Conclusion

As we have seen, there were centuries of futile attempts before the first successful measures of stellar parallaxes were made. By modern standards the instrumentation used for these measures was crude, and thus the results obtained were remarkable. Even with modern instrumentation, such as the new Navy telescope, all possible precautions must be taken to attain the required precision. The displacements to be measured on the photographic plates are in all cases small, only a fraction of the diameters of the photographic star images from which the parallactic shifts are determined. Even with the fine optics of the new telescope the photographic images will have diameters of the order of 100 to 150 microns (1.3 to 2.0 seconds of arc), while the parallactic shifts to be measured will in most cases be less than 5 microns, and the mean error for the resulting parallax will be about 0.5 micron. With such tolerances there is little room for either instrumental or human error.

References and Notes

1. J. T. Mayer, *Mathematischer Atlas* (Augsburg, 1745).
2. One parsec = 3.1 × 10^{13} km = 3.3 lt yr—the distance corresponding to a parallax of 1 second of arc.
3. *Astrometry* is defined in *Webster's New World Dictionary* as "the branch of astronomy dealing with the measurement of planets, stars, etc. and their positions and movements."
4. S. Newcomb, *The Stars* (Putnam, New York, 1901), pp. 323–326.
5. L. F. Jenkins, *General Catalogue of Trigonometric Stellar Parallaxes* (Yale Univ. Observatory, New Haven, Conn., 1952).
6. K. Aa. Strand, *Basic Astronomical Data* (Univ. of Chicago Press, Chicago, 1963), pp. 58–59.
7. S. L. Lippincott, *Astron. J.* **62**, 55 (1957).
8. K. Aa. Strand, *ibid.* **67**, 706 (1962).
9. *Cassegrain focus* refers to the optical arrangement of a reflector in which the secondary mirror reflects the convergent beam of the primary mirror through a hole in the center of this mirror to the focal plane behind it.
10. The coma is the comet-shaped image, produced by an optical system, of a point source of light not on the optical axis.
11. A. van Maanen, *Contrib. Mt. Wilson Obs. No. 111* (1915); *No. 391* (1929).
12. F. E. Ross, *Astrophys. J.* **77**, 243 (1933).
13. W. J. Luyten, "Final Report of Bruce Proper Motion Survey," *Publ. Obs. Minnesota No. 15* (1960), vol. 2.
14. H. L. Giclas *et al.*, *Lowell Obs. Bull. No. 89* (1958); *No. 102* (1959); *No. 112* (1961); *No. 120* (1963).
15. F. E. Ross, *Astrophys. J.* **81**, 156 (1935).
16. S. Vasilevskis, *Astron. J.* **67**, 464 (1962).
17. R. H. Weitbrecht, *Review Sci. Instr.* **28**, 122 (1957).
18. The Hartmann test plates were evaluated by R. K. Riddle of the U.S. Naval Observatory. The detailed data will be published elsewhere.
19. A. B. Meinel, *Astrophys. J.* **124**, 652 (1956).

CURRENT PROBLEMS IN RESEARCH

The Role of Afterimages in Dark Adaptation

Bleached receptors continue to signal in darkness, causing afterimages and elevated visual thresholds.

H. B. Barlow and J. M. B. Sparrock

Our knowledge of dark adaptation is in a curious state, for photosensitive pigments certainly regenerate in the dark, but the increase in the amount of pigment is insufficient to account for the drop in threshold. Granit, Munsterhjelm, and Zewi (*1*) obtained the first experimental evidence of this when they compared the electroretinogram response and the pigment concentration of frog and cat retinas after exposure to bleaching lights, and Rushton (*2*) has given a convincing demonstration in man. He showed that, during dark adaptation, the rods do not normally start functioning until over 90 percent of their rhodopsin has been regenerated. Since this final 10 percent increase in pigment concentration accompanies a greater than hundred-fold drop in visual threshold, sensitivity is obviously not directly proportional to pigment concentration, but there appears nonetheless to be a definite relation between them. Dowling found in rats (*3*), and Rushton found in human cones (*4*) and rods (*5*) that it is the logarithm of sensitivity which is directly proportional to pigment concentration. This is a neat empirical relation, but it is theoretically puzzling, and the mechanism underlying the drop in threshold remains unexplained.

Since the changes in threshold during dark adaptation are not accounted for by changes in the proportion of incident quanta absorbed, it is logical to ask if changes in noise level are involved. This is a major factor limiting the performance of radiation detectors, and Barlow has argued both that it is important at the absolute threshold of human vision (*6*) and that it is the noise level that changes during dark adaptation (*7*). The experiment reported here was designed to test this idea, and the results are consistent with it. First, some supporting psychophysical evidence must be given.

When investigating factors influencing the shape of dark-adaptation curves, Crawford (*8*) found a simple way to represent the results. He determined the steady background light that would raise the threshold of a superimposed test stimulus to the value for that stimulus alone after a particular time in the dark. In this way Crawford looked upon dark adaptation as the decrease, with time, of a hypothetical veiling light which he called the "equivalent background." The important simplification achieved by this approach is that the plot of equivalent background against time turns out to be independent of the parameters (for example, area) of the test stimulus used to determine threshold. Rushton (*9*) has recently confirmed and extended these observations in many important ways.

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The intrinsic noise of the retina, which is thought to limit the absolute threshold (*6*), can be expressed in terms of "dark light" (*10*), and it is natural to think of the equivalent background as an elevation of this dark light. According to this idea the presence of bleached pigment in the receptors elevates their dark light, which then slowly subsides to its final value as the pigments are regenerated in the course of dark adaptation, but there is an obvious objection which must be met before this notion can be generally accepted. If intrinsic noise raises the threshold more than 1000 times, why is this not obvious subjectively? Why, at the start of dark adaptation, are we not dazzled by this intrinsic light? What we do see after the bleaching of a restricted region of the retina is the dim, evanescent, positive afterimage, and the question now asked is whether this is bright enough to be the equivalent-background light of dark adaptation.

Craik and Vernon (*11*) were thinking along these lines when they tried to estimate the brightness of the afterimage by matching it with real light. They were able to make measurements on the afterimage for only 2 minutes, but they found that from 30 seconds to 1½ minutes it was sufficiently bright to account for a large part of the total reduction in sensitivity. It was too feeble to have any effect in the remaining 5 minutes of cone-phase dark adaptation, and they found it impossible to use this method to investigate the rod phase of dark adaptation. However, in measuring the brightness of the afterimage they overlooked one of its important features—namely, that it does not move over the retina as do the images of all objects seen in the external world. The eye cannot be kept absolutely still even with careful voluntary fixation; as it moves, real images shift over the retina, whereas afterimages do not. It is true that our subjective impressions tell us the opposite—the external world appears stationary and afterimages appear to move—but this is because eye movements are allowed for before we perceive movement.

Techniques have now been developed (*12, 13*) whereby real images can be stabilized or stopped in one position on the retina. In the simplest method, a light-weight aluminum cup is held by suction on the anesthetized cornea and the test object to be observed is mounted directly on the cup at the focus of a suitable lens (see Fig. 2). No method produces perfect stabilization, but this technique, originated by Yarbus (*13*), is probably the most effective (*14*). When a well-stabilized image is observed it is at first seen clearly, but after a few seconds sharply defined contours become blurred and fine detail disappears. Furthermore, contrast fades, so that what originally appeared as a bright patch of light comes to look grey, differing only slightly from its background. The cause of these changes is itself a matter of great interest, but what concerns us here is that the afterimage, being stationary on the retina, fades like a stabilized image, whereas the image of a patch of light viewed in the ordinary way does not. Clearly, then, to achieve a fair comparison between a real light and a positive afterimage the real light should be presented as a stabilized retinal image.

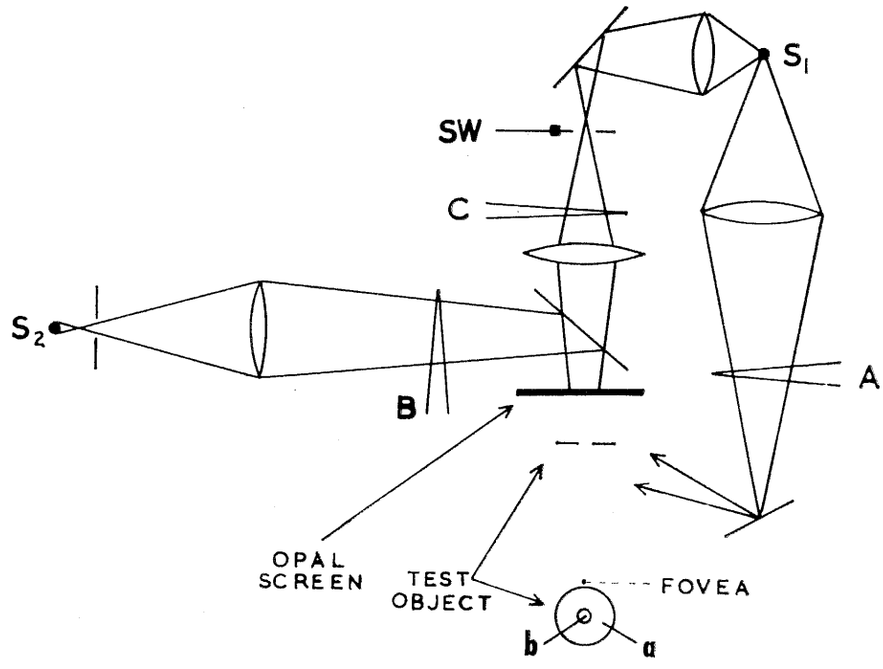

Fig. 1. Schematic representation of the apparatus used for (i) matching a positive afterimage with a stabilized image of variable intensity; (ii) matching two stabilized images; and (iii) determining increment thresholds and dark-adaptation curves. S_1, S_2, low-voltage tungsten lamps operated at controlled voltage; *A*, *B*, *C*, photometric neutral wedges; *SW*, a rotating shutter. The test object is mounted on a Yarbus-type contact lens and moves with the eye. In this diagram the subject would be in the foreground, in line with the test object and the screen.

In the experiment described here a patch of light of variable intensity was presented as a stabilized image and adjusted until it looked as bright as the positive afterimage remaining from previous exposure of the eye to an intense bleaching light. This matching intensity was called the equivalent luminance of the afterimage, and it was converted to trolands, the conventional unit of retinal illumination. To summarize the result, the equivalent luminance of the afterimage was found to be the same as Crawford's equivalent background light, and the subjective appearance of the matching stabilized image is very similar to the afterimage both in its positive and in its negative guises.

Methods

The full experiment requires, first, the production of an afterimage by bleaching a region of the retina, and then the determination of (i) the illumination of the stabilized image that matches the positive afterimage and (ii) the decline in threshold that follows the bleach. In addition one needs to know (iii) the increment-threshold relation for the test light used in determining the decline in threshold (step ii) against a background provided by a real light in place of the afterimage. It is possible to make all these measurements with the final model of the apparatus shown schematically in Fig. 1, but observations on the qualitative similarity of stabilized images and

afterimages were in fact made with a simpler apparatus. With this, it was also possible to produce the stabilized-image equivalent of the negative afterimage, as described later.

In all forms of the experiment the test object was mounted in the focal plane of a Yarbus-type suck-on contact lens modified to give better optical performance. With a lens of this type the image can be stabilized to about ±1 minute (*14*); the residual movements are unlikely to be important in peripheral vision under the low-luminance conditions of this experiment. The test object was mounted on an arm 2 centimeters long attached to the aluminum cup of the contact lens (see Fig. 2). It was a white, plastic, annular screen whose external diameter subtended 28 degrees; the internal diameter subtended 7 degrees. This screen lies eccentrically in the field of view, the center of the hole being 16 degrees from the fovea in the lower visual field. The annular screen is illuminated, on the side toward the subject, by light whose intensity the subject controls by changing the setting of wedge *A* (Fig. 1). Wedge *B* controls the intensity of a beam that falls as a uniform patch of light on an opal screen about 5 centimeters beyond the test object; the subject's view of this patch is limited by the boundary of the hole in the test object. When the subject is matching an afterimage (as discussed later), this beam is turned off. Wedge *C* controls the light with which increment thresholds and dark-adaptation curves are determined. This stimulus light is presented in flashes (of 0.1-second duration) by means of the sectored wheel *SW*. This light, too, falls on the opal screen, hence the subject sees it through the hole of the test object. Light beams were passed through green filters (Ilford 624). With this arrangement (incorporating suggestions made by W. A. H. Rushton) it was possible to determine the dark-adaptation curve and the decline of equivalent luminance of the afterimage following a single bleaching flash, and in the same session the position of the increment threshold curve could be fixed. Furthermore, important control experiments on the feasibility of matching stabilized images could be performed.

Experiments have been made on a total of four subjects, the two authors having been the subjects in the experiments described here. The procedure was as follows. The subject put the contact lens on his eye, which had been anesthetized with Amethocaine, and positioned his head, stabilizing it by the usual headrest and dental bite. He looked at a small red fixation point which was not attached to the contact lens but was movable in a plane just distal to the test object. The subject adjusted it until he saw the central part of the opal screen through the hole in the annular test object. Small movements of the eye around the fixation point, thus adjusted, caused no change in the luminance of *b* (Fig. 1).

It is not easy to adjust the luminances of two stabilized fields to equality, and in order to acquire confidence the subject made some preliminary adjustments of the luminance of *a* while *b* was set at various known values (see the section headed "Controls"). At the same time some preliminary determinations of increment threshold were made by adjusting wedge *C*, *a* and *b* being set to equal luminance. The subject then went across to a subsidiary apparatus (see Fig. 2) in which the bleaching flash was delivered. A flash bulb (Phillips PF5; duration, 24 msec; estimated total luminous flux, 1.7×10^4 lumen-seconds) was placed just beyond the hole in the test object and discharged when suitably aligned. This flash produced a bright afterimage which appeared to fill the hole in the test object. This done, the subject returned as quickly as possible to the main apparatus and proceeded to adjust wedge *A* until the luminance of the annulus *a* matched that of the afterimage occupying the hole *b*. The lights through *B* and *C* were turned off during this procedure. The subject

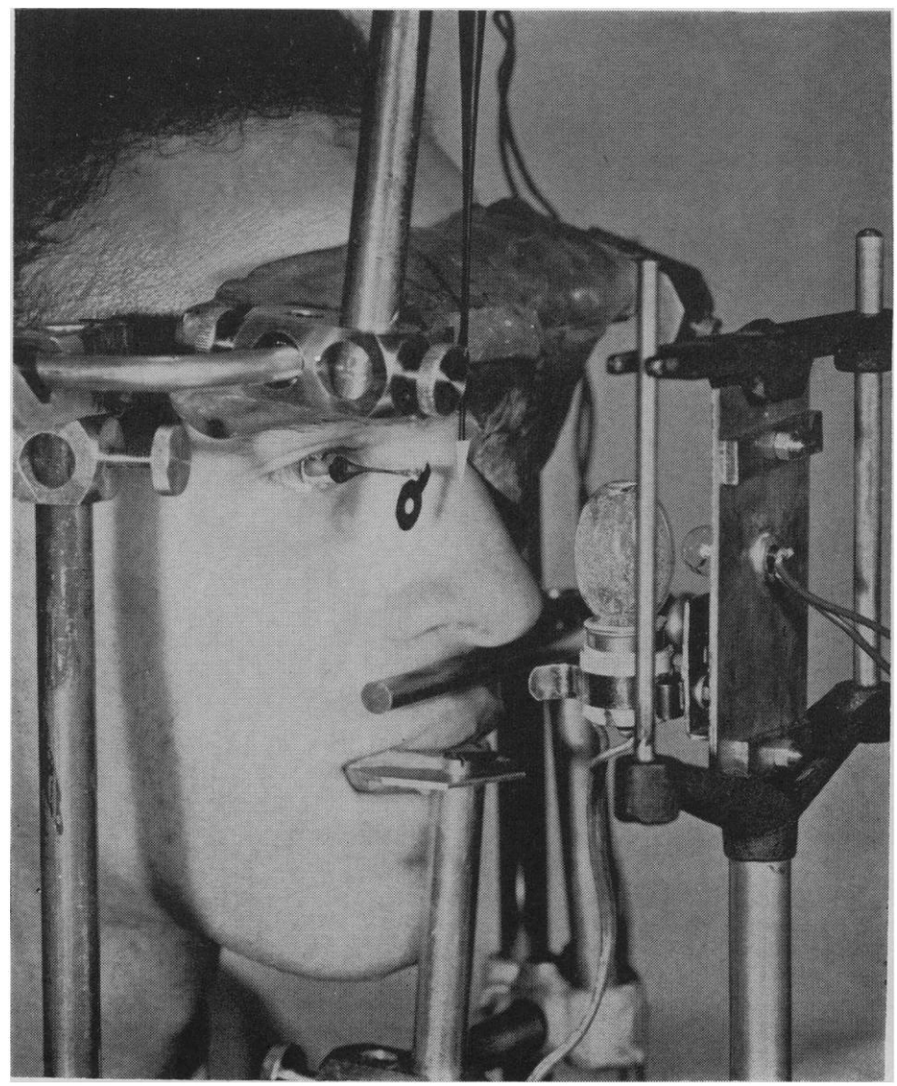

Fig. 2. The subject in position for receiving the bleaching flash. Shields have been removed. The fixation light is indicated by a white triangle.

indicated when he was satisfied with a match, and the operator noted the time and wedge setting, then turned on the stimulus light for determining a threshold. The subject adjusted wedge *C* until he could just detect the flashes in the central hole of the test object. This was the region occupied by the afterimage, and it was surrounded by the annular image that had just previously been adjusted to match the afterimage. Thus he matched the afterimage and determined the threshold alternately until the afterimage finally disappeared, after which the subject made a few determinations of his absolute visual threshold. This entire procedure took about an hour; since a subject cannot comfortably wear this special contact lens much longer than an hour at a time, it was not practical to plot a complete increment-threshold curve in the main testing session. This curve was plotted in a subsequent session, and the preliminary determinations of increment threshold obtained in the main session were used to correct for any slight differences in calibration caused by differences in the alignment of subject, test object, or apparatus.

Quantitative Results

Figure 3 is a plot of results obtained in a single test with H.B.B. as subject. It illustrates the way in which Crawford's "equivalent background" is determined. The solid circles at upper left give the retinal illumination of the stabilized image that matched the afterimage at various times after exposure to the bleaching light. A small correction (described in the section headed "Controls") has been made to offset the fact that when the subject adjusted the annulus to match a central spot of known luminance, he was found to set it at a value 0.11 log units (on the average) below that of the central spot. The points at lower left (open squares) are the thresholds (in arbitrary units) recorded at various times during dark adaptation. Those at lower right (solid squares) are the increment thresholds determined with the same apparatus just before the bleaching flash was delivered. The latter two curves give us the equivalent background—the real background that would have raised the threshold to the value found at a particular stage of dark adaptation. This equivalent background is plotted (open circles) in the upper left coordinate system by reading from the straight line at upper right. The values for equivalent background and for equivalent luminance of the afterimage can then be directly compared. It will be seen that there is no significant difference either in the shapes of the curves or in the absolute values.

Figure 4 shows results obtained on subject J.M.S. for various degrees of bleaching. The circles are results for the full bleaching flash; triangles, for the flash attenuated by a 1.0 density filter; squares, for the flash attenuated by a 2.0 density filter. In each case the open symbols are the equivalent background, derived as described for Fig. 3, and the solid symbols are the equivalent luminances of the afterimages. Again there is good agreement between the two, especially in the later, rod, parts of the curves; here, and quite frequently in other curves, we have noted some disagreement in the levels of the cone plateaus.

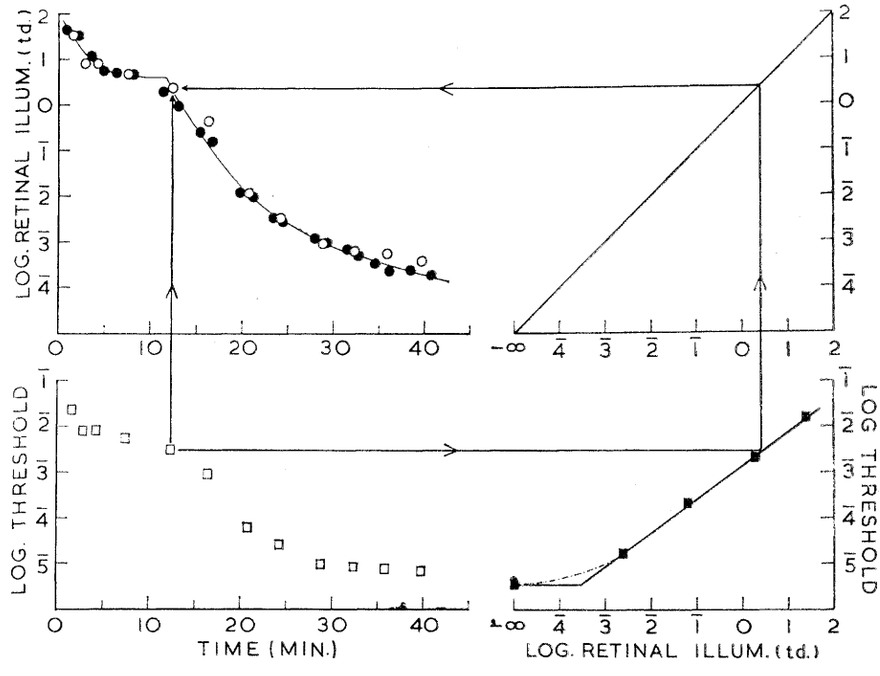

Fig. 3. Comparison of the "equivalent-background" light postulated by Crawford and the equivalent luminance of the positive afterimage. (Bottom left) Logarithm of threshold (arbitrary unit) during dark adaptation; (bottom right) logarithm of increment of threshold (same arbitrary unit) as a function of logarithm of background (in trolands). The absolute threshold is the average of several estimates. (Top left, open circles) Equivalent background obtained by reading from the points of graph at bottom left across to the graph at bottom right, then transposing to the vertical scale by means of the line at top right; (top left, solid circles) equivalent luminance of positive afterimage obtained from the stabilized image that matched it. (Subject, H.B.B.)

Controls

This experiment depends critically on the ability to perform matches when the two fields that are adjusted to subjective equality are both stabilized and do not move over the retina. Such stabilized images fade, and it might well be thought that, after a lapse of time, any difference of brightness would become invisible. Indeed, when one views nonmatching fields under stabilized conditions one is at first struck by the diminution of the contrast between them, but with careful observation it is possible to detect a difference that persists (*14*), and one can learn to use this difference to make matches.

Figure 5 represents an experiment in which the intensity of spot *b* (Fig. 1) was first held at a steady value while a succession of matches was made. Then wedge *B* was moved in such a way as to reduce the intensity of *b* by 0.05 log unit every 10 seconds, while the subject adjusted wedge *A* to maintain a match as well as he could. He made a gesture each time he obtained what he considered a good match, and the times and readings were noted. After the intensity of *b* had been reduced by 4 log units it was held constant for a period, then it was gradually increased to the initial value. The results indicate that an experienced subject can match two stabilized im-

ages, but it should not be thought that this is as easy or as accurate a procedure as ordinary photometric matching. It requires training to acquire the knack of discounting misleading transient effects, and to confine one's attention to the persistent cloudy images (see *14*). There are, furthermore, two sources of error which we have tried to avoid or to offset. The first error occurs when the two fields which are being matched are held at unequal values for a time before the beginning of the matching procedure. After such treatment the subject adjusts the variable field to reduce the mismatch, but he does not move it enough, and for a few minutes he will accept "matches" which are very far from correct. This source of difficulty was minimized by adjusting the stabilized image to a value matching the afterimage as soon as possible after the bleaching flash, and maintaining as good a match as possible thereafter. The second source of error was the tendency—visible in Fig. 5—for the variable annulus to be set at a value lower than the central spot. In Fig. 5 this error averaged 0.03 log unit, and for all available results the average was 0.11. A correction of the latter value was applied in estimating the equivalent luminance of the afterimage.

We have found no difference between thresholds measured against a background decreasing as in Fig. 5 and thresholds measured against steady backgrounds. Finally, control experiments have shown that the intensity of the central spot has a dominating influence on the threshold of a flash added to this spot, the intensity of the matching annulus having only a small effect.

Qualitative Results

With the apparatus so far described, the afterimage was a central disc seen within a stabilized annular image. Though it was possible to get good matches between the disc and the annulus—matches in which the border was scarcely visible—it was not possible to assess how similar an afterimage and a stabilized image appear when each is viewed by itself. This could be done better in an earlier form of the apparatus, in which the test object mounted on the contact lens was a thin plate of opal glass subtending 12 by 24 degrees. The back of the plate was covered with opaque paint except for a square window to the right of the center which was illuminated by a beam of light of variable intensity. The center of the rectangle fell on the foveal region, and the afterimage was delivered (without wearing the contact lens) in such a position as to lie to the left of the fovea. Thus, the subject saw two squares, each of side about 8 degrees, with their centers 6 degrees on either side of the fovea. One of these squares is the stabilized image, the other is the afterimage.

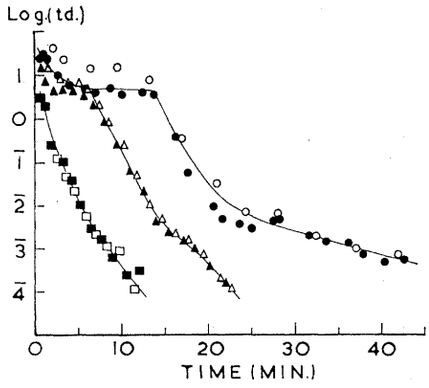

Fig. 4. Equivalent backgrounds (open symbols) and equivalent luminances (solid symbols) of the positive afterimage. All were obtained as described for Fig. 3, but for triangles and squares the intensity of the bleaching light was reduced. Approximate percentages of pigment bleached: circles, 80 percent; triangles, 20 percent; squares, 2 percent. (Subject, J.M.S.)

Such an arrangement is favorable for comparing the subjective qualities of stabilized images and afterimages. Here is what one sees. Both squares of light fade, color desaturating and brightness decreasing, and this fading occurs at about the same rate in the two images if they appeared equally bright initially; both suffer a blurring or loss of detail in the first few seconds, which leads to a characteristic milky, smooth, textureless quality; both disappear and regenerate spontaneously, but the fine detail, color, and contrast lost in the first few seconds are lost for good and do not regenerate. The loss of detail leads eventually to the appearance of a pair of dim clouds, one on either side of the point of fixation. Thus, the subjective appearances of a positive afterimage and a patch of light stabilized on the retina are astonishingly similar.

It might be thought that to reproduce the appearance of a negative afterimage would require complicated manipulations of intensities in the stabilized image. This is not so: the stabilized patch of light appears negative under the same conditions that afterimages appear negative. A region of the retina that has been exposed to a bright light appears as the positive afterimage in darkness, and when it is viewed against a uniform white surface it appears as a region darker than the surround—the negative afterimage. When the opal plate forming the test object is illuminated from the side facing the eye, the afterimage changes from positive to negative in the expected manner, and the stabilized image changes in the same way. This is a surprising result, for light is being added to the whole of the test object: the luminance of the square of opal illuminated from behind as well as in front is higher than its surround, illuminated only from the side facing the eye, but in spite of this, to the subject viewing the image under stabilized conditions, it appears dimmer.

It is therefore possible to mimic negative as well as positive afterimages by a stabilized patch of light, but the matches are not quite perfect. Initially a color difference is noticeable, though this can be reduced by changing the color of the stabilized image. Residual movements of the stabilized image occur and spoil the match, especially at the edges of the test areas. Finally, we have noticed that, although it is usually possible to find a matching intensity for the stabilized image that holds when viewed both positively and negatively (that is, without and with illumination of the front of the opal screen), there are phases of dark adaptation where this is not possible. These occur early in both the cone and the rod phases, when the threshold and the matching intensity of the stabilized image are changing rapidly.

Discussion

The quantitative results show that, irrespective of the extent of bleaching, there is good agreement between the equivalent luminance of the afterimage and the equivalent background. In other words, the threshold during dark adaptation is a differential threshold against the background provided by the positive afterimage. The continued activity causing the positive afterimage is what elevates the threshold when bleached pigment is present; as pigment is regenerated this spurious dark light, or intrinsic noise, de-

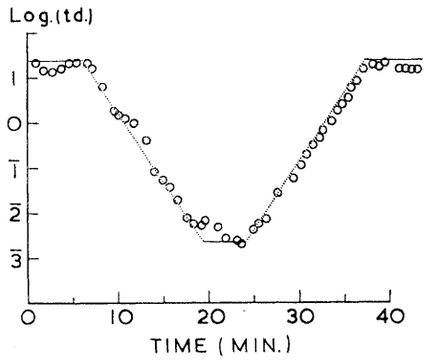

Fig. 5. Control experiment in which brightness matches are made on two stabilized images. (Circles) Settings of wedge *A* that produced satisfactory matches to the center spot *B*, whose luminance is represented by the line. (Subject, H.B.B.)

clines and allows the threshold to drop. Bleached pigment does not make the receptors unresponsive, it makes them noisy.

One may well ask why this explanation for the changes in sensitivity during dark adaptation was not obvious to the earliest investigators, and why Crawford's notion of equivalent background light was not more enthusiastically taken up. The answer is that stabilized images fade, and that as they fade the bright equivalent-background light is converted into the dim positive afterimage. But there is more to this than simple adaptation analogous to the decline of a steady signal in a condenser coupled system. When light is added equally to two faded but unmatched stabilized patches of light there is a reversal in appearance—the brighter patch now appears dimmer, even though the intensity of light falling on it is actually higher. This is intelligible if fading corresponds to the reduction of amplification rather than to the passive decline of signals in a linear system, and it is hard to avoid the conclusion that fading is caused by a mechanism analogous to "automatic brightness control." Furthermore, the fact that the negative afterimage and the negative-appearing stabilized image match when the positive images match suggests that the feedback is actuated equally by genuine light-evoked signals and by the spurious signals which occur when the receptors contain bleached pigment. This must be the mechanism which prevents us from being keenly aware of Crawford's equivalent-background light.

One feature of these results must be pointed out. Just before the break in the dark-adaptation curve the dark light of the rods must be very high, but one finds that at this time the equivalent luminance of the afterimage is constant and apparently determined by the cones. Just after the break the dark light of the cones must be higher than that of the rods, yet it is the dark light of the rods that one matches. Thus, in both cases the brightness of the afterimage is found to depend upon the system which has the lower dark light. The implications are not easy to discern because of the uncertain relation between subjective brightness and luminance in rod and cone systems; it is a strange result for which we do not have a satisfactory explanation.

Conclusion

We can now suggest a definite viewpoint on the relation between the neural and photochemical parts of dark adaptation. Bleached pigment in the receptors does not make them unresponsive to light, it makes them noisy, and in the positive afterimage we actually see this spurious, light-like, disturbance that persists long after the bleaching light has been extinguished. The retina responds to the continued input by reducing the effectiveness of the signals from the receptors in the region, and we see this "automatic brightness control" in operation when a stabilized image or a positive afterimage fades. We observe its consequences when additional light of uniform intensity falls upon the retina and we see the negative afterimage, or the corresponding negative stabilized image. The fact that the equivalent luminance of the afterimage was found to equal the equivalent background light suggests that the increased noise of receptors containing bleached pigment is the fundamental cause of all the changes that occur during dark adaptation.

Summary

When the photosensitive pigments in a patch of retina are bleached, the threshold is elevated for 30 minutes or more, and one is aware of a continuing sensation of light from this region. This positive afterimage was matched by a stabilized image in an adjacent retinal region. The threshold was found to be the same for light falling on the afterimage and for light added to a stabilized image of matching luminance. Thus, the threshold during dark adaptation is the increment threshold against the background of the positive afterimage. It is concluded that the elevation of threshold associated with bleaching is due to a spurious disturbance or "noise" generated in the receptors, and that reduction in the fraction of quanta absorbed is comparatively unimportant. This noise is not normally obvious because afterimages fade like stabilized images. There are indications that fading results from a feedback process akin to an "automatic brightness control."

References and Notes

1. R. Granit, A. Munsterhjelm, M. Zewi, *J. Physiol. London* **96**, 31 (1939).
2. W. A. H. Rushton, *ibid.* **156**, 166 (1961).
3. J. E. Dowling, *Nature* **188**, 114 (1960).
4. W. A. H. Rushton, *J. Physiol. London* **168**, 374 (1963).
5. ———, *ibid.* **156**, 193 (1961).
6. H. B. Barlow, *J. Opt. Soc. Am.* **46**, 634 (1956).
7. ———, in *Photophysiology*, A. C. Giese, Ed. (Academic Press, New York, 1963), p. 163; *Vision Research*, in press.
8. B. H. Crawford, *Proc. Roy. Soc. London* **B123**, 69 (1937); **B134**, 283 (1947).
9. W. A. H. Rushton, *J. Physiol. London*, in press.
10. H. B. Barlow, *ibid.* **136**, 469 (1957).
11. K. J. W. Craik and M. D. Vernon, *Brit. J. Psychol.* **32**, 69 (1941).
12. R. W. Ditchburn and D. H. Fender, *Optica Acta* **2**, 138 (1955); L. A. Riggs, F. Ratliff, J. C. Cornsweet, T. N. Cornsweet, *J. Opt. Soc. Am.* **43**, 495 (1953).
13. A. L. Yarbus, *Biophysics* **2**, 165 (1957); *ibid.*, p. 683.
14. H. B. Barlow, *Quart. J. Exptl. Psychol.* **15**, 36 (1963).
15. This research was supported by grants from the Medical Research Council, London.