standard' curve towards a maximum at about 3–4° is apparent, as pointed out above. Observer II consistently (Fig. 2) reaches the maximum at a smaller visual angle than observers I and III, and the post-maximal shortening is not always recorded.

The continuous lines are plotted from corresponding experiments by scotopic vision—to apply the excellent term introduced by Parsons (11)—

the figures against them showing the amount of light passing through the glass used and thus indirectly the degree of dark-adaptation. It will be noted that the adaptation curves in all the diagrams lie below the 'standard' curves, at least in the theoretically important area between their maxima and their right-hand minima. The general tendency of the scotopic curves is to order themselves in the co-ordinate system according to the degree of dark-adaptation, but there also seems to be a minimum of duration, below which the after-effect does not go as long as the moving drum is clearly visible. At high degrees of dark-adaptation the image, when falling upon the rod-free area, was faint, and did not give rise to any measurable after-effect. Hence the shortening of the lowest curves on the left in Figs. 2 and 3. Observer I noticed an increase in the duration of the illusion at short distances at extreme degrees of scotopic vision, one example of which is given in Fig. 1. It seems probable that this is a case of predominance of the peripheral effect over the faint central one. But these cases, where the sensitivity of the fovea is negligible compared with the highly sensitized periphery, are not the theoretically interesting ones. The curves representing experiments at lower degrees of scotopic vision allow of far more reliable conclusions, especially as there is one outstanding feature common to them all, *i.e.* the low position of the curves in the region between their maxima and right-hand minima at large visual angles. There the influence of dark-adaptation is relatively greatest. In most cases also the maxima are lower than in the standard curves, but nevertheless, the values of the upper curves again approach each other further to the left where the image is becoming purely foveal. Observer II reaches a higher maximum with his uppermost adaptation curve (1/10), but in spite of that the curve is much below the 'standard' one with the intermediate values. These observations all seem to agree about the important point, showing that the impairment in the perception of the after-effect of movement at slight degrees of dark-adaptation is relatively strongest, where, indeed, on our hypothesis, it would be expected to occur. At short distances the values even for a completely light-adapted eye are small and therefore cannot decrease very much, especially as the dark-adaptation might tend to bring out the peripheral long-lasting effect, since so great a part of the image falls upon sensitized rods. An increase in the inhibition would naturally make itself felt at distances where the corresponding retinal areas include comparatively few rods which, only if highly sensitized, could display their inhibitory activity. The reduction of the maximal durations at about 3–7° of visual angle is similarly to be explained. As mentioned above, this area is not to be regarded as wholly rod-free, but the rods are few and surrounded by groups of cones, and thus might well be supposed to be negligible in good illumination, whereas dark-adaptation reveals their influence in the shortening of the after-effect of movement. As the upper adaptation-curves again approach the 'standard' curves when the image becomes purely foveal, the effects described above can hardly be wholly accounted for in terms of the decreased amount of stimulating light reaching the retina through the eye-glass used. This factor does not explain why the region of short-lasting after-effects at relatively slight degrees of scotopic vision is extended to distances further out from the revolving drum, but is not extended to the point where the image becomes restricted to the fovea. Besides, it is to be remembered that dark-adaptation, although limited in degree, takes place also in the fovea. The careful measurements recently made by Hecht (6) show it to be less, only about 17 times zero value, than previously estimated, but for glasses letting through 1/10 and 1/50 respectively of the 'good' illumination[1] used its sensitizing influence on the cones is not to be disregarded. There seems to be no doubt about the values of Hecht relating to the cones, as the development of the foveal adaptation in his experiments follows a different course from the one found for rod-vision.

It will be noticed that there are appreciable individual differences between our observers, and in our experiment somewhat surprising are the short-lasting after-effects of observer III, which also soon ceased in purely foveal vision at higher degrees of dark-adaptation.

6. DISCUSSION.

The general findings of the experiment, as pointed out above, tend to support the hypothesis previously put forward to account for the peculiar influence of the observation distance on the after-effect of movement. They also render the alternative hypothesis of a struggle between two phenomenologically different impressions of movement (see above, p. 151) less plausible. But another fact would, on this last-mentioned hypothesis, be at least as difficult to understand: why, namely, the duration of the illusion does not increase as the retinal image is diminished by actually diminishing the moving object, the observation distance being kept constant. It then decreases as stated above. Why does the after-effect only increase in duration when the

[1] Lacking a photometer we had to be content with this rather arbitrary estimation of the illumination used.

diminishing of the retinal area stimulated is brought about by lengthening the observation distance? Here seems to be an apparent discrepancy; in the former case a shortening, in the latter a lengthening of the duration of the after-effect[1], and in both cases the alteration introduced implies a diminishing of the retinal area stimulated. Evidently the decrease in the size of the object at a given constant distance is the less complex relation, and when this leads to a shortening of the after-effect of movement it must be regarded as an elementary functional connection, the course of which a concomitant decrease in the inhibitory influence of the rods cannot but retard. But when the stimulating objects occupy nearly the whole field of vision, the after-effect again becomes very faint[2], probably owing to the inhibition again being capable of appearing when strengthened to an extraordinary degree. Otherwise the duration of the after-effect increases and decreases with the size of the image. Again, when lengthening the observation distance, the apparent size of the object does not alter appreciably within the distances in question, and the drum also seems to present an apparent constancy in the speed of its movement. Now there are numerous experiments on vision showing that the apparent qualities of objects (see *e.g.* (4), pp. 210–14) as regards measurable data of sensations have an influence similar to the corresponding objective qualities. In our experiments therefore one would expect the duration of the after-effect of movement to remain, within limits, constant, or slightly to diminish with increase of the observation distance. This is, as it were, a background against which the inhibitory influence of the rods can be demonstrated with smaller objects than otherwise would be needed, there being no working principle of opposite sign to encounter.

7. General problems involved.

Whether this inhibitory effect of the rods upon the function of the cones, as postulated above, is something peculiar to the perception of movement or has a bearing upon retinal function in general, is a question the answer to which further experimenting must furnish. But it should be mentioned that G. E. Müller (9, 10) has brought forward some evidence tending to show that the rods display a similar activity with

[1] It might be noted that parallel series showing this discrepancy are to be found in the previous paper on p. 101.

[2] Wohlgemuth (14), p. 72) states that no after-effect occurs when the moving object is very large, occupying almost the whole field of vision, whereas von Szily (13), p. 124) has noticed an after-effect running in the *same* direction as the primary movement.

regard to colour vision. From a biological point of view there is much to be said in favour of the existence of such an inhibition, at least as far as the perception of movement is concerned. A danger approaching an animal from the periphery of its field of vision would, if the centre be subject to inhibition, strike its attention in a still more efficient way than a higher sensitivity to peripheral movement alone could bring about.

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