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THE DISCRIMINATION OF AFTER-IMAGES

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This paper is concerned with the illusions observed, in darkness or on looking at a moderately dim uniformly illuminated surface, after part of the visual field of one or both eyes has been exposed to bright light. Those seen in darkness are usually called 'positive after-images', and are often similar in colour to the inducing light. Those seen in moderate illumination are called 'negative after-images', and are often of approximately the complementary colour. The problem of why after-images look precisely as they do is a very complex one, for the appearance is likely to depend on many factors acting together. The sequences of chemical changes which occur in receptors after light has been absorbed by the receptive pigments certainly differ between rods and cones, and probably between different classes of cones; and adaptational changes can certainly occur in nerve cells of the retina and of the brain. All these may well play a part in determining the appearance of an after-image. We give ourselves a better chance of obtaining a complete answer to part of the problem, and a securer foundation for beginning to solve the rest of it, if at present we restrict discussion to the following simple question: 'Under what conditions do two stimuli of different physical composition give indistinguishable after-images?' When we have found two such stimuli, we shall have good grounds for supposing that the structures or processes in the retina or visual pathway which are concerned in the persistence of their after-images are affected alike by them. We shall see that there are pairs of stimuli which produce identical after-images though the immediate or 'primary' sensations are very different, and other pairs which produce distinguishable after-images though the primary sensations are indistinguishable. From these observations, inferences will be made about the probable nature of the lasting change responsible for the persistence of after-images, and about some properties of the receptive pigments of human foveal cones.

METHODS

Figure 1*a* shows the very simple apparatus used in the experiments of Part I and in the preliminary experiments of Part II (p. 198). The apparatus used in the accurate experiments of Part II (p. 199) to provide the same quantity of light (integral of luminance with respect to time) either in one short flash or in a series of flashes distributed over a longer time, is shown in Fig. 1*b*. When very brief stimuli were required, in the experiments of Part II (p. 199), two Mazda FA5 krypton-filled flash tubes were arranged as in Fig. 1*c*. Each was connected to a 50 μF condenser charged to 2200 V. The condensers were charged from the same power supply through separate resistors of 70,000 Ω; thus on suddenly discharging one, the initial rate of discharge of the other into it corresponded to a time constant of more than 7 sec. The flash tubes were triggered by separate induction coils, the primary circuits of which were broken by a Lucas spring contact breaker, giving an interval which could be continuously adjusted in the range 0–32 msec, and

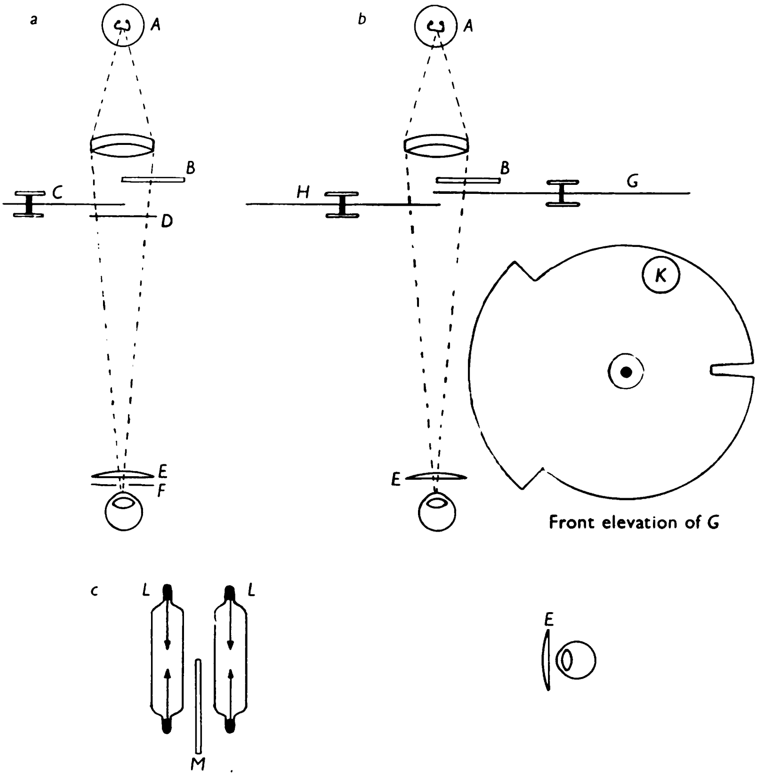

Fig. 1*a*. Plan of the apparatus used in Part I. *b*, plan of the apparatus used in Part II (p. 198), with front elevation of the double pendulum shutter. *c*, side elevation of the apparatus used in Part II (p. 199). *A*, ribbon filament lamp; *B*, neutral filter or wedge, which could be moved to cover either half of the field, or both halves; *C*, simple pendulum shutter, giving an exposure of 0·112 sec—it could be moved to cover either half of the field or both halves; *D*, camera shutter, adjustable to give various exposures; *E*, spectacle lens correcting the refraction of the homatropinized eye for the required distance; *F*, 4 mm artificial pupil; *G*, double pendulum shutter giving exposures of 15·7 msec and 1·68 sec; *H*, continuously rotating 1/107 sectored disk; *K*, weight; *L*, Mazda FA5 flash tube; *M*, brass sheet.

set with an accuracy of about $\pm 20\ \mu$sec. Of the light in each flash, as measured with a vacuum photocell and cathode-ray oscilloscope, 95% was emitted within 200 μsec.

In nearly all the experiments the subject's pupil was dilated and fixed with homatropine. In the experiments of Part I an artificial pupil of 4 mm diameter was used. Elsewhere light was admitted through the whole of the natural pupil.

To examine the after-image the usual procedure was to turn the eyes towards a uniform white surface, and alternately to open and close that eye which had received the inducing stimulus, the other eye being continuously covered. In this way the after-image, alternately negative and positive, remained always easily visible. If the test eye was kept continuously open or closed, it was more difficult to keep the after-image under observation. The reader can readily obtain for himself evidence that this difficulty is due to binocular rivalry.

The luminances of flashes produced by filament lamp and shutter were measured with an S.E.I. photometer previously tested against a lamp calibrated by the National Physical Laboratory. The errors of this measurement, together with those of the densities of the neutral filters (measured with a Hilger Uvispek photo-electric spectrophotometer at intervals of 20 mμ through the spectrum) may amount cumulatively to as much as 0·2 log. unit in the important range around 10^6 cd. m^{-2}.sec, but are unlikely to be greater. The more difficult task of absolute calibration of the Mazda FA5 flash tubes was not attempted.

RESULTS

PART I. The Weber fraction for the discrimination of after-images

If two uniform fields of light presented side by side are examined by eye, and a decision made, whilst still looking at them, which is the brighter, it is found that the least difference of luminance that can be detected is roughly proportional to the luminance of the dimmer field ('Weber's law': Bouguer, 1760 and many later writers). It is interesting to inquire to what extent this law is valid when the discrimination is made not on the sensations produced while the stimuli are still present, but on the after-images. For dim or prolonged stimuli this is not easy to investigate satisfactorily; if the after-images differ, the discrimination can always also be made on the primary sensations, and it may be difficult for the subject of the experiment to discount his prior knowledge of the correct answer in deciding whether the after-images are discriminable. For short flashes of luminance-time product (or integral of luminance with respect to time) greater than about 100 cd. m^{-2}.sec, the investigation becomes easier; such flashes, even when they differ sufficiently to be easily discriminated on their after-images, produce indistinguishable primary sensations. The ratio of the least difference in luminance that can be detected to the luminance of the less bright field ('Weber fraction') is only slightly greater for these bright flashes, discriminated on their after-images, than for dim flashes of similar duration discriminated on the primary sensations, provided that, in the after-image experiment, the luminance-time product does not exceed about 3×10^5 cd. m^{-2}.sec; Weber's law, as can be seen in Fig. 2, is approximately valid over the very large range from

$$3 \times 10^{-3} \text{ to } 3 \times 10^5 \text{ cd. m}^{-2}\text{.sec.}$$

The increase in the Weber fraction seen in Fig. 2 at very low luminances has long been familiar; even in Bouguer's book published posthumously in 1760 there is indirect reference to it. The more conspicuous increase for very bright flashes has not previously been reported, though a closely related phenomenon was discovered, whilst investigating a military technical problem, by J. L. Russell of the Royal Aircraft Establishment, Farnborough, Hampshire, in 1937. The amount of light required to produce it is sufficient to cause a photochemical change in a large fraction of the molecules of visual pigment in the region of retina on which it falls, if the relevant pigments have photosensitivities similar to those measured objectively in the human fovea (Rushton, 1958) or to that inferred for the red-receptive pigment from the disturbance of colour matches by adaptation (Brindley, 1955). Making due allowance for uncertainties in the absolute photometric calibrations and in the corrections for size of pupil and spectral distribution of the light, we can say roughly that if the pigments have the properties described by Rushton (1958), bleaching of 85 % of the molecules can, and of 99·0 % cannot, be distinguished from bleaching of 99·99 % of them; if they have the properties

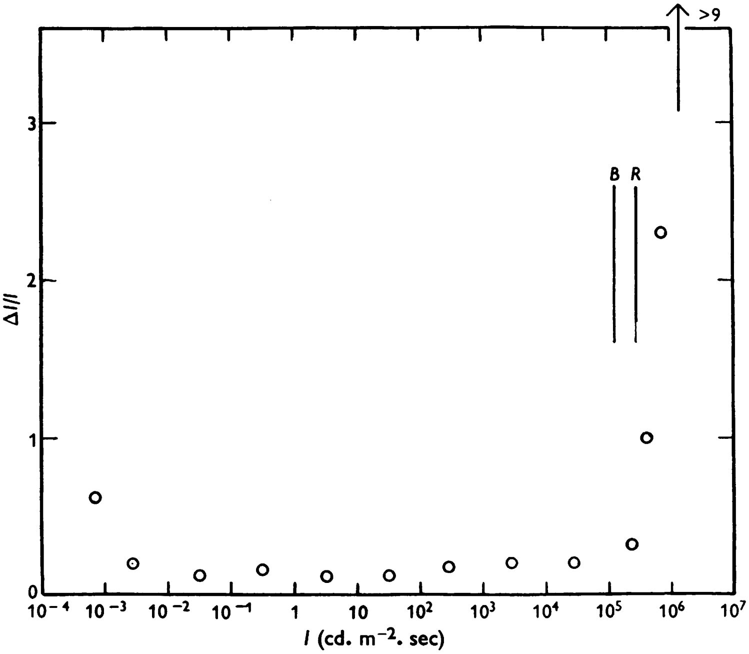

Fig. 2. The Weber fraction $\Delta I/I$ for brief flashes of light. Artificial pupil 4 mm; field diameter 2°; duration of stimulus 0·112 sec, except for the strongest stimulus (not discriminated from one 10 times as bright); this was of 0·63 sec. The discriminations were made on the primary sensations up to and including 31 cd. m^{-2}.sec, and on the after-images above this. The vertical line *B* shows the amount of light required to bleach all but 1/e of the red-receptive pigment of the fovea, estimated from the subjective measurements of Brindley (1955), and the vertical line *R* a similar estimate from the objective measurements of Rushton (1958).

inferred by Brindley (1955), bleaching of 99·0% can, and of 99·99% cannot, be distinguished from bleaching of all but one in 10^8. These fractions are so large as to make it very probable that the cause of the observed increase in the Weber fraction is the bleaching of most of the visual pigment, and not the saturation of some later stage in the transmission of visual information. This conclusion is further strengthened by the evidence, to be given in Part II, that the persistence of after-images under conditions closely similar to those of the experiments of this Part depends on chemical events which follow the absorption of light by visual pigments, and not on adaptational effects upon nerve cells.

PART II. Discrimination of the after-images of stimuli which differ in duration

Identical after-images produced by the same luminance-time product differently distributed in time

There is a substantial range of conditions over which the primary sensation produced by a flash of light depends on its luminance-time product (or in general, the integral of luminance with respect to time) independently of its temporal distribution ('Bloch's law': Bloch, 1885). For regularly repeated flashes this relation was discovered by Talbot (1834), verified very critically by Hyde (1906), and extended to extremely short durations by Beams (1934). For single flashes it was discovered by Bloch, and has been confirmed at threshold by a number of authors. Above threshold it certainly holds for durations down to $4{\cdot}1 \times 10^{-7}$ sec and retinal illuminations up to 3×10^8 trolands (Brindley, 1952), and is likely to be valid for indefinitely short durations and high intensities. The *greatest* duration at which Bloch's law is valid has never been systematically examined above threshold. For a 3° foveal field at luminance-time product 0·5 cd. m^{-2}.sec, I have found it to be 0·027 sec; it is greater for dimmer flashes, and may perhaps be smaller for brighter ones.

For after-images, preliminary experiments to investigate the conditions under which Bloch's law holds, using the crude but flexible apparatus of Fig. 1*a*, indicated that for stimuli lasting not more than about 2 sec the whole course of the positive or negative after-image, excluding its first 15 sec, was determined by the total quantity of light in the stimulus, independently of its distribution in time. For stimuli lasting between 2 and 5 sec, the same was very nearly but not quite exactly true. The apparatus shown in Fig. 1*b* was built to confirm this finding accurately over a limited range of conditions. The left half of the circular photometric field subtending 3° at the eye was illuminated with a single flash of duration 15·7 msec. The shutter which determined this flash also exposed the right half of the field for 1·68 sec, the 15·7 msec flash occurring in the middle of this exposure; but light reached the subject's eye from the right half of the field only during a fraction 1/107 of the 1·68 sec during which it was exposed, i.e. a total of 15·7 msec, because of the rotating sectored disk interposed between the source and this part of the shutter. Thus if no filters were inserted, or the same filters in each path, the integral of luminance with respect to time was the same for the right half of the field as for the left at all wave-lengths, but the temporal distribution was very different.

Experiments with this apparatus very clearly confirmed the preliminary ones. At 8×10^4 cd. m^{-2}.sec, with the sectored disk rotating at any speed between 15 and 40 rev/sec, the after-images, excluding their first 15 sec, were alike in the right and left halves of the field when no filter was inserted. If a filter was placed in the path for one half-field, the after-image, both positive (i.e. seen against a dark background) and negative (i.e. seen against a bright background) was weaker on this side. Practised subjects could consistently discriminate in this way a neutral filter of density 0·1 on one side. Even to unpractised subjects the effect of a filter of density 0·2 was very obvious. The sensations experienced during the stimuli and during the first second or two after them were very different for the right and left halves of the field, whether the sectored disk was rotated at more or at less than the flicker fusion frequency; and the relative amounts of light delivered on the two sides could not, even after much practice, be estimated from these primary sensations with the accuracy that was very easily achieved by waiting for 15 sec and then examining the after-images. During the first 15 sec the after-images of the two halves of the field usually differed in colour, and no adjustment of the relative luminances by adding neutral filters would cause them to match perfectly.

Deviations from Bloch's law at very short durations

Since Bloch's law holds for after-images in the range from 15 msec to 2 sec or so, it might be expected, by analogy with the corresponding law for the primary sensations, that it would hold also at very much shorter times. For stimuli of less than 10^5 cd. m^{-2}.sec, the available evidence does not contradict this expectation. For extremely bright stimuli, however, it is certainly false. Two Mazda FA 5 flash tubes were set up as shown in Fig. 1*c*, and discharged at an interval of 0·28 msec. The upper and lower halves of the after-image produced were found to be distinguishable; the 240-J flash from the nearer tube was evidently bright enough to produce a saturation similar to that found in the experiment of Fig. 2, and the additional light from the further tube made no difference to the after-image.

The interval between the flashes was increased to 4 msec. The upper and lower halves of the after-image were then found to be clearly different; whether seen against a dark background or a bright one, the upper half, where light had been received from both tubes, was stronger than the lower half, where light had been received only from the nearer tube. Intervals intermediate between 0·28 and 4 msec gave intermediate results, the upper and lower halves of the after-image being neither as easily distinguished as at 4 msec nor as clearly alike as at 0·28 msec.

All the five subjects tested with this apparatus could consistently distinguish, without sensory clues other than the after-image, whether the tubes had been fired 4 msec or 0·28 msec apart. For three of them the above description applies exactly. For the other two subjects the upper and lower halves of the after-image were not quite indistinguishable at 0·28 msec, but the difference then seen was very much smaller than at 4 msec. Provided that certain controls are satisfied, these findings imply a deviation from Bloch's law: two flashes separated by 4 msec give an after-image which differs from that seen when the same two flashes are separated by only 0·28 msec.

Controls. When the time course of the flashes was recorded with a vacuum photocell and cathode-ray oscilloscope, no influence of either flash on the intensity or duration of the other could be detected. In each flash 95 % of the light was emitted within 0·20 msec. Thus when the farther tube was fired first, as was usually done (though the same results were obtained when it was fired second) almost all the light from it had been emitted before the nearer tube, through which the light had to pass to reach the subject's eye, had been activated. The question of whether the transparency of the nearer tube alters after its activation need not, therefore, be considered.

DISCUSSION

There is good theoretical reason to expect that, for durations short compared with that required for substantial regeneration of the photosensitive substance, the extent of a photochemical reaction should be determined by the total amount of light received, independently of its distribution in time. At very short durations this relation certainly breaks down for rhodopsin and probably for human foveal pigments (see below); but between these very short durations and the 5 sec or so that are probably required for any substantial degree of regeneration, it would be more surprising to find it false than true for a human receptive pigment, especially since it has been verified in part of the relevant range by Campbell & Rushton (1955) for rhodopsin and by Rushton (1958) for foveal pigments. The finding that a given amount of light produces the same after-image (except for the first 15 sec), whether it is delivered within 15·7 msec or spread over 1·68 sec, is thus fully consistent with the hypothesis that the after-image of a brief stimulus, from the fifteenth second until its disappearance 100–300 sec later, depends upon photochemical effects, and not at all upon adaptation or potentiation of neural mechanisms in the retina or brain as a result of the intense activity that presumably occurs during and immediately after the stimulus. The fairly close agreement between the time of persistence of after-images and the time necessary for the regeneration of foveal pigments (Brindley, 1955; Rushton, 1958) suggests further that the relevant photochemical effect, i.e. the condition whose presence determines that an after-image shall be observable, is either the absence of molecules of receptive pigment from the places where they should be, or the presence of primary or secondary products of photolysis which during regeneration disappear by being reconverted to receptive pigment.

To what extent are alternative hypotheses admissible? The sensations produced by the 15·7 msec and the 1·68 sec stimuli are very different indeed. So also, if we may extrapolate slightly from Ronchi & Moreland (1957), are their electroretinograms, which probably represent the electrical activity of the rods and cones (see Brindley, 1959). None of the very many kinds of retinal ganglion cells whose electrical activity has been recorded would be likely to give similar responses to stimuli differing as these do, and the same applies to the less abundant information available about spike discharges from the inner nuclear layer (Brindley, 1956; Brown & Wiesel, 1958) and about intra-retinal slow electrical activity (Tomita, 1950; and later writers). If, then, adaptation or potentiation of nerve cells is concerned, it must either be confined to cells of a kind not yet detected electrically in experimental animals, or depend on a functional process in them that is scarcely at all correlated with their electrical activity. These ways of escape are not easy to accept, and the evidence seems strong that the persistence of the after-images of brief stimuli, excluding the first 15 sec, depends solely on the chemical consequences, within the receptors, of the absorption of light by the receptive pigments.

The inequality of the after-images during the first 15 sec is most reasonably explained by supposing that neural effects are then contributing. In the first 5 sec or so the inequality is very great, as if neural effects then much predominate over photochemical ones. After the fifth second it diminishes swiftly, so that at 10 sec the after-images are nearly alike, and at 15 exactly so.

It would be rash to extrapolate far beyond the conditions of the present experiments. Strong though I believe the evidence to be for the purely receptoral origin of the after-images of *brief* stimuli, it does not follow that neural factors are not concerned when the stimuli are longer. Nevertheless, the possibility, even under a limited range of conditions, of producing after-images whose place of origin is known and fairly simple, provides a new tool for investigating the function of the human retina.

The deviation from Bloch's law found at very short durations

This is almost certainly related to a phenomenon discovered by Hagins (1955). Hagins measured by reflexion densitometry the amount of rhodopsin in the eyes of albino rabbits before and after exposing them to a flash lasting less than 1 msec. He found that a single flash, however bright, never bleached more than half the rhodopsin present; but a second flash, if delivered several tens of milliseconds later, would bleach half the remainder. Two plausible explanations can be suggested: absorption of a quantum of light may bring a molecule of rhodopsin into a state from which, during the following few milliseconds, it can, with about equal probability, be bleached or return to its original state; or light may not only convert rhodopsin into a substance X, but also convert X into rhodopsin. In the second explanation, it must be assumed that X spontaneously loses, within a few milliseconds, the capacity for being reconverted into rhodopsin by light. The work of Hubbard & Kropf (1958) makes it probable that the second explanation is correct, and that X is a compound of opsin with all-*trans* retinene, or perhaps a mixture of compounds of it with retinene isomers other than 11-*cis* and 9-*cis*.

The deviation from Bloch's law shown by human foveal after-images when the inducing stimuli are very short can be completely explained by supposing that the receptive pigments of the foveal cones share this property. If so, the time required for the dark reaction which restores part of the manifest photosensitivity after a flash must be between about 0·4 and 4 msec.

SUMMARY

1. For the discrimination of the after-images of brief flashes, Weber's law, $\Delta I/I$ = constant, holds approximately up to 3×10^5 cd. m^{-2}.sec. At higher intensities the Weber fraction $\Delta I/I$ increases very much. This 'saturation' of discrimination is probably due to bleaching of nearly all the photosensitive pigment.

2. The after-images (excluding their first 15 sec) produced by stimuli of duration between 15·7 msec and 1·68 sec (and approximately up to 5 sec) are determined by the total quantity of light delivered, independently of its distribution in time. This is the counterpart, for after-images, of Bloch's law. From this it is argued that the persistence of after-images under these conditions depends on the chemical consequences, within the receptors, of the absorption of light, and not on adaptational changes in nerve cells.

3. For very short flashes (0·4–4 msec), a conspicuous deviation from Bloch's law occurs at high intensities but not at low. A closely analogous property of rhodopsin was discovered by Hagins (1955), and it is suggested that the receptive pigments of human foveal cones resemble rhodopsin in this respect.

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