J. Physiol. (1962), **164**, *pp.* 168–179
With 1 *plate and* 4 *text-figures*
Printed in Great Britain

TWO NEW PROPERTIES OF FOVEAL AFTER-IMAGES AND A PHOTOCHEMICAL HYPOTHESIS TO EXPLAIN THEM

By G. S. BRINDLEY
From the Physiological Laboratory, University of Cambridge

(*Received* 15 *June* 1962)

This paper has its origin in the following simple observations, which, as far as I can discover, have not been described before except in my preliminary report (Brindley, 1961).

1. *Progressive loss of resolution in foveal after-images.* If a brief and very bright flash of light is cast upon the retina, it produces an after-image which can still be seen 15 or even 20 min later. If the flash falls on the fovea, any fine detail that may be present in the optical image on the retina can during the first minute or two be easily resolved in the after-image, whether this is in its 'negative' form as seen against a bright background or in its 'positive' form as seen in darkness. In later minutes, however, the detail becomes progressively blurred, its finer features disappearing entirely.

2. *The green halo.* If a brief and very bright flash of light of long wave-length is cast upon the foveal retina, its negative after-image is found to be surrounded by a conspicuous green halo which remains visible for at least 15 min. If light of short wave-length is added to the flash, the green halo either does not appear or disappears before the end of the second minute.

A simple photochemical explanation of these phenomena will be introduced and discussed.

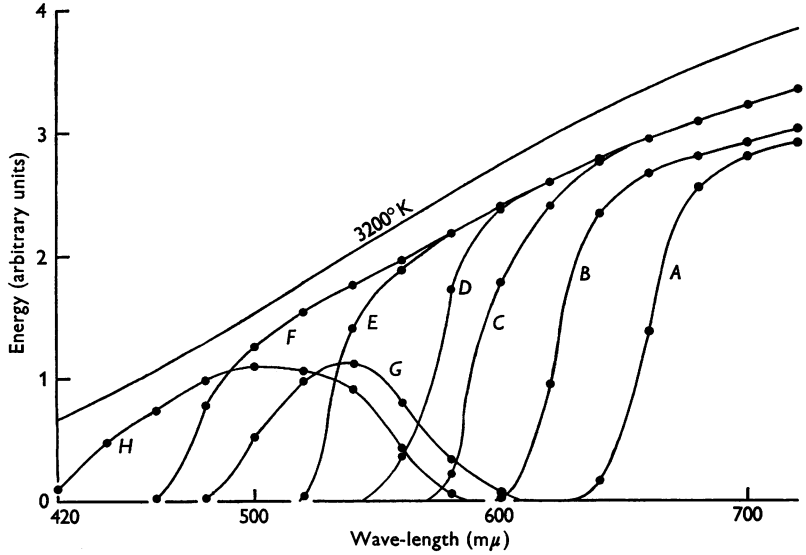
METHODS

Text-figure 1 shows the apparatus used. The horizontally placed helical filament of a 48 W 12 V car headlamp bulb J was imaged by an achromatic doublet on the pupils of the subject's two eyes. Light was admitted through the whole of the natural pupils, which were dilated with homatropine. The camera shutter K was set to give exposures of 0·67 sec. The lens L subtended an angle of 1·5° at either eye. A grating consisting of alternate opaque and transparent bars of equal width could be placed at M, and colour filters either at M or at N. Spectacle lenses corrected the subject's homatropinized refraction, so that L or M was imaged on the retina of each eye. The spectral compositions of the stimuli used are shown in Text-fig. 2. The lamp was over-run at 19·5 V during each stimulus.

After-images were observed on a uniform white screen whose luminance was usually 10 cd.m^{-2}. Observations were usually made every 2 min during the 20 min after an inducing stimulus, and each observation occupied 5–10 sec. Except where the contrary is stated, the eye or eyes were kept in darkness between observations. An interval of 40 min was usually allowed between successive experiments on the same eye.

The detailed observations in this paper were made by the author as sole subject, but the following properties were verified by six other subjects who had normal colour vision as judged from their readings of the Ishihara test: progressive loss of resolution in after-images (p. 170), greater blurring in the older of two after-images of equal strength (p. 171), the presence of a green halo around the pink late after-image of stimulus *C* and its absence around the otherwise similar pink late after-image of stimulus *F* (p. 172), and visibility of the green halo on a screen illuminated with monochromatic light (p. 174). The speed with which resolution was lost and the size and time course of the green halo were similar in all these six subjects.

Text-fig. 1. Diagram of apparatus in plan. *J*: 48 W 12 V car headlamp bulb. *K*: camera shutter. *L*: lens forming an image of the filament of *J* on *P* and *Q*. *M*: colour filter or grating. *N*: colour filter. *O*: spectacle lens. *P* and *Q* right and left eyes of subject.

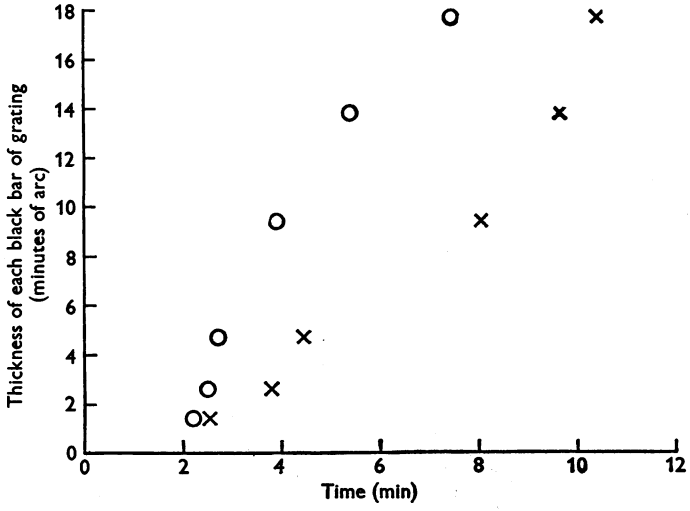


Text-fig. 2. Spectral composition of the stimuli used, calculated from the transmissions of the filters as measured with a Hilger Uvispek spectrophotometer and an assumed colour temperature for the over-run bulb *J* of 3200° K. The filters used were Ilford gelatine filters with the following catalogue numbers: *A*, 206; *B*, 205; *C*, 204; *D*, 202; *E*, 111; *F*, 108; *G*, 404; *H*, 302. The luminance of stimulus *F* was $1{\cdot}1 \times 10^7$ cd.m^{-2}. A 0·67 sec exposure to this through a fully dilated pupil should bleach very nearly all the chlorolabe and erythrolabe of the retina.

RESULTS

General description of the late after-images of brief very bright stimuli

The negative after-images of deep blue stimuli remain yellow in appearance from the first few seconds until they disappear after many minutes. Those of deep red stimuli (e.g. *A* of Text-fig. 2) similarly remain green until they disappear. Stimuli of other colours, including *B*, *C*, *D*, *E*, *F* and *G* of Text-fig. 2, produce after-images which are at first very various in colour, often approximately complementary to the stimulus. After the third minute, however, all these after-images become pink, and their pink colour is independent of the spectral composition of the stimulus, except that if the stimulus contains any blue (as *F* does but *B*, *C*, *D*, *E*, and *G* do not), the after-image is tinged with orange.



Text-fig. 3. Time during which the after-image of a grating remains resolvable as a function of the fineness of the grating. ○: red stimuli of spectral composition *A*. ×: green stimuli of spectral composition *G*.

Progressive loss of resolution

The permanently green after-image of stimulus *A* retains sharp traces of the finest details of the stimulus for about 90 sec, but after this time it becomes blurred rapidly. The after-images of stimuli *B*, *C*, *D*, *E*, *F*, and *G* retain an appearance of perfect sharpness for a little longer than does the green after-image of stimulus *A*, and are first noticeably blurred at about 2 min. When their blurring does begin, it proceeds less than half as fast as after stimulus *A*. A convenient rough measure of the speed of blurring is

the time taken for the after-image of a grating to become so blurred that the direction of the bars can no longer be recognized in it. Text-figure 3 shows this time for various gratings in light of spectral compositions *A* and *G*.

Another measure, less objective but of some interest in connexion with the theory to be discussed, is the time taken for the after-image to bridge a gap. If the inducing stimulus is a uniform circular 1·5° field of green light (spectral composition *G* of Text-fig. 2) crossed by a single black bar subtending 10′ at the eye, the pink negative after-image seen 10 sec after the stimulus has a complete 10′ gap in it corresponding to the black bar, the sensation within this gap being uniform and almost white. After 1 min there are still sharp boundaries 10′ apart, but the edges of the gap, just within these sharp boundaries, are tinged with pink. After 2 min (see Pl. 1, *a*) the sharp boundaries are fainter but still in the same positions, and the pink tinge has advanced about 2′ from each boundary. After 4 min (Pl. 1, *b*) the sharp boundaries have quite disappeared, and only the central 2′ of the gap remains uncontaminated with pink. After 8 min (Pl. 1, *c*) the gap is bridged, but can still just be seen as a band of fainter pink on the stronger pink after-image. After 16 min (Pl. 1, *d*) the after-image can still be seen, but the gap is not distinguishable.

The loss of resolution is not due merely to fading. The following experiment illustrates this. A grating is presented to the left eye at 8×10^5 cd.m^{-2}.sec. Five minutes later the same grating is presented to the right eye at 8×10^4 cd.m^{-2}.sec, and the after-images are examined 2 min after the second stimulus. The after-image that was formed first is found to be the stronger, but much the more blurred.

If a stimulus is weak enough for its after-image to last less than 2 min, then fine detail in it (even as fine as that of a grating with 1′ bars) can be resolved almost until the after-image disappears. But if the stimulus is strong enough for its after-image to last 15 or 20 min, detail as coarse as that of a grating with 10′ bars becomes unresolvable while the after-image is still very easily seen.

The slow loss of resolution proceeds at the same speed when the eye is exposed to light as when it remains in darkness. If at any time after an inducing flash a uniform white surface is steadily fixated, the after-image fades and disappears after an interval of between 10 and 50 sec, but can be brought back by briefly closing the eye and opening it again. This is analogous to the well-known 'stabilized retinal image' phenomenon described by Troxler (1804) and many later writers. During the steady fixation fine detail becomes invisible a few seconds before the whole after-image disappears. Thus illumination of the retina has some short-term influence on the resolution of detail in after-images. However, the following two

experiments show that it has no influence on the slow progressive loss of resolution with which this paper is mainly concerned.

1. Identical patterned stimuli are presented simultaneously to the right and left foveae. For the next 6 min the left eye is kept in darkness, while the right looks steadily at a uniform white screen whose luminance is 10 cd.m^{-2}. A flash of white light of 1200 cd.m^{-2}. sec is then presented to the whole visual field of the left eye to make the general adaptational states of the two eyes roughly equal, and for the next 30 sec both eyes are kept in darkness. If the negative after-images are examined against the white screen at the end of the 30 sec period in darkness, they are found to have become blurred to the same extent (namely that characteristic of an after-image 6½ min old), and to be in all respects indistinguishable.

2. Identical patterned stimuli are presented simultaneously to the right and left foveae. For the next 6 min the left eye is exposed continuously to 10 cd.m^{-2}, the right alternately for 10 sec to darkness and for 10 sec to 20 cd.m^{-2}. Under these conditions the subject is aware of the right eye's after-image throughout almost the whole of the 6-min period, for though it fades during each 10-sec exposure to light or to darkness, each sudden change to the other state renews its strength and conspicuousness. At the end of the 6 min both eyes are kept in darkness for 15 or 30 sec, and the two after-images are then compared against either 10 or 20 cd.m^{-2}. They are found to be in all respects indistinguishable.

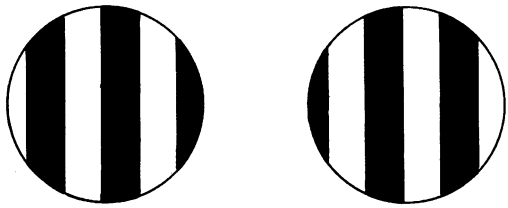
Resolution persists in extrafoveal after-images. If a grating with 10′ bars is presented simultaneously in yellow light (*E* of Text-fig. 2) at 5×10^5 cd.m^{-2}.sec to the fovea of one eye and to the 8° extrafovea of the other, the detail can easily be resolved 1, 2 or 3 min later in the pink after-image of the foveal stimulus and in the greyish after-image of the extrafoveal. It appears sharper in the foveal after-image, as would be expected from the ordinarily inferior resolving power of extrafoveal retina. Six minutes after the stimuli both after-images have faded about equally, but the foveal has become very blurred, while the extrafoveal is as sharp and easily resolved as it was at 2 min. Twelve minutes after the stimuli the grating can still be resolved in the extrafoveal after-image, but the foveal has become blurred to a uniform pink in which no detail can be seen.

The green halo

The after-image of a yellow or green stimulus (*E*, *F* or *G* of Text-fig. 2) is wholly pink from the end of the second minute until it finally disappears after 15 or 20 min; its outer boundary is one between pink and the pure white of the background on which it is seen, and the two are separated only by a zone of weaker pink which is narrow at first but becomes progressively wider as time passes.

The late after-image of a red or orange stimulus such as *B*, *C* or *D* of Text-fig. 2, though very similar in its own colour to the late after-image of a yellow or green stimulus, differs in that it is surrounded by a green zone, whose width varies with time and with the composition of the stimulus between about 0·5° and 2°. Two minutes after the stimulus this halo is a good deal less strongly coloured than the after-image itself, but it fades more slowly, so that after the sixth minute the pink after-image and the green halo are about equally conspicuous. Pl. 1, figs. *e*, *f* illustrate the appearance of the halo.

It can be seen from Text-fig. 2 that the yellow stimuli *E* and *F* which produce no green halo contain all the light that was contained in the red and orange stimuli *B*, *C* and *D*. They differ only in containing light of shorter wave-lengths in addition. Thus light of long wave-length, which by itself would have produced a green halo, can be prevented from doing so if light of shorter wave-lengths is added to it.



Text-fig. 4. Stimuli designed to show that the green halo is not due to stray light (see text).

The green halo is not due to simultaneous contrast. It is well known that a white surface lying close to a pink one can sometimes appear greenish by simultaneous contrast. The very close similarity in colour between the after-images of stimuli *C* and *E*, of which the first is surrounded by a green halo and the second is not, makes it very unlikely that the green halo can be merely of this nature. The influence of any slight difference of hue that there may be between the pink after-images of *C* and *E* can be eliminated by viewing them on a white screen on which is mounted a circular black patch of the same angular subtense at the eye as the inducing stimulus. When the centre of the black patch is fixated, the central after-images are invisible, but the green halo can still be seen with the eye that has been stimulated with *C* and not with the eye that has been stimulated with *E*.

The green halo is not due to stray red light falling outside the geometrical image of the stimulating field. The following experiment demonstrates this: the coarse grating of Text-fig. 4*a* is presented to the left fovea and its 'negative' counterpart of Text-fig. 4*b* simultaneously to the right fovea, both

being illuminated with yellow light of spectral composition *F*. Five seconds later the grating of Text-fig. 4*a* is presented to both foveae, illuminated with red light of spectral composition *B*. It is found that a green halo develops around the right eye's after-image, for which the red stimulus fell on unbleached retina, but none around the left eye's after-image, for which the red stimulus fell on bleached retina. Yet the stray light must have been exactly the same for both eyes.

A given quantity of light of a given spectral composition produces the same green halo independently of its distribution in time over the range 20 *msec to* 2 *sec.* I have already reported (Brindley, 1959) that after-images, excluding their first 15 sec, are determined by the total quantity of light in the inducing stimulus, independently of its distribution in time over the range 15·7 msec to 1·68 sec. The same property holds in the range 20 msec to 2 sec for the green halo; if, with both pupils dilated with homatropine, stimulus *D* is presented to the left eye for 20 msec and to the right for 2 sec with a neutral filter of density 2 in front of the right eye, the green haloes, like the after-images, remain indistinguishable in the two eyes from about 15 sec after the stimuli until their final disappearance about 15 min later. Addition of a supplementary neutral filter of density 0·2 in front of either eye during the stimulus causes this eye's green halo to be conspicuously weaker.

The green halo can be seen on a screen illuminated with monochromatic light. On a screen illuminated with sodium light the late after-image of stimulus *B*, *C* or *D* appears pink and its halo green.

Light which falls on extrafoveal retina is relatively ineffective in producing a green halo. When presented on a 1·5° field centred 2° from the fixation point, stimulus *B*, *C* or *D* produces an after-image surrounded by almost as strong a halo as when presented on a central field of the same diameter; but if the field is centred 6° from the fixation point, little or no green halo is produced. The difference appears to depend on properties of the retinal region illuminated, and not on those of the region corresponding to the halo, for in the same zone 4° from the fixation point appropriate stimulation of the fovea induces a strong green, but similar stimulation of adjacent peripheral retina only a very weak green.

The temporal and spatial conditions for prevention by light of short wave-length of the halo produced by light of long wave-length. We have already seen that light of long wave-length, which by itself would have produced a halo, can be prevented from doing so if light of short wave-length is added to it. This light need not be added at the same time; if a given area of retina receives a blue-green stimulus of spectral composition *H* 3 sec before or 3 sec after an orange-red stimulus of spectral composition *C*, the green halo that would have been produced by the orange-red stimulus alone

is completely prevented. I have tried in vain by several methods to detect a difference in effectiveness in preventing the green halo depending on whether the stimulus of short wave-length immediately precedes or immediately follows that of long wave-length; if there is such a difference it must be very slight.

If the short-wave-length stimulus follows or precedes the long-wave-length by more than 3 sec, it is only partly effective, but its effectiveness when it follows can be increased by increasing its size. For example, a stimulus *H* that is 10′ larger than a stimulus *C* in all directions (diameters 1° 10′ and 50′), and follows it by 10 sec, is as effective as one that is 20′ larger (diameters 1° 30′ and 50′) and follows it by 25 sec; both leave a very faint but clearly detectable green halo.

Failure to obtain perfectly matching haloes with stimuli of different spectral composition. It would simplify the analysis of these phenomena if, whenever two stimuli of different spectral composition were found both to give green haloes, it were always possible by dimming all components of one stimulus by a constant factor to produce with it a halo indistinguishable from that produced by the other stimulus. This, however, is not possible. The halo produced by stimulus *B* is both larger and stronger than that produced by stimulus *D*. If the duration or intensity of stimulus *B* is reduced three times, its halo becomes weaker than that produced by stimulus *D*, but remains larger.

DISCUSSION

The observation that the late after-image and the green halo are independent of the temporal distribution of the stimulus in the range 20 msec to 2 sec makes it probable that these phenomena depend on photochemical effects of the stimulus and not on its action on nerve cells of the retina, for no known aspect of the electrical activity of retinal nerve cells is independent of the time course of the stimulus above about 50 msec.

If the late after-image depends on products of photochemical reactions that have occurred in the receptors, two plausible hypotheses can be suggested to explain the loss of spatial resolution. Either the relevant products of photochemical reactions do not remain where they were produced, but diffuse away and affect other structures; or they and their immediate effects remain confined to the receptors in which they were produced, and the loss of resolution is due to progressive failure of the nervous pathways to transmit the spatial information contained in the message sent to them by the receptors. The second hypothesis makes the progressive loss of resolution analogous to what probably happens when stabilized retinal images become invisible, and in these it is well known that fine details are lost before coarse. I reject it on three grounds. The first is that progressive

loss of resolution does not occur in extrafoveal after-images, though it does in extrafoveal stabilized retinal images. The second is that the loss of resolution in after-images is some fifty times slower than that in stabilized retinal images. The third and strongest ground is that it is independent of whether the eye is kept in steady light or in darkness. It would be easy to suppose that when presented with a constant message the nerve cells learn, over the course of several minutes, to neglect fine details of the spatial pattern in the message and transmit only its coarser features. But there is no reason why the nerve cells should learn anything relevant while the eye is in darkness; they could do so only if the message then sent to them by the receptors (corresponding to a positive after-image) could teach them to ignore detail in the quite different message (corresponding to a negative after-image) that they were to receive on subsequent illumination of the retina. By analogy with properties of stabilized retinal images one would not expect this; in particular, it would be very surprising if darkness were exactly as effective in making the nerve cells accustomed to the spatial detail as the white screen used for the observations.

Diffusion of products of photolysis can explain loss of resolution only if these products are the *sole* basis of the after-image. If those receptors that have been bleached remain less sensitive than their neighbours for some other reason, for example lack of receptive pigment, then this insensitivity should permit resolution of detail in the after-image even in the presence of another kind of insensitivity due to diffusible products. It is likely (though not proved) that rods do remain insensitive for many minutes after bleaching because of lack of rhodopsin, so the persistent resolution of extrafoveal after-images does not allow us to conclude that the products of photolysis of rhodopsin do not diffuse or do not affect the sensitivity of retinal structures. For foveal cones a diffusional theory of the loss of resolution in after-images must postulate that any insensitivity from lack of receptive pigment is negligible after the end of the second minute, and that later stages of the after-image depend only on diffusible substances.

The pink after-image and green halo are not due to pink and green products of photolysis, respectively, screening the receptors from incident light. This is proved by the possibility of seeing them in monochromatic light.

If late foveal after-images are due to diffusible products of photolysis, the action of these products must almost certainly be on cones, not on bipolar cells or ganglion cells, because of the regular manner in which the after-images, both pink and green, of linear stimuli placed just to one side of the fixation point advance across the foveal centre. The bipolar cells and ganglion cells that are connected to the central foveal cones are

displaced to the margins of the fovea, and it appears from the drawings of Polyak (1941) that the region that is free from them has a diameter of about 250 μ (corresponding to about 52′ of visual field). Substantial diffusion through such a distance requires some minutes. The delay in diffusion from the relevant structures of one side of the central fovea to those of the other side could thus hardly fail to be detectable if these structures were either bipolar cells or ganglion cells.

On the grounds given above and others that will mostly be obvious, the following hypothesis is put forward.

The fovea contains red-sensitive and green-sensitive cones (as well as blue-sensitive with which we are not here concerned). Photolysis of the receptive pigment of the red-sensitive cones (presumably the erythrolabe of Rushton, 1958) yields a substance, to be called e_1, which diffuses through the retina and diminishes the sensitivity of any red-sensitive cone that it reaches, but has little or no effect on green-sensitive cones. It is the sole cause of those negative after-images and haloes that are seen 2 min or more after a brief bright stimulus and appear green. Photolysis of the receptive pigment of the green-sensitive cones (presumably Rushton's chlorolabe) similarly yields a diffusible substance, to be called c_1, which diminishes the sensitivity of green-sensitive but not of red-sensitive cones. It is the sole cause of those negative after-images that are seen 2 min or more after a brief bright stimulus and appear pink. e_1 moves faster through the retina than does c_1.

The speed with which e_1 and c_1 need to move through the retina, in order to account for the present phenomena, seems to be easily compatible with diffusion. For the loss of resolution in after-images it is difficult to discuss this quantitatively because we know nothing of the relation of the strength of the after-image to the amount of c_1 or e_1 causing it. For the green halo a measure is given by the observation that a blue-green stimulus that is 10′ larger and 10 sec later than a red one attenuates the halo as much as an otherwise similar stimulus that is 20′ larger and 25 sec later (p. 172). Let us assume that the indistinguishability of these haloes indicates that the same amount of e_1 diffuses more than 10′ (0·0487 mm) in 10 sec as diffuses more than 20′ (0·0974 mm) in 25 sec, and that the diffusing e_1 is confined to the layer of rods and cones, so that diffusion is effectively one-dimensional. Equation (37) of Barrer (1951) is then applicable, and we require the value of D such that

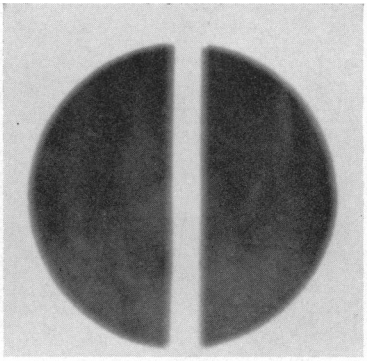
$$\int_{x_1}^{\infty} \operatorname{erf}\frac{x}{2\sqrt{Dt_1}}\,dx = \int_{x_2}^{\infty} \operatorname{erf}\frac{x}{2\sqrt{Dt_2}}\,dx,$$

where $x_1 = 0{\cdot}0487$ mm, $x_2 = 0{\cdot}0974$ mm, $t_1 = 10$ sec and $t_2 = 25$ sec. The only solution is $D = 1{\cdot}49 \times 10^{-6}$ cm^2 sec^{-1}, but the ratio of the integrals

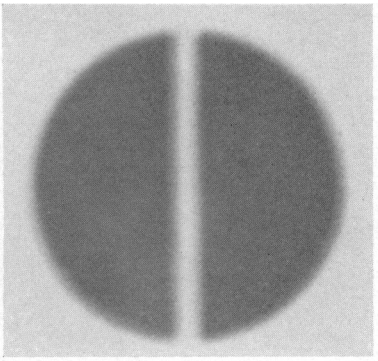
changes rather slowly with D, so that the observations do not fix the value of D very closely; for example, at $D = 2{\cdot}36 \times 10^{-6}$ cm^2 sec^{-1} it is 0·86:1 and at $D = 0{\cdot}93 \times 10^{-6}$ cm^2 sec^{-1} is 1·24:1, and any value within this range would probably be consistent with the observations.

There remains one very striking observation for which I have not yet given any explanation: the prevention of the green halo by addition of light of short wave-length. The hypothesis as stated above explains the facts that a red stimulus A, such as may be supposed to bleach practically only erythrolabe, produces only e_1 and hence a rapidly spreading green after-image, that a green stimulus G such as may be supposed to bleach practically only chlorolabe produces only c_1 and hence a slowly spreading pink after-image, and that an orange stimulus C or D that must bleach both chlorolabe and erythrolabe and produce both c_1 and e_1 is followed by a pink after-image surrounded by a spreading green halo. The fact that addition of green and blue light to the orange stimulus C or D abolishes the green halo without affecting the pink after-image demands for its explanation that light of short wave-lengths destroys or in some way inactivates e_1. It might be supposed that e_1 is itself photolabile, and is converted by light of short wave-length to a substance e_2 which has no effect on the sensitivity of receptors. But this hypothesis can only with some difficulty and artificiality be reconciled with the fact that light of short wave-length is just as effective in preventing the green halo when it immediately precedes a stimulus of long wave-length as when it immediately follows it. More plausibly it can be supposed that bleached cones tend to capture e_1 and prevent it from diffusing further. When red-sensitive cones only are bleached, enough diffuses away to cause a green halo, but when green- and blue-sensitive cones are also capable of capturing it, little escapes beyond the region of the retina that was illuminated by the stimulus.

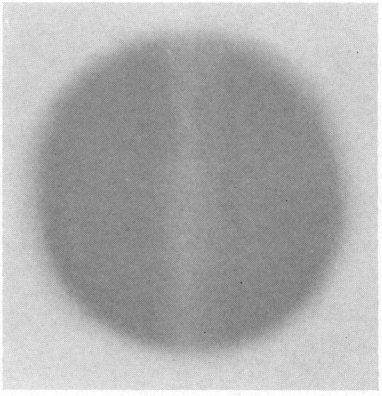
I believe that the hypothesis of desensitization of cones by diffusible products of photolysis is the only simple hypothesis that explains all the present observations on after-images, and that it has also the merit of making biological sense. It might at first be thought strange that green-sensitive cones should be especially apt to be desensitized by the product of photolysis of chlorolabe, and red-sensitive cones by that of erythrolabe; but it is not strange if these products of photolysis are the means by which the photochemical reactions normally provoke the cones to send their signals to the nerve cells of the retina. The desensitization produced by continued presence of the 'transmitter substance' then becomes analogous to the desensitization of motor end-plates by continued presence of acetylcholine (Katz & Thesleff, 1957), and the specific sensitivity of each kind of cone to its own 'transmitter substance' becomes a useful means of pre-



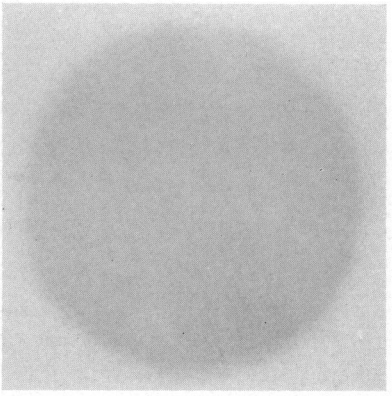
a



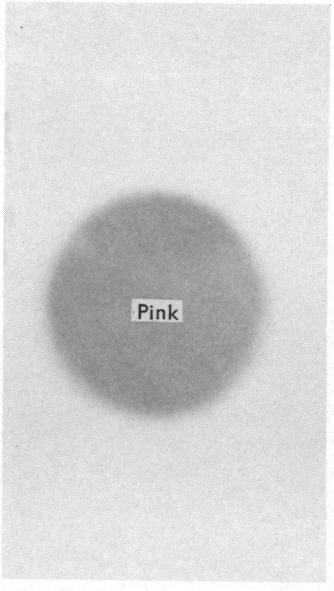
b



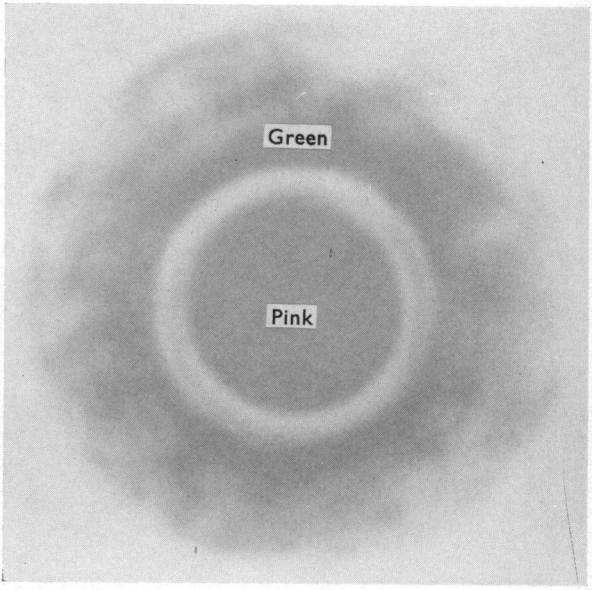
c



d



e



f

(*Facing p.* 179)

venting excitations and changes of excitability of a kind that would convey no visual information.

SUMMARY

1. If a brief and very bright flash of light is cast on the fovea, its negative after-image shows sharp spatial detail at first, but becomes progressively blurred during the following 15–20 min.

2. The blurring is substantially faster for the green after-images of deep red stimuli than for the pink after-images of stimuli of shorter wavelength. It does not occur in extra-foveal after-images.

3. The blurring is not merely due to fading, and is independent of whether, after the stimulus, the eye is kept in darkness, in light, or in alternating darkness and light.

4. The negative after-image of an orange-red or orange flash is pink, but is surrounded by a conspicuous green halo which remains visible for at least 15 min. If light of short wave-length is added to flash, the colour of the after-image is unaffected, but the green halo either does not appear or disappears within 2 min.

5. It is suggested that late foveal after-images depend wholly on products of photolysis of cone pigments, which diffuse from the cones in which they were produced and decrease the sensitivity of other cones of the same spectral type. This hypothesis explains the blurring of after-images and all the observed properties of the green halo.

REFERENCES

BARRER, R. M. (1951). *Diffusion in and through Solids*, p. 9. Cambridge University Press.

BRINDLEY, G. S. (1959). The discrimination of after-images. *J. Physiol.* **147**, 194–203.

BRINDLEY, G. S. (1961). Two new properties of foveal after-images. *J. Physiol.* **158**, 20*P*.

KATZ, B. & THESLEFF, S. (1957). A study of the 'desensitization' produced by acetylcholine at the motor end-plate. *J. Physiol.* **138**, 63–80.

POLYAK, S. (1941). *The Retina*, Fig. 38. Chicago: University of Chicago Press.

RUSHTON, W. A. H. (1958). Visual pigments in the colour-blind. *Nature, Lond.*, **182**, 690–692.

TROXLER (1804). Ueber das Verschwinden gegebener gegenstände innerhalb inseres Gesichtskreises. *Ophthalm. Bibliothek.* (ed. HIMLY, K. & SCHMIDT, J. A.) Bd **2**, Stück 2, pp. 1–53.

EXPLANATION OF PLATE

a–d, sketches of the negative after-image of stimulus *G* presented for 0·67 sec in a 1·5° circular field crossed by a black bar 10′ wide. *a*, 2 min after the stimulus; *b*, 4 min. *c*, 8 min; *d*, 16 min. *e*, *f*, sketches of the negative after-images of stimulus *E* (left-hand sketch) and of stimulus *C* (right-hand sketch) as seen 8 min after the stimuli. The green halo produced by stimulus *B* would be very similar to that shown for *C*. That produced by stimulus *D* would be slightly weaker and substantially narrower.