

The equivalent background of bleaching

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Abstract. Stiles and Crawford proposed that a retinal region bleached by preexposure to intense light behaves as if it were illuminated by some steady veiling or background luminance. We test this notion by comparing the afterimage of a bleaching light with a steady (and retinally stabilized) light of adjustable intensity, in the manner of Barlow and Sparrock. With their matching procedure, and also with a new procedure, we find as they did that during the rod phase of recovery the afterimage does look like a stabilized field of an intensity which, presented as a background, brings visual sensitivity to the same level. It is as if the two conditions produce equal signals at some stage of the visual pathway. Like Barlow and Sparrock we observe a rod-cone break in the afterimage matches. However, we argue that the appearance of the rod-cone break presents a paradox and we show a way to resolve it.

1 Introduction

A light exposure that bleaches an appreciable fraction of visual pigment causes a large rise in visual threshold. The well-known dark-adaptation curve plots the recovery of log threshold as the pigment is regenerated. A difficulty in using this curve as an absolute measure of pigment regeneration is that its shape depends upon the parameters of the test flash used to measure it. For instance, Craik and Vernon (1941) using either a very large or a very small area of test flash obtained, for the same dark-adaptation conditions, curves that were not only different in their threshold levels (as was to be expected) but also quite different in their shape. Thus, the relation between log threshold rise and the amount of pigment bleached is not simple, for it depends upon the parameters of the test flash used.

Stiles and Crawford (1932), however, demonstrated a simplifying relationship. Steady backgrounds also raise the visual threshold, and that to an extent which likewise depends upon the parameters of the test flash. What Stiles and Crawford showed was that if we choose a background that raises the threshold for a superposed flash as much as bleaching does at some given stage of recovery, then these two threshold elevations when matched for one kind of test flash, are matched for all. Though the actual log threshold rise depends upon the test parameters, it does so equally for bleaches and for backgrounds. So, we may say, "At this stage of recovery the threshold is raised as though there were a background of this particular luminance; for, in both conditions, the threshold is raised equally no matter what kind of test flash is used". The matching luminance is called the 'equivalent background of bleaching'. So, at every stage of pigment regeneration, the visual threshold behaves as though there were a bright background at the retinal region bleached.

† Deceased. William Rushton was an enthusiastic admirer of Stiles's work and often sought his advice on psychophysical or colorimetric problems. The experiments reported here were carried out in 1971-72, and a draft of the paper was written (mostly by Rushton) shortly afterwards. The interpretation and analysis are Rushton's; his participation as a subject was terminated when a corneal abrasion became infected.

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But, as Craik and Vernon (1941) pointed out, there is such a bright background and it is situated just there; namely, the afterimage. Perhaps the afterimage is Stiles and Crawford's equivalent background. At first sight it looks as though this attractive view could not possibly be right. A background that raises the increment threshold four or five log units, as rod bleaching does, is dazzlingly bright. The brightness of an afterimage does not look at all of this order. Moreover, if we observe the effect of a background by projecting a lantern slide on to a screen illuminated with another source of light gradually made stronger and stronger, the projected picture may fade to invisibility, but it will never reverse its contrast and become a negative image as afterimages do. Thus if an afterimage is a background, it must be a rather special kind of background.

Barlow and Sparrock (1964) pointed out that what is special is that the afterimage is *stabilized* on the retina. Stabilized images rapidly fade and the afterimage likewise must be a faded image, appearing only a small fraction of its 'true brightness'. Moreover, as Barlow and Sparrock showed, and as we shall demonstrate in this paper, even real images, when they are stabilized on the retina, turn into negative images with change in background luminance, just as afterimages do. Thus, Barlow and Sparrock (1964) took seriously the idea that the afterimage is the equivalent background and set about proving it. First, the luminance of a stabilized field of light was adjusted to be of equal brightness to the afterimage. Second, the threshold of a flash of light was measured when it fell (a) upon the afterimage (this is, the dark-adaptation threshold) and (b) upon the equally bright field of real light.

1.1 *The experiments of Barlow and Sparrock*

Barlow and Sparrock did the following:

- (i) They surrounded an afterimage with a stabilized image of real light whose intensity was adjusted to look equally bright. In this way they measured the brightness of the afterimage throughout dark adaptation. They produced stabilization by the method of Yarbus (1967), with a device attached to the cornea by a sucker so that it moved exactly with the eye. The device carried a target on a short stalk and also a short-focus lens that imaged the target on the retina. The target consisted of a white circular disc with a circular hole in the middle. A very bright light when flashed through the hole into the eye caused bleaching so that the hole appeared to be exactly filled with the afterimage. Light falling on the white circular surround illuminated the surface towards the eye, and by adjusting the intensity of this light, the surround could be matched in brightness to the afterimage in the centre. The image brightness so measured from minute to minute during dark adaptation resulted in a curve of log luminance against time very similar to the familiar dark-adaptation curve at the centre of the afterimage. So at each stage of recovery they knew both the luminance of the surround that matched the afterimage, and also the dark-adaptation threshold for a flash projected upon that image.
- (ii) After recovery, the increment threshold was found for a similar flash projected through an opal screen that was illuminated to various intensities and also viewed through the central hole. In this arrangement the illuminated opal screen 'replaced' the afterimage. A striking result was found. When the screen was given the luminance that had matched the afterimage at some moment of recovery in experiment (i), the increment threshold through the screen in experiment (ii) was the same as the dark-adapted threshold (through the afterimage) at that moment in experiment (i). Thus the threshold was raised equally by an afterimage and by an opal screen of the same brightness. Now the background that raises threshold equally is the equivalent background of Stiles and Crawford. Thus, Barlow and Sparrock showed that the equivalent background has the brightness of the afterimage. This goes a long way to support their view that the afterimage is a background that raises the threshold just as backgrounds of real light do.

1.2 Difficulties

There are three difficulties in Barlow and Sparrock's paper.

(a) Though ordinarily in photometry, contiguous fields may easily be set to have the same brightness, this is not so with stabilized images. Any two stabilized fields will soon appear equal, as their differences fade away. To test their procedure Barlow and Sparrock compared the brightness of two contiguous real stabilized images: the first fixed in intensity, the second variable. As we describe below, if the second remains fixed at any intensity, its brightness soon drifts to be the same as that of the first, so that brightness judgements in steady conditions are useless to determine the equality of the fields. If on the other hand the second light fluctuates in intensity, now brighter, now dimmer than the steady comparison, a level can be found where these ups and downs appear equal; and here the mean level is found to be when the two lights are physically equal. Barlow and Sparrock applied this method to match the variable stabilized image with the fixed afterimage, and in this way measured its brightness at various stages of recovery during dark adaptation.

(b) When the brightness of the afterimage that filled the hole in the target was compared with the brightness of the illuminated white target around the hole, it was assumed that the surround was viewed by normal unbleached retina. But on account of the scatter of light in the eye some of the bleaching light destined for the afterimage must have fallen on the surround and raised its threshold and dimmed its sense of brightness. Thus the brightness of the afterimage was compared with that from a stabilized field falling upon a somewhat desensitized retina, and this field would consequently have to be made brighter than it should to duplicate the modest brightness of the afterimage.

(c) The 'dark-adaptation curve' of image brightness not only has the late rod branch, it also has what looks like an early cone branch—a branch that is almost superimposable upon the true cone branch of the dark-adaptation curve (given by white squares in their figure 3). This is surprising, as Barlow and Sparrock admit. With thresholds it is always the lower threshold of two independent systems that is plotted, cone thresholds at first where cones are more sensitive than rods, then rod thresholds from the moment when the curves cross and rods become more sensitive than cones. But with brightness something quite different would be expected. The brightnesses of rods and cones should add together and be greater than either component alone; however, as Barlow and Sparrock say, "The brightness of the after-image is found to depend upon the system which has the lower dark light" (Barlow and Sparrock, 1964, page 1314).

We have repeated Barlow and Sparrock's experiments with minor modifications. We have confirmed the validity of their method, not only with their own procedure (experiment 1 below), but also with a new matching method (experiment 2); and we have been able (in experiment 3) to explain the surprising break in their image-brightness dark-adaptation curve.

2 Experiment 1. Replication of Barlow and Sparrock's experiments

2.1 Method

2.1.1 *Contact shell.* As in the experiments of Barlow and Sparrock, stabilization was achieved by the method of Yarbus (1967), the target being mounted firmly on a square-sectioned stalk attached to a contact shell fixed fairly rigidly to the eye. We used a plastic contact shell moulded tightly to the eye of the subject DM and bearing a 40 D lens worked on to the optical axis and also (in some experiments) a short closed length of cycle valve tubing for suction. When the target was 25 mm from the lens, it was in sharp focus on the retina. With this specially moulded shell, an anaesthetic was not required. The arrangement is indicated in figure 1. The lens on the shell was surrounded by an artificial iris painted in black on the contact shell with a clear 'pupil' 4 mm in diameter

at the centre. The target, as shown in figure 1, consisted of four layers: (i) (nearest the eye) an opaque photographic negative perforated by two holes, one for a window within which the fixation light appeared, the other to limit the test fields; (ii) a 'Polaroid' (P); and (iii) a quarter-wave plate ($\frac{1}{4}\lambda$) with axis at 45° to that of the Polaroid [the combination (ii) and (iii) constituted a right circular analyzer with the property that incident right circularly polarized light was admitted to the eye and left circular light was excluded (see Appendix)]; and finally, (iv) (furthest from the eye) a sheet of ($\frac{1}{2}\lambda$) cellophane that acted as a half-wave plate. Right circular light passing through this cellophane became left circular, left became right. The cellophane sheet had a hole punched in it so that when left circular light fell on the cellophane, that which passed through the punched hole was excluded by the right circular admitter, so the hole looked black. But the rest of the field passing through the cellophane was transformed into right circular light and was admitted; so the subject saw a bright field with a black centre. Likewise, when right circular light fell upon the punched cellophane of the target, the hole appeared bright in a black field. Since rotation of the target about the light axis does not affect circularly polarized light, the intensities are not altered by rotation of the eye on its axis, the shell on the eye, or target on its stalk.

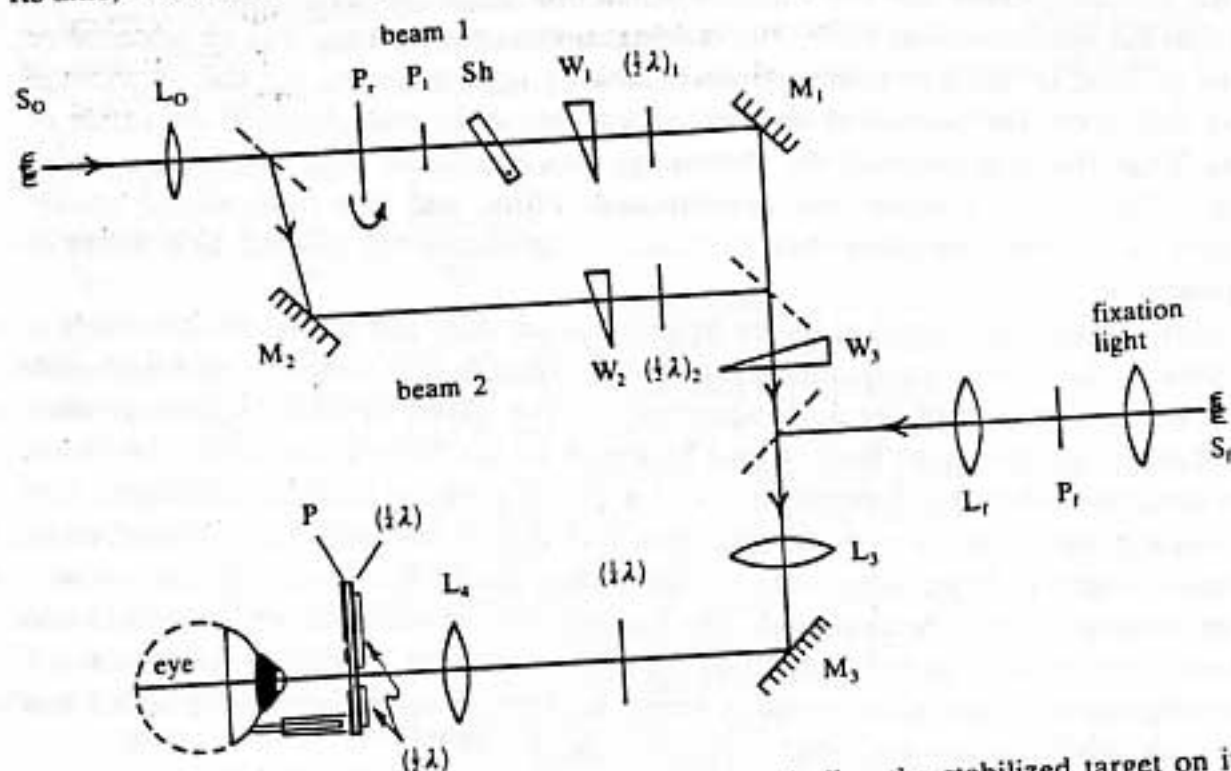


Figure 1. The optical arrangement (not to scale) including the stabilized target on its stalk. See the text for a description of the components.

2.1.2 Optical equipment. This also is shown in figure 1. The light source S_0 was a 6 V, 6 A tungsten filament collimated by lens L_0 . The parallel light falls upon the glass plate at the polarizing angle and about 25% is reflected, this being entirely polarized in the plane perpendicular to the paper. The transmitted light (beam 1) is fully polarized in the plane of the paper by passing through the 'Polaroid' P_1 . Both beams can be attenuated by the neutral filter and wedge combinations W_1 , W_2 , and their planes of polarization can be adjusted by the half-wave plates $(\frac{1}{2}\lambda)_1$, $(\frac{1}{2}\lambda)_2$ mounted on rotatable frames. If the angle between the polarization plane of incident light and the (λ) axis is θ , then the plane of the transmitted light will be rotated through 2θ .

After reflection at front surface mirrors M_1 , M_2 , the two beams are united at the beam splitter, and pass on to illuminate the target and enter the eye. Lenses L_3 and L_4 secure uniform illumination of the target by imaging L_0 upon it, and they focus the image of the filament upon the artificial pupil of the contact lens to maximize the light

entering the eye. The quarter-wave plate ($\frac{1}{4}\lambda$) turns incident light polarized at $+45^\circ$ to the vertical into right circular light and that at -45° to the vertical into left circular light. Incident light polarized vertically is passed unchanged. [Since light polarized at any angle may be resolved into two components, one at $+45^\circ$ and one at -45° , the effect of ($\frac{1}{4}\lambda$) upon it will be to produce a mixture of right and left circular lights in amounts proportional to these components.]

Beam 1 could provide either flashes or sinusoidal variations by interposition of either the revolving 'Polaroid', P_1 , driven by a motor, or the electromagnetic shutter, Sh , programmed by pulse generator modules. The subject maintained alignment in the apparatus by a dental bite and brow rest, and directed his gaze to the unstabilized fixation light.

The fixation light, S_1 , to hold the subject's eye from drifting is introduced from the side by the glass plate near L_3 . An incandescent filament is focused on to a pinhole, and by adjusting the lens L_4 , the image of the pinhole is made to fall within the 'fixation aperture' of the opaque sheet in the target plane and is brought into focus on the retina.

2.1.3 The bleaching flash. The bleaching source was an electronic flash tube which was imaged on to the artificial pupil by lenses L_5 and L_6 (figure 2). The opaque artificial iris prevented illumination of the retina through iris or sclera. It was important to obtain a bleached image on the retina with crisp edges exactly located and a minimum of stray light.

The bleaching stimulus filled the hole B in the metal plate M. This plate was attached to the bleaching stimulator and not to the contact lens. It was also perforated by a tiny fixation hole F. The holes were drilled and bevelled to have sharp crisp edges. When the subject took up his aligned position with bite and brow rest, the metal plate was so close to the target that holes and target cellophane could be in focus simultaneously on the retina. The subject directed his gaze at the tiny hole F which was lit up by the steady fixation source S. The hole B then subtended an angle of 4 deg, centred 8 deg from the line of sight. The afterimage we studied was produced by a flash through hole B. To match the afterimage, we had to produce a stabilized field that exactly enclosed it, with no visible gap or overlap. This was achieved with the help of the hole in the ($\frac{1}{4}\lambda$) target cellophane, which was exactly in register with the bleaching hole B. Left circularly polarized light fills the unbleached surround with light that has passed through the cellophane but leaves the hole dark except for the afterimage there. This is the Barlow and Sparrock situation.

In order that the bleaching hole B should coincide exactly with the hole in the cellophane, the two holes were equal in size and were brought into register at the moment of releasing the flash in the following way. The steady fixation source S was left circularly polarized by means of the circular polarizer P. Thus S could illuminate the hole B only when B was overlapped by the ($\frac{1}{4}\lambda$) cellophane, which converted the left circular light to right circular light capable of passing through the contact lens target's right circular analyzer. The cellophane hole was like the moon in an eclipse of the sun. In general,

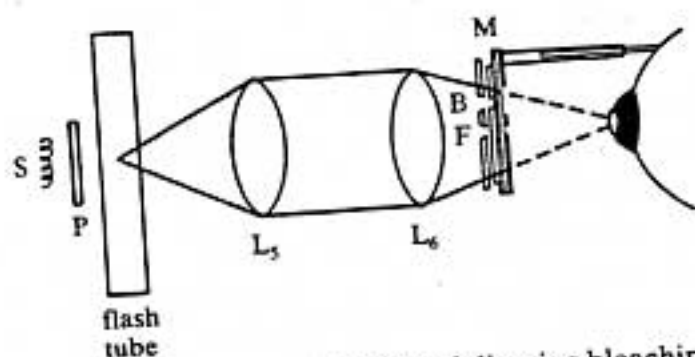


Figure 2. The arrangement for delivering bleaching flashes. See the text for a description.

light was seen at the edges, but by careful adjustment the eclipse could be brought to totality. At that moment the flash was discharged. Now the afterimage was fixed exactly coincident with the cellophane hole, and when left circular light was presented, it illuminated precisely the surround and left the afterimage glowing in the hole - two stabilized fields that had to be matched in brightness.

2.1.4 Afterimage brightness. For these measurements the half-wave plates $[(\frac{1}{2}\lambda)_1$ and $(\frac{1}{2}\lambda)_2$ in figure 1] were set so that both beams supplied left circular light (blue-green, Ilford filter 603) continuously to the annular surround, shaded in the inset to figure 3. The unshaded central area corresponds to the holes in the plate and the cellophane. It was filled with afterimage and no appreciable light fell there. To overcome the difficulty that steady stabilized lights fade and become hard to compare, we found it useful to make the surround intensity fluctuate in a regular and controlled way. A slow constant-speed motor drove a rotating 'Polaroid' P, placed in beam 1 (figure 1) between the glass and P₁. This produced a nearly sinusoidal fluctuation in the intensity of that beam, extinguishing it every 3 s. Beam 2 at the same time added steady light to the annulus; it was always more intense than the peak intensity of beam 1. The observer controlled the intensity of beam 1 (by means of wedge W₁) so as to keep the fluctuation just clearly visible. The steady and fluctuating components of the annulus light were attenuated together by means of the neutral density wedge W₃ in the common path. The observer used this wedge to match the brightness of the surround to that of the afterimage, and as this faded during dark adaptation, measurements were made as often as was feasible.

The fluctuation in the intensity of the surround prevented the afterimage from fading away; it seemed kept alive by contrast. When the surround was black the image looked brighter (positive phase); when the surround was near peak the image looked dimmer (negative phase). The relative prominence of the positive and negative phases depended upon the average surround intensity set by wedge W₃. If the surround intensity was too low, the positive phase lasted the longer; if too high, the negative phase lasted the longer. The observer tried to set W₃ so that the two phases were equal in duration. The validity of this is discussed later. (Other criteria led to approximately the same choice of surround intensity: this was also the intensity that made the positive and negative phases of the afterimage within the fluctuating surround equally noticeable, and that made the transition from positive to negative appearance most noticeable. A slight discrepancy between the 'equally noticeable' criterion and the 'equal duration' criterion was that at equal duration the positive afterimage was somewhat more noticeable during the first 15 min or so of recovery, and the negative afterimage was more noticeable thereafter.)

2.1.5 Equivalent background of bleaching. This is the background that raises the threshold as much as bleaching does. To measure it we need to obtain two measurements: (a) the ordinary dark-adaptation curve, i.e. the threshold for a flash to be detected when superimposed on the afterimage at various times of recovery; and (b) the threshold when the flash is superimposed instead on steady backgrounds of various intensities. (a) To obtain the dark-adaptation curve, beam 2 was cut off, and a diaphragm was placed in beam 1 to provide a blue-green circular patch subtending 2 deg which fell in the centre of the 4 deg bleached area. An electromagnetic shutter in beam 1 (near W₁) could be operated by touching a key. This gave an exposure of 0.1 s. If the key was held down the exposures were repeated at the rate of 1 s⁻¹. By controlling the wedge W₁, the flashes could be brought to threshold and the dark-adaptation curve obtained. (b) The increment threshold was obtained by flashes in the same way, but now the eye was initially dark-adapted, and beam 2 unblocked to present an 8 deg blue-green background field upon which the flashes were projected. Before each threshold measure-

ment the experimenter set the background intensity at some value from a set that covered the scotopic and photopic ranges in 0.6 log unit steps.

By combining the results of (a) and (b) the equivalent background may be found at all times during the recovery from bleaching. The threshold flash was the same in the two cases and the threshold was raised (a) by bleaching or (b) by background. We may therefore plot by direct substitution what is the 'equivalent background' in the sense of Stiles and Crawford: the steady luminance that raises the threshold as much as it was raised by bleaching at t minutes of recovery.

2.2 Results

In figure 3, the open circles show on a logarithmic scale the equivalent backgrounds at various times during recovery from a bleaching flash administered at $t = 0$. The filled circles show the average intensity of the surround that matched the afterimage in brightness. Because the brightness measurements varied a good deal from one session to another, data from eight sessions have been interpolated and averaged. The vertical line accompanying each filled circle subtends twice the standard error of the mean for that measurement. It is clear that the surround intensities that matched the afterimage in brightness are comparable in absolute level and time course with the background intensities that equalled the bleach in threshold. But the cone plateau between 5 and 10 min after the bleaching flash that is conspicuous in the curve of equivalent backgrounds is not nearly so well-defined in the brightness matching data. This divergence is to be expected and will be explained later (see experiment 3).

2.2.1 Resolution of doubts. The foregoing account and the results of figure 3 are substantially the same as those of Barlow and Sparrock, and confirm them. They are consequently subject to the same doubts that we raised earlier (section 1.1) with regard to their work. These doubts were: (a) How reliable is the judgement of equal brightness when the fields judged are stabilized? (b) Did the scattered bleaching light desensitize somewhat the surrounding area upon which the comparison light fell? (c) Why in the recovery curve of image brightness (figure 3) does cone brightness replace rod brightness instead of adding to it? We shall now try to resolve these doubts, first to validate

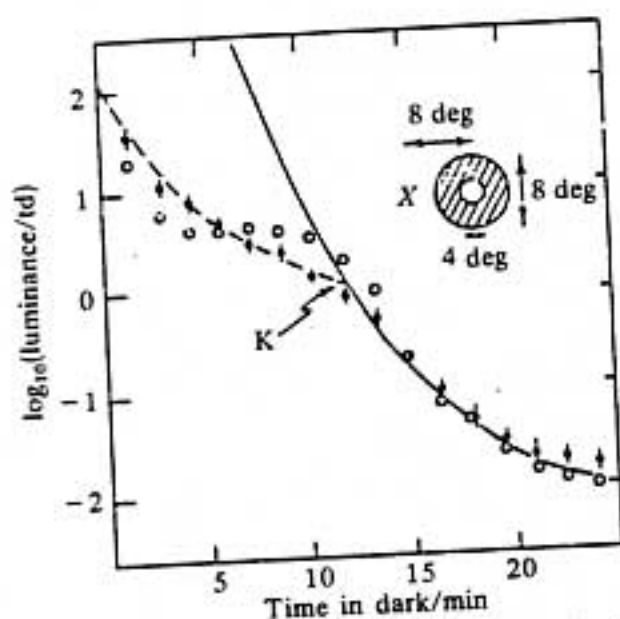


Figure 3. Equivalent luminance (filled circles) and equivalent background (open circles) during recovery from bleaching. Curves are explained in the text for experiment 3, section 4.2. Inset shows the layout of the display. The fixation point is indicated by the cross. The shaded area is the stabilized annular surround, enclosing the circular afterimage of the bleached centre.

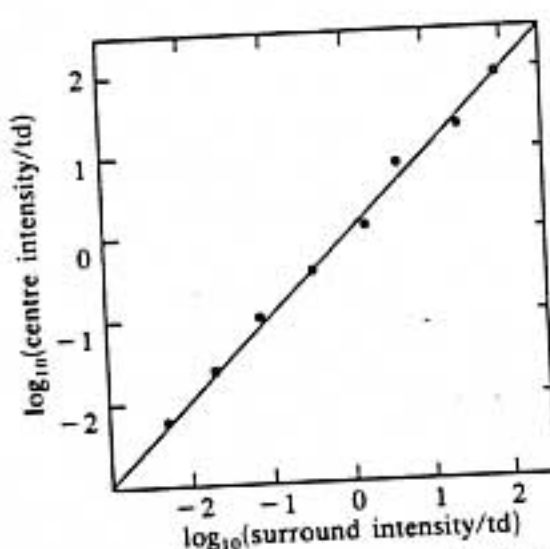


Figure 4. Steady centres matched to fluctuating surrounds in stabilized vision.

(a) by a method very similar to that of Barlow and Sparrock. The procedure described for matching the afterimage brightnesses is unorthodox and, although it clearly gave determinate settings, there is no a priori reason to suppose them accurate. We therefore performed a subsidiary experiment in which the same procedure was used to match the gently fluctuating stabilized surround, not to an afterimage but to a stabilized light having no fluctuation in its intensity, that occupied the dark centre instead. This steady light, like the steady component on the annulus, was provided by beam 2. The half-wave plate ($\frac{1}{2}\lambda$)₂ in beam 2, instead of being set by the experimenter to provide left circularly polarized light (that would not pass through the centre of the ring), was controlled by the observer so as to admit to the centre an adjustable amount of light, that could greatly exceed the light supplied to the annulus. All lights passed through an Ilford 603 filter. As before, a subjectively positive phase and a negative phase succeeded one another during each fluctuation cycle of surround intensity, and a critical setting of the half-wave plate ($\frac{1}{2}\lambda$)₂ could be found that made the durations of these two phases equal. The true physical intensities of centre and surround were then measured by projecting the fields on to a white screen and observing the screen with an SEI photometer.

Figure 4 shows the centre intensities that were chosen to match a range of (time-average) surround intensities in stabilized vision. There are no large deviations from the physical equality shown by the 45° line. Our matching procedure does permit accurate matches between stabilized images.

We ran a second subsidiary experiment to see (b) whether bleaching of the surround might have distorted our measurements of afterimage brightness. We followed the procedure used in obtaining the dark-adaptation curve except that instead of using the test flash to probe the sensitivity of the highly bleached central region, we projected it within the annular surround, at a point approximately equidistant from its inner and outer boundaries. The results showed that within 4 min following the bleaching flash, the sensitivity of the surround had increased to within 1 log unit of its dark-adapted value. After 10 min the sensitivity loss was below 0.4 log unit. Thus the results of figure 3 during the rod phase of recovery are not greatly distorted by unwanted bleaching of the surround. A further experiment provided more support for this conclusion, with brightness matches, rather than the visibility of flashes used as a criterion. This criterion agreed with the threshold criterion: the ratio of the intensities required for a brightness match between centre and surround was equal to the ratio of the thresholds, with a tolerance of less than 0.2 log unit, in every phase of dark adaptation.

The final difficulty, concerning the rod-cone break, is the subject of experiment 3 below. But first we try to test Barlow and Sparrock's conclusion with a different matching procedure.

3 Experiment 2. An alternative matching procedure

The procedure of matching the afterimage to a fluctuating surround in a concentric display has two drawbacks: it requires control experiments to establish its validity, and it is inconvenient in practice because it demands that the stabilized surround remain accurately in register with the central bleached area for 30 min after the bleach—a condition that was never strictly satisfied in our experiments. Blinks frequently displaced the target, which would then drift back into visually acceptable alignment with the afterimage. To escape from these difficulties we have also made observations with an overlapping display.

3.1 Method

The display is shown in the inset to figure 5, where B is the bleached 4 deg patch, and A the stabilized comparison field (the solid circles in the inset). They are both quite steady but are prevented from fading by fluctuations in the intensity of a uniform background

field that extends over both. The circular comparison field A was defined by the hole in the cellophane and was illuminated originally from beam 2 (figure 1) where the half-wave plate ($\frac{1}{2}\lambda$)₂ was set to provide, at the target, right circularly polarized light that was reduced to 2.5% of its full intensity if it first passed through the cellophane, but was fully transmitted where the cellophane was absent. The uniform background was supplied by beam 1, polarized in the vertical plane. This coincided with the vertical axis of the half-wave plate and of the cellophane on the target so that it was unaffected by either and fell uniformly over the circular analyzer of the target whether passing through the cellophane or through a hole in it. It illuminated the retina therefore as a uniform field.

When the rotating 'Polaroid', P, in figure 1, brought beam 1 to extinction, the background was seen to go dark over most of its area, but there remained two cloudy, weakly luminous images, the afterimage occupying the bleached area B, and the comparison field A. The greater the intensity supplied by beam 2 to the stabilized image of the comparison field, the brighter was the positive image that persisted there on extinction of the background. By controlling the wedge W₂ the observer could set the intensity of the stabilized image so that this positive afterimage from it matched the afterimage observed in the bleached area.

Matches made in this way were not much dependent on the intensity of the background supplied by beam 1, but it was difficult to make the match with precision if the background was very bright or very dim. The observer therefore set the background intensity at a convenient level, and this was never very far above the threshold intensity on the bleached area.

With this display (figure 5, inset), it was possible to determine thresholds and equivalent backgrounds in a single session. The electromagnetic shutter was substituted for the rotating polarizer in beam 1, and a diaphragm was introduced so that beam 1 when flashed did not illuminate the entire background but only illuminated, with the same intensity, the two small (2 deg) spots shown by the dashed lines, one at the centre of the bleached area, the other at the centre of the comparison field. First attending to the spot on the bleached area, the observer used wedge W₂ to reduce it to threshold. Then he used wedge W₁ to set the comparison field intensity at a level that made the second spot likewise just visible. This is the equivalent background intensity, that duplicates the threshold of the bleached area.

3.2 Results

The results of these experiments are plotted in figure 5, where filled circles show the log luminance of the stabilized comparison field that was equal in brightness to the positive afterimage at various stages of recovery when the uniform background was extinguished. The open circles show the log equivalent background. Each point is based on the interpolated and averaged data of four sessions. The standard errors are about equal to the heights of the circles.

These results confirm those of figure 3. Over the later rod branch there is reasonable coincidence between the two curves. The coincidence of the curves tells us that when afterimage and a stabilized field of light have the same incremental threshold, they will be similar in appearance when a uniform background covering both is changed in intensity. With the cone branch the two curves diverge: the equivalent background lies higher. Unless the various classes of cone were excited in the same proportion by bleaching, background, and threshold flashes, we could not expect them all to respond in the same way, and so the two cone branches would be expected to diverge. However, a more important question, in both figure 3 and figure 5, is why on the cone branch of the equal brightness curves the cone brightness of the afterimage instead of adding to the rod brightness appears to suppress and replace it. This is the question we next address.

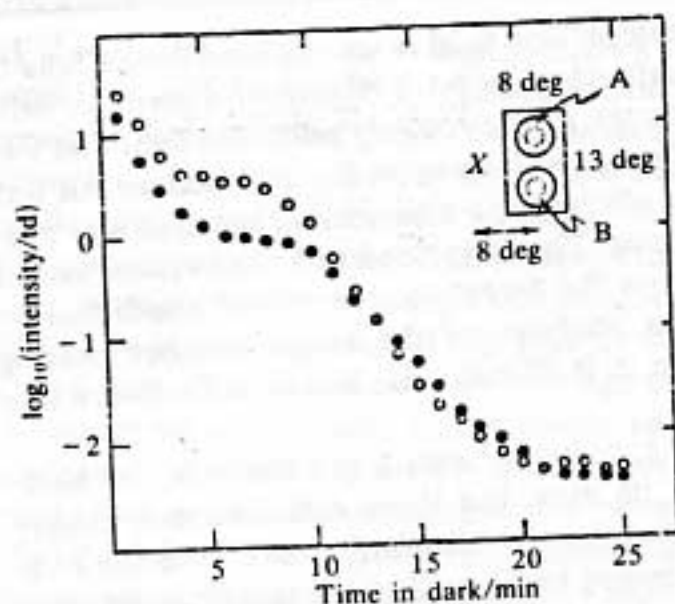


Figure 5. Filled circles trace the fading of afterimage brightness measured by the alternative procedure. Open circles, equivalent backgrounds under the same conditions. Inset shows the layout of the display with rectangular background, bleached region B, and stabilized comparison field A. Dashed lines show the small test spots used for measuring equivalent backgrounds.

4 Experiment 3. The rod-cone break and afterimage brightness

In figures 3 and 5 we have confirmed Barlow and Sparrock's observations almost exactly, even to the sharp kink in the equivalent background curve and the more gradual transition in the log equivalent luminance. Let us examine what these measurements signify. Starting late during recovery and going backwards in time (figure 3) we start well below the cone threshold; rods only are involved in the comparison field, and also in the afterimage where cones have quite recovered. The two curves here run nicely together. This continues at shorter times nearly to the place where the kink appears (after about 10 min of recovery). This point is where the cone threshold has become relatively constant. Cones have fully recovered, and produce no afterimage (Hayhoe et al, 1976). This is particularly clear in the fovea, where like Miller (1966) we find that all afterimage contours vanish irreversibly many minutes before the rod-cone break. The parafoveal image surviving at later times appears with the colour characteristic of rod stimulation. The cones during this plateau phase can add nothing to the brightness of this sensation from rods—still less can they subtract from it. The 'cone branch', observed to extend for more than 10 min in the records of afterimage brightness obtained by us and by Barlow and Sparrock, is therefore a mystifying result.

What we should expect of the afterimage brightness at this time is shown by the continuous curve in figure 3, the continued exponential rise of log intensity up to high values, reflecting the exponential recovery of rod sensitivity. If this requires an equal real stabilized luminance on the comparison patch to match it, the matching log luminance plotted in figure 3 by the filled circles would similarly show a simple exponential time course. But as this luminance is progressively raised (for shorter recovery times) the point will be reached when the cone threshold is exceeded and the comparison patch will then stimulate cones as well as rods, both of which might be expected to contribute to the brightness by which the afterimage is now matched. We now ask: can this change in response to the comparison patch explain the Barlow and Sparrock cone plateau?

4.1 Method

In order to see what is the effect on brightness matching if the centre receives signals only from rods but the comparison annulus excites cones also, we used a modification of the display of figure 3: two stabilized images, one in blue-green light at the centre and one in red light at the annulus.

The equipment was the same as that used in the measurement of afterimage brightness by Barlow and Sparrock's method, except in the following respects. The half-wave plates in the two beams were set so that beam 1 illuminated only the centre of the display and beam 2 only the surround. The two beams passed through differently coloured filters: deep red (Ilford 608) in beam 2, and blue-green (Ilford 603) in beam 1. This meant that at mesopic intensities the centre (1) lay below the cone threshold but stimulated rods, whereas the surround (2) stimulated cones as well as rods. The cellophane in the observer's target cannot be a half-wave plate for both these lights of different wavelength; nevertheless it was possible in practice to extinguish both beams to less than 3% in the regions where they were not wanted. For this experiment, the rotating polarizer that had been used to vary the intensity of the surround in the earlier experiment was removed from the apparatus. Fluctuations of the surround intensity were still a prerequisite for unique matches, but this time the observer produced them himself by imposing continual small excursions on the graded density filter W_2 while he tried to make a setting.

For each of a range of centre intensities produced by inserting neutral filters into beam 1, the observer used the graded filter W_2 to choose (in the way described previously, see section 2.1.4) a surround intensity that matched the centre. He then repeated the setting in unstabilized vision (holding the target stalk between his fingers—an uncomfortable but effective expedient).

A second phase of the experiment was devoted to the determination of the Fechner fractions of the rods and the cones. For this purpose both beams supplied light of the same green colour (Ilford 625 filter): beam 1 over a uniform unstabilized 8 deg field, beam 2 over an unstabilized 2 deg field that could be flashed (200 ms). Scotopic and photopic background intensities were tried, and the flash intensity found that could just be detected against each background. The cone absolute threshold was measured by bleaching the eye and noting the level of the plateau in the dark-adaptation curve.

4.2 Results

Figure 6 shows the red surround intensities chosen in stabilized vision (filled circles) and unstabilized vision (open circles) to match the green centre at various scotopic and mesopic intensity levels.

Plainly the setting made does not depend on whether stabilized or unstabilized vision is used. At low intensities the matching surround intensity is proportional to the centre intensity, as is natural. This relation is shown by the line oriented at 45° which fits the low-intensity data points. But at intensities where the surround appreciably stimulates cones, a different behaviour is observed: a line of gradient $\frac{1}{3}$ fits the points, implying that

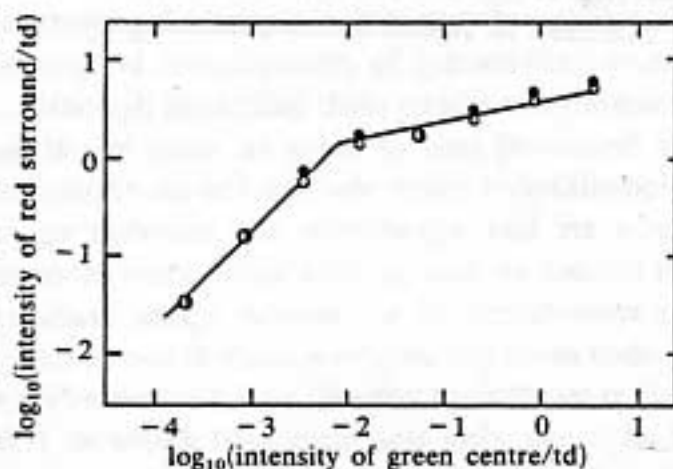


Figure 6. Red surrounds matched to green centres of various intensities. Filled circles stabilized vision; open circles, unstabilized vision. The kink in the curve only slightly exceeds the threshold for seeing the red surround presented as a 200 ms flash during the cone plateau of dark adaptation. Straight lines have slopes 1 and $\frac{1}{3}$.

the intensity of the green centre must increase as the fifth power of the red surround intensity if a match is to be maintained. At intensities where this happens, the centre is stimulating mainly rods: only the two highest surround intensities are above cone threshold. But the red surround stimulates cones as well as rods, and this is the reason for the nonlinearity: if the surround is blue-green like the centre, and therefore does not stimulate cones at these levels, we find (as in figure 4) that no elbow appears in the matching function, but surround and centre increase in a fixed ratio up to the highest intensities.

Figure 7 shows the increment threshold ΔI as a function of the background intensity I ; the data have been fitted by a cone branch and a rod branch in the manner of Stiles (1939). Each branch is of the form

$$\Delta I = F(I + I_0),$$

where F , the Fechner fraction, and I_0 , the critical background intensity at which the threshold is doubled, take very different values for rods and cones, just as they do in Stiles's far more comprehensive and exact investigations. The results of the two experiments are easily related by applying to the rods and the cones Fechner's theory of the relation between the increment threshold and the way that the visual effect of a stimulus grows with intensity. For intensities I much greater than the critical background I_0 , the visual signal (ψ) is given by

$$\psi = \left(\frac{1}{F}\right) \log_{10} I,$$

where F is the Fechner fraction derived from increment threshold measurements. When a stimulus of real or equivalent intensity I_r in the rods is matched in brightness to a comparison stimulus of intensity I_c applied to cones (supposing that equality of brightness corresponded to equality of ψ), these intensities should satisfy

$$\log_{10} I_r = \left(\frac{F_c}{F_r}\right) \log_{10} I_c,$$

where F_r and F_c are the Fechner fractions of the rods and the cones respectively. With F_r/F_c equal to 5 (figure 7) this becomes the equation of the line of shallow slope in figure 6. At lower intensities where the matched stimuli work through rods only, the Fechner fractions are equal and the predicted matches fall on a straight line of slope 1, as at the lower intensities in figure 6.

In our repeat of Barlow and Sparrock's experiment (figure 3), the centre was a pure rod afterimage, so that we may associate with it an abscissa in figure 6; the matching

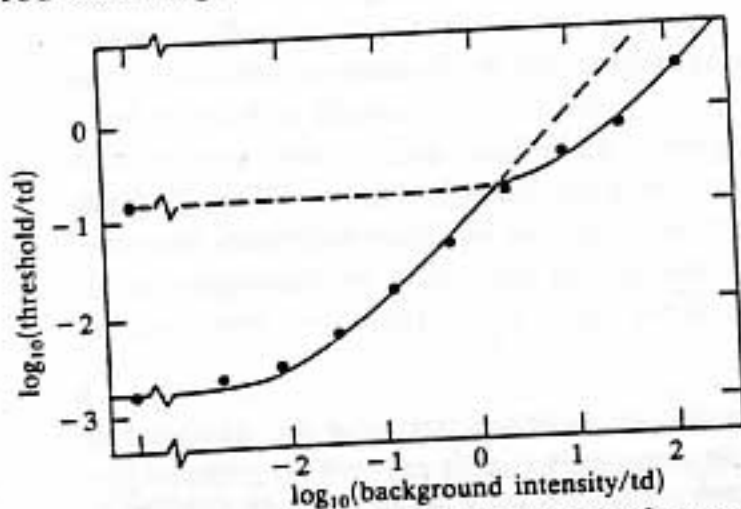


Figure 7. Increment threshold ΔI versus background intensity I , to show the Fechner fractions of the rods and cones. The equation of the rod branch is $\Delta I = 0.1(I + 0.015)$. The equation of the cone branch is $\Delta I = 0.02(I + 8)$. Fechner fractions are 0.1 and 0.02, respectively.

intensities (ordinates in figure 6) show that the matches made during the 'cone phase' of dark adaptation fall on the line of slope $\frac{1}{5}$ in figure 6, and those made during the 'rod phase' on the line of slope 1. The difference in gradient between these lines shows us precisely what we must expect in the experiment of figure 3. In figure 3 the continuous curve is simply the late rod dark-adaptation curve extrapolated backwards to give the earlier rod values similar to those in figure 5. The curve is an exponential of half-decay 4.5 min, so the extrapolation is easy. A horizontal is drawn through K, the kink in the curve, and the dashed line is obtained by scaling down points on the early rod branch so that the ordinates erected from the horizontal through K are decreased five times. This is the appropriate scaling factor to compensate for the compression of the ordinates in the control experiment of figure 6. The kink (point K) occurs at an intensity about 1 log unit above cone threshold.

We thus explain the Barlow and Sparrock kink:

- (i) The centre contained only a rod afterimage for a few minutes before the kink and at all later times.
- (ii) Earlier than the kink this needed a light well above cone threshold on the annulus to match it.
- (iii) Figure 6 shows that the brightness of the mixed rods and cones increased with the logarithm of intensity five times as fast as the brightness from rods only.
- (iv) Thus, measuring the afterimage of rods by the rod-cone mixture needs a fivefold increase in vertical scale as compared to when measured by rods only in the annulus.
- (v) When a correction is made for this, the kink disappears and rod brightness continues on the exponential that defines the log equivalent background of the rods.

5 Discussion

We have given evidence that the matching procedure we derive from Barlow and Sparrock makes it possible to equate the visual signals produced by stabilized fields that would ordinarily fade to nothing. The matches made to afterimages with this procedure (figure 3) confirm earlier indications (Barlow and Sparrock 1964; Miller 1966) that a bleach and its equivalent background are similar in their effects on sensitivity simply because they generate identical signals at the input to the sensitivity-regulating mechanism.

This physiological identity is the simplest, though not the only, way in which Stiles and Crawford's principle of equivalence-for-sensitivity could arise. It is a surprising identity, since the bleach and background conditions are quite different at the pigment level and also quite different subjectively (except under the special conditions of image stabilization). The identity is probably not exact: although departures from equivalence in psychophysical experiments may be attributable to retinal image motion, one electrophysiological investigation of mammalian rods (Penn and Hagins 1972) has revealed that, although bleaching does produce a persisting change in receptor photocurrent, this signal is not quite as great as that produced by the equivalent background. Our own observations do not exclude exact equivalence: we have, in some conditions, noted differences between the afterimage and its equivalent stabilized background, but the differences were never striking and we cannot exclude the possibility that they were due to residual image motion, or to stimulation of cones by a stabilized field that was matched to an afterimage originating from rods.

An alternative to the identity hypothesis is the feedback scheme described by Rushton (1965), in which bleaching acts only upon the feedback of the 'gain box' that modifies sensitivity, without affecting the input to the gain box in the way that backgrounds do. This is contradicted by our results. The scheme can successfully account for the fading of stabilized images, if we assume that there is enough feedback from the output to make the gain the reciprocal of the input, and the output therefore almost constant

(Gosline and Rushton 1973); but if, after bleaching, a signal from bleached receptors increases the feedback without increasing the input, it will drive the output down, and so the afterimage should appear dark against its unbleached surround. If we let bleaching affect the input and not the feedback of the gain box, we are left with a restatement of the identity hypothesis.

The feedback alternative could be saved, however, by abandoning the idea that the gain box is the whole cause of the fading of afterimages—for instance, by supposing that the output from each gain box is subjected to a differentiation in time (Sparrock 1966; Carpenter 1972) so that only the fluctuation in gain box output (and not its time average) would be centrally available as a basis for matching. In one model of this sort (MacLeod 1974, pages 247–254), it is argued that in our fluctuating-surround display the greatest output fluctuation will come from units close to the centre-surround border that receive sensitivity-controlling influences from both regions, and that the amplitude of this fluctuation will be greatest when the intensity of the surround is adjusted so that the sensitivity-controlling signal received from the surround is equal (in time average) to that from the centre. A match made by maximizing the subjective fluctuation in brightness in this display will then be a match between the *sensitivities*, and not the sustained signals, present in centre and surround. On this view, a bleach must be matched by its equivalent background in the sense of Stiles and Crawford, no matter what physiological model is assumed for the sensitivity-regulating mechanism. Leaving aside this reservation, our results support the hypothesis of physiological identity between bleaches and backgrounds for the rod phase of human dark adaptation.

Acknowledgements. Cindy Gosline gave indispensable help in running the experiments. Professor Lorrin Riggs gave advice on the fitting of the contact lenses. Dr A Stockman and Dr G B Henning read drafts and made useful suggestions. The work was supported by NIH grant EY01711.

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APPENDIX

Note on circularly polarized light

If the Y -input to a cathode ray tube is a sine-wave voltage, and if the same is connected in phase to the X -input, the spot will oscillate sinusoidally along a straight line at 45° that can be considered as the resultant of two linear excursions, one vertical and one horizontal, of equal amplitude and in phase.

Now let the X -input remain unchanged, but the Y -input, though unaltered in amplitude and frequency, be advanced 90° in phase. This will cause the cathode ray spot to describe a circle in the clockwise direction. When X is at peak, Y will be at centre; when X is at centre, Y will be at peak. If the Y -input had been retarded (not advanced) by 90° , the spot would traverse the same circle in the reverse direction. The light analogy is when the vertical and horizontal components of light vibrations instead of being in-phase, are delayed one with respect to the other by 90° or $\frac{1}{4}$ of a vibration. This is called circularly polarized light and it may be clockwise (right) or counterclockwise (left) when viewed in the direction of light propagation. How are we to produce a 90° delay in one component of the light? We can pass it through a birefringent material such as cellophane that has orthogonal 'fast' and 'slow' axes, so called because light polarized along the fast axis is transmitted with a greater velocity than light polarized along the slow axis. If the thickness of the birefringent layer is just right, the transit will introduce a net phase difference of 90° between the orthogonally polarized components. Then if the incident light is linearly polarized in a direction 45° clockwise from the fast axis, it will emerge right circularly polarized; and if anticlockwise, left circularly polarized.

Thus it is clear that a sheet polarizer placed in front of a quarter-wave plate ($\frac{1}{4}\lambda$) at 45° clockwise from the fast axis will generate right circularly polarized light. We call this combination a right circular analyzer.

Suppose a second similar right circular analyzer is initially placed orientated just like the first and is then rotated 180° about the 45° axis so that the fast and slow axes are interchanged and the sheet polarizer which was in front is now behind. If the right circularly polarized light generated by the first analyzer now falls on the $\frac{1}{4}\lambda$ of the second, this $\frac{1}{4}\lambda$ will promptly neutralize the wave retardation produced by the first $\frac{1}{4}\lambda$, since now both the vertical and the horizontal components have made one fast transit and one slow one. The result is that the initial light, plane polarized at 45° , is still plane polarized in this direction after the second $\frac{1}{4}\lambda$, and is in a position to pass through the final sheet polarizer which is in this direction.

Now, circularly polarized light is completely symmetrical about the direction of propagation, so the second analyzer described above may be rotated to any extent about this axis of propagation and receive light in exactly the same way. The only difference is that the plane polarized light that finally emerges will be in the direction defined by the final sheet polarizer, which is part of the analyzer and rotates with it. We may summarize these considerations. If the $\frac{1}{4}\lambda$ plate lies with the fast axis vertical, then incident light polarized in the positive diagonal generates right circular light, in the negative diagonal left. A right analyzer will accept right polarized light and transmit it polarized in the plane of the final sheet polarizer; a left analyzer will similarly accept left circular light. Each analyzer will convert circular light of the opposite kind into light polarized at right angles to the final sheet polarizer, and thus occlude it.

A half-wave plate is twice as thick as a quarter-wave plate and introduces double the delay. Placed after the first $\frac{1}{4}\lambda$ with its fast axis coinciding with the slow axis of the $\frac{1}{4}\lambda$, it will obviously change this beam from 90° retard to 90° advance, or change the light from right to left circular polarization.