

INTERCHANGEABLE BACKGROUNDS FOR CONE AFTERIMAGES

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Abstract—Observations of afterimages indicate that red and green cone sensitivities can be modified independently by bleaching, providing a way to estimate their sensitivities in the normal eye. The foveal afterimage of a red and green bipartite field is allowed to fade against a steady red background. A change of background color from red to green generally revives a bipartite afterimage. If two conditions are met, however, a uniform, borderless afterimage is revived instead. These conditions are: (1) the radiances of the bleaching hemifields must be equated for one of two spectrally selective mechanisms and (2) the substituted backgrounds must be equated for the other mechanism. Derived spectral sensitivities of the two mechanisms in the red-green range agree with the spectral sensitivities of protanopes and deuteranopes obtained from visual matches, and also with those derived from temporary artificial protanopia and deuteranopia in normals. The mechanisms are therefore identified with the normal red- and green-sensitive cones, and it is concluded that the sensitivity losses that generated these afterimages were applied independently to separate signals originating from the two cone types.

INTRODUCTION

Attempts to isolate the three cone mechanisms in normal vision have met with only moderate success. Stiles (1978), measuring threshold for test flashes of various wavelengths superimposed on bright steady backgrounds that also differed in wavelength, derived seven photopic spectral sensitivities attributed to the hypothetical underlying processes which he termed Π mechanisms. Though Π_3 , Π_4 , and Π_5 correspond crudely to the *b*, *g*, and *r* cones, respectively, substantial and consistent discrepancies exist between Π mechanisms and cone pigment spectral sensitivities derived from the study of color blindness. For example, if Π_4 and the long-wavelength protanopic spectral sensitivity are normalized at their peaks, Π_4 is more than twice as sensitive in the long wavelength end of the spectrum (Stiles, 1978; Vos and Walraven, 1970). Clearly, either the normal pigments differ from those of dichromats, a possibility suggested by Estévez and Cavonius (1977) and Pugh and Sigel (1978), or the three cone types do not regulate their sensitivities autonomously in the presence of steady backgrounds (Boynton, 1963; Enoch, 1972).

The use of isolation techniques different from those of Stiles might help resolve this issue. If indeed the Π mechanisms are not identifiable with single cone types because the different cone types interact in setting each others' sensitivity in steady-state light adaptation, it may still be possible to tease apart the photopic system into its three receptor components if conditions can be found under which the cones act independently of one another. We report experiments designed to examine the question of cone-cone independence in dark adaptation. The familiar dark adaptation curve is typically two-branched: the upper branch reveals the recovery of the cones while the lower branch reveals the more sluggish recovery of rods, suggesting that the rod and cone systems recover more or less independently during dark adap-

tation (Hayhoe *et al.*, 1976). If the three photopic mechanisms behave autonomously in the same way, one might expect inflections in the photopic branch of dark adaptation corresponding to the independent recoveries of the *r*, *g* and *b* mechanisms. In fact, Auerbach and Wald (1954) and Du Croz and Rushton (1966) demonstrated that under appropriate conditions photopic dark adaptation does reveal such inflections. For example, a two-branched curve was obtained from the rod-free fovea with a blue test flash following a bleaching exposure of orange light. Du Croz and Rushton attributed the upper branch to Stiles' blue (Π_1) mechanism and the lower branch to his green (Π_4) mechanism. Similarly, the red (Π_3) and green (Π_4) mechanisms can be isolated during recovery with a deep red bleach and a red test flash viewed against a green background. However, Du Croz and Rushton's report does not make clear whether the channels corresponding to the separate branches of cone dark adaptation are Stiles' mechanisms or the slightly different pigment spectral sensitivities inferred from work on color defectives, nor is there any indication that their measurements were precise enough to distinguish between these possibilities.

I. THE BACKGROUND SUBSTITUTION TECHNIQUE

The present study uses the properties of afterimages to provide a stringent test of the independence of photopic mechanisms during recovery from bleaching and to obtain estimates of the *r* and *g* cone spectral sensitivities in the long wavelength spectral range. The appearance of an afterimage induced by exposure to a bright bleaching flash depends on the intensity of the background upon which it is viewed. In general, an afterimage initially glows dimly against a dark background (the positive afterimage) but appears dark against a bright background (the negative afterimage). However, against any steady back-

ground, afterimages tend to fade from sight within a few seconds. An afterimage which has faded in this way can be revived by any sudden change in the radiance of the background. If a brighter background is suddenly substituted for the first, the revived afterimage appears negative; if a dimmer background is substituted, the afterimage looks positive. Thus the appearance of an afterimage induced by a bleaching flash depends not on the absolute radiance of the background upon which it is viewed, but on the change in the radiance of that background. The revived afterimages that occur when the background is changed can be understood as perceptual consequences of the depression of sensitivity in the bleached region (Rushton, 1971; MacLeod and Hayhoe, 1974a; Hayhoe *et al.*, 1976). If the introduction of a new background provides an increase in stimulation, unbleached retinal areas will register it with full sensitivity. The bleached retina, however, gives a reduced response to the incremental stimulus, making this region appear less bright than the surround, so producing a negative afterimage. In general, the greater the bleach, the less the sensitivity and the darker the negative afterimage. The positive afterimage seen with a decremental stimulus can be understood in the same way.

Now suppose that the fovea is exposed to a bright bleaching flash consisting of a bipartite field with red and green hemifields. Suppose also that the radiances of the hemifields are adjusted so that the quantum catch for the r cones, say, is the same on both sides of the field during the bleach. The quantum catch of the g cones must then be different on the two sides of the field: the g cones will catch more quanta from the green side of the bleaching field than from the red side. Such a bleaching stimulus is diagrammed in the upper half of Fig. 1. Consider now the effects of this bleaching stimulus on the observer's sensitivity to stimulation of the r or g cones. The lower half of Fig. 1 depicts the distribution of sensitivity across the bleached area and its immediate surround. Sensitivity is shown separately for r and g cone stimuli (right and left diagrams, respectively). Two different hypotheses are considered. Suppose first that the depression of sensitivity due to bleaching is applied independently to signals originating within each type of cone, and that sensitivity to r or g cone stimuli depends only on the bleaching of r or g cones, respectively. This *cone-cone independence* hypothesis is not inconsistent with post-receptoral adaptation so long as there is no significant sensitivity regulation in cells receiving *both* r and g cone input. On the independence hypothesis the depression of sensitivity to r cone stimuli should be uniform across the bipartite bleached region, since the r cones were uniformly bleached to begin with. [At the same time, for g cone stimuli (left diagrams in Fig. 1) there will of course be a greater depression of sensitivity on the side bleached with green light.] But on the alternative, *interaction* hypothesis, bleaching of one receptor type would affect sensitivity for stimuli applied to other receptors, and so the unequal bleaching of the g cones would generally upset the balance of sensitivity even for r cone stimuli, as indicated at the bottom of Fig. 1.

To decide between these hypotheses experimentally,

we need to be able to examine the spatial variation of sensitivity to r cone stimuli in situations like that of Fig. 1. We have already pointed out that afterimages, revived (after fading) by a change of background, provide a convenient indicator of the spatial variation of the observer's sensitivity to the stimulus provided by the background exchange. All that is needed, then, is a change of background that stimulates the r cones without at the same time exciting the g cones. The exchanging of two backgrounds of different color, as in the lower half of Fig. 2, can provide a "pure" r cone stimulus in this sense, if the relative radiances of the two backgrounds are set so that the g cones (but not, of course, the r cones) absorb the same number of quanta from the substituted background as from the original. (The principle of this technique follows previous studies, notably those of Rushton *et al.*, 1973.) The afterimage revived by such an exchange of backgrounds can serve as a visible rendering of the distribution of sensitivity for r cone stimuli. If the sensitivity is uniform despite the bipartite bleach (as predicted by the independence hypothesis in the situation of Fig. 1), then the revived afterimage should appear uniform rather than bipartite.

Similarly, it should be possible to determine whether the r mechanism affects the recovery of the g mechanism by equating the bleaching hemifields, this time for the g cones, while isolating the g mechanism afterimage by equating the backgrounds for the r cones during the test condition.

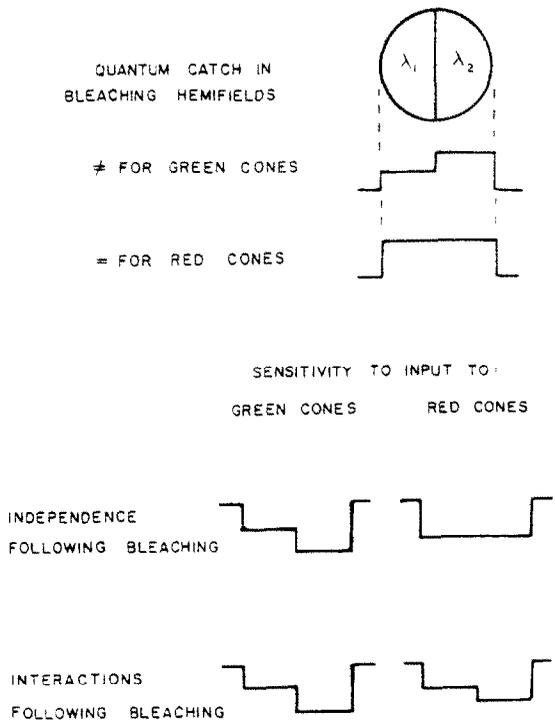


Fig. 1. (top) A bipartite bleaching field ($\lambda_2 < \lambda_1$), showing its bleaching effect on the r and g cones when the relative radiances have been adjusted to make the r cone bleach uniform. (bottom) Distributions of sensitivity after the above bleaching exposure, as predicted by two alternative hypotheses. Sensitivity is shown separately for g cone stimuli (at left) and for r cone stimuli (at right).

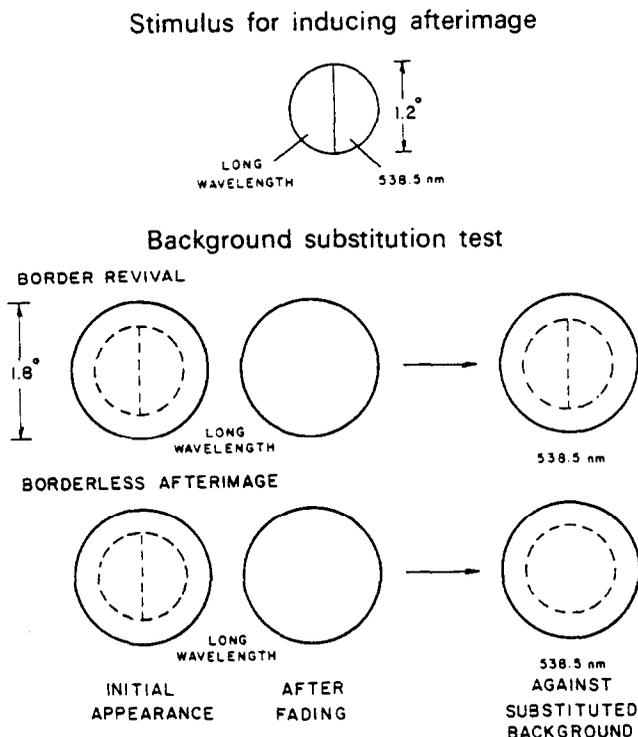


Fig. 2 (top). 1.2° bipartite field with long wavelength and green (538.5 nm) hemifields used for inducing afterimage. (bottom) Technique of fading afterimage on long wavelength background, substituting 538.5 nm green background and noting whether the revived afterimage was uniform.

In practice, we do not know *a priori* what precise ratios of the radiances of the bleaching hemifields (bleaching ratios) or what ratios of the radiances of the test backgrounds (background ratios) will actually produce equal quantum catches for either the *r* or *g* cones. That information would be available only if we knew exactly the spectral sensitivities of the specific observer. Consequently, it is necessary to investigate a wide range of bleaching ratios, and for each bleaching ratio, a wide range of background ratios to determine if *any* particular pairs of bleaching and background ratios actually yield afterimages which are uniform and borderless when viewed against the neatly substituted background. If these borderless afterimages can be found, then the two "interchangeable backgrounds" must be equal for one of two visual channels and the bleaching hemifields must be equal for the other underlying channel. If borderless afterimages can be found for several wavelengths, then the spectral sensitivities of the channels can be plotted. If these sensitivities compare favorably with the spectral sensitivities of the *r* and *g* cones derived by other methods, then within the limits of the background substitution technique the *r* and *g* cones can be said to recover independently during dark adaptation.

Methods

Apparatus and calibration. Stimulus displays for this experiment and those that follow were generated with the two-channel Maxwellian view system shown in Fig. 3. In order to produce high luminances, the tungsten lamp (General Electric 200 W, 120 V Quartzline Lamp) was overrun

at 135 V and the filament image was focused by a lens near the source so that part of a single coil completely filled the artificial pupil (3.2 mm in diameter). The artificial pupil was small enough to ensure that the observer's natural pupil never occluded the incoming light. This was checked subjectively by noting that the pupillary constriction which followed the onset of the bleach did not vignette the field. Observers in all experiments used dental impressions to maintain fixed and repeatable head position.

All stimuli were produced by passing light through monochromatic interference filters (bandwidth at half height ≤ 14 nm) whose spectral transmissions were calibrated with a Cary spectrophotometer. Ealing 577, 601, and 639 nm interference filters and Baird-Atomic 620 nm and 538.5 nm filters were used for observer DRW. MMH was tested with the 538.5, 601, 620, and 639 nm wavelengths. The bipartite field subtended 1.2° visual angle with hemifields produced by beams passing through a semicircular aperture in each channel and united at a beamsplitter. A translational stage in Channel 1 allowed the observer to juxtapose precisely the two razor-edged hemifields to eliminate any gap or overlap between them. Backgrounds shared a circular aperture subtending 1.8° visual angle. Radiometric measurements of all stimuli were made with a silicon photodiode (EG & G Radiometer/Photometer, model 450-1) which was checked against a thermopile. All radiance measurements, made with the same filters and wedge settings used for the observer, were in μW at the pupil and were corrected for infrared radiation. Infrared was measured by interposing a # 70 (passing > 678 nm) filter into the beam and the correction was made by subtracting the radiance value thus obtained (always very small) from the total energy without the filter. Microwatts were converted to lumens using 1931 C.I.E. conversion factors. Troland values were obtained by dividing by the solid angle of the field. Bleaching exposures for the long wavelength hemifields (577, 601, 620, 639), which were fixed in

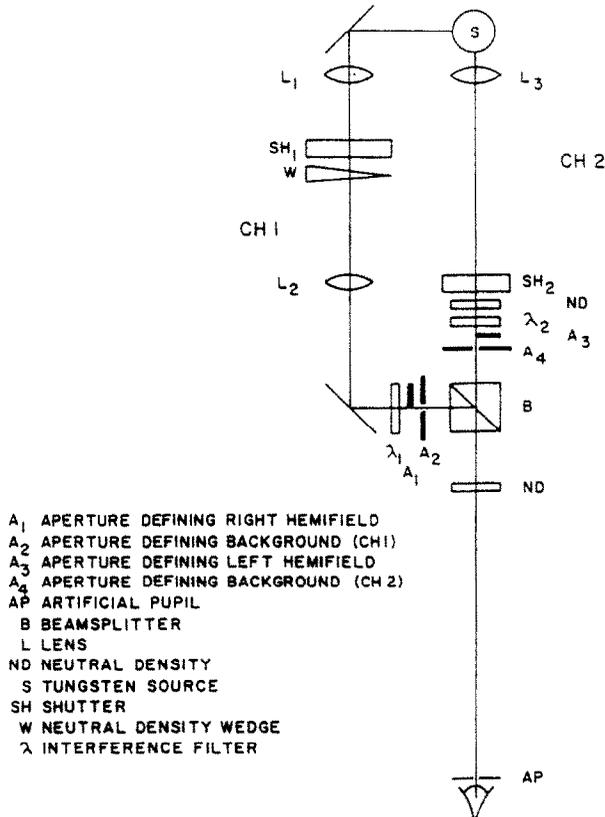


Fig. 3. Two-channel Maxwellian view system used in all experiments.

intensity while the 538.5 nm standard was varied from trial to trial, were $10^{3.30}$, $10^{3.46}$, $10^{3.66}$ and $10^{3.43}$ td, respectively. Backgrounds for these wavelengths ranged from 40 to 440 td.

Procedure. Two observers (DRW and MMH) were used in the background substitution experiment; both had normal color vision. Each trial consisted of two parts:

(1) a foveal afterimage was induced with a bright bleaching exposure and

(2) the afterimage was viewed against steady backgrounds in the test condition.

During the 10 sec bleaching exposure the observer carefully fixated the center of the bipartite field (see Fig. 2). Rod intrusion was avoided by using small stimuli (1.2° visual angle in diameter) projected onto the fovea. (Polyak, 1941, assessed the foveal rod-free area to subtend $1.5\text{--}1.7^\circ$ visual angle on the basis of anatomical evidence and we have verified this psychophysically for one of our observers (DRW) by mapping thresholds for a small test flash.) The left hemifield was a long-wavelength light (whose wavelength was varied from session to session), while the right hemifield was a standard 538.5 nm green light. Since all stimuli used fell in a spectral range equal to or longer than 538.5 nm, the contribution of the blue-sensitive cones can be ignored. With careful fixation the bleaching exposure induced a crisp bipartite afterimage of the original stimulus display.

Immediately following the bleaching exposure the hemifield apertures were removed from each channel to reveal the 1.8° background field. Uniblitz shutters in the two channels were driven in counterphase so that opening the shutter in one channel simultaneously closed the shutter in the other. Thus the observer could exchange one background for the other. Background wavelengths were always the same two that had been used in the bleaching exposure.

The afterimage of the bipartite field was projected on the long-wavelength background and allowed to fade (see Fig. 2). Fading occurred within 10–15 sec for both observers; MMH reported total disappearance of the afterimage, DRW reported that a very faint amorphous tinge, showing no distinction between the halves and roughly coextensive with the bleached circle, was visible in the center of the background after fading. The observer then neatly substituted the green (538.5 nm) background for the long-wavelength one, noting the appearance of the afterimage on the substituted background. If the revived afterimage was nonuniform, as usually happened, the observer then returned to the long-wavelength background and adjusted the radiance of the green background beam (using the neutral density wedge in Channel 1) in preparation for the next background exchange. The observer's task was to locate, if possible, a radiance of the green background against which the afterimage appeared uniform and borderless. The appearance of the revived afterimage followed simple principles which the observer could use to guide his search. These are best illustrated for the case shown in Fig. 1, where the two halves of the bleaching field are equated for the r cones. In this case the polarity of the revived afterimage was appropriate to the stimulation of the g cones. Thus if the substituted background was too bright, there appeared a negative afterimage of the bleaching field as seen by the g cones, that is, the green-bleached side of the field appeared darker (and less green) than the red-bleached side. If the substituted background was too dim, there was again a bipartite afterimage but with the opposite color difference between the two sides. With practice it was straightforward for the observer to use the observed afterimage to decide whether the radiance of the substituted background needed to be increased or decreased for the next exchange. The time required for the

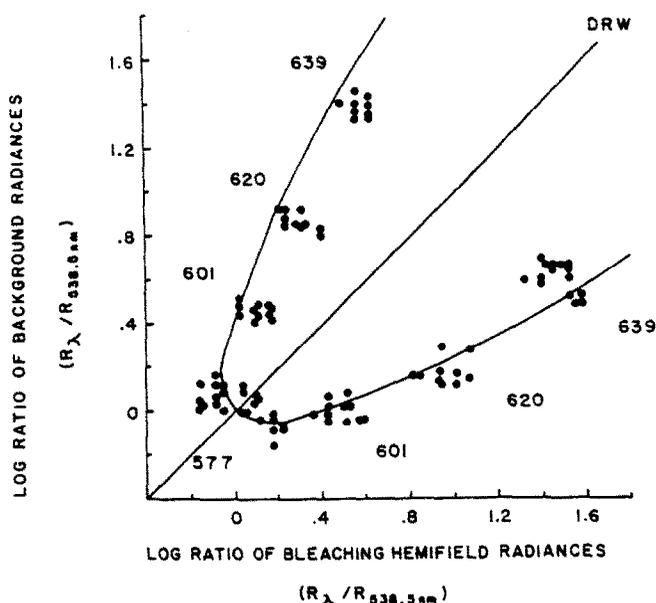


Fig. 4. Dots indicate the ratios of the radiances of bleaching hemifields (vertical axis) and test backgrounds (horizontal axis) which together yielded borderless afterimages for observer DRW. Clusters are numbered according to the long wavelength light paired with the 538.5 nm reference green which was used to find those particular borderless afterimages. The curve represents the prediction from Vos and Walraven's r and g functions.

search process was usually 15 sec or more, and by 60–90 sec after the bleach the search had to be abandoned because the afterimage was too weak to be useful.

The typical result of such a trial was that no borderless afterimage could be achieved, and that whatever the radiance of the substituted background, the two halves of the afterimage remained different in color if not in brightness. Borderless afterimages could, however, be achieved with the addition of the second degree of freedom provided by the ratio of the radiances of the hemifields during the bleaching exposure. This was varied between trials, in steps of 0.06 or 0.12 log units over a range of 1.2 log units, with either two (MMH) or four (DRW) bleaching exposures at each

step. Five minutes were allowed between trials to ensure that the cones were recovered from their bleaching on previous trials. On any trial where a borderless afterimage was achieved, the required radiance of the substituted background was recorded along with the ratio of the bleaching hemifields. This procedure was repeated for additional long-wavelength stimuli, each paired with the same reference green (538.5 nm).

Results and discussion

Borderless afterimages could be obtained by both observers for each pair of wavelengths tested. Figure 4 maps these borderless afterimages for observer DRW. The ordinate shows the logarithm of the ratio of the two test background radiances; the abscissa shows the logarithm of the ratio of the bleaching hemifield radiances. Pairs of bleaching and background ratios which yielded a uniform and borderless afterimage against the neatly substituted background are represented by dots in the figure.¹ The distinct clusters of points show that for each pair of wavelengths there existed two ranges of paired bleaching and background ratios which yielded borderless afterimages.² If either the bleaching ratio or the background ratio did not fall in the appropriate range, the afterimage viewed against the substituted background was always nonuniform and marked with a border. Each point in Fig. 4 is derived from a single bleach and recovery on which a borderless afterimage was found. The different points belonging to one cluster were generally measured in the same session, but different clusters were investigated in different sessions.

The symmetry of the clusters of points about a line of unit slope passing through the origin reflects the fact that, for a particular pair of wavelengths, the bleaching ratio of one of the two clusters is roughly the same as the background ratio for the other cluster

¹ In the case of 639 nm paired with 538.5 nm, DRW reported that it was not possible to find a background radiance which entirely eliminated the border down the center of the afterimage even though the two halves of the afterimage were identical in appearance. This was counted as a match, since the faint border may have been an artifact of alignment of the bleaching hemifields. The two wavelengths are sufficiently far apart to introduce the problem of chromatic aberration; an achromatizing lens was not used. MMH found uniform and borderless afterimages against the substituted backgrounds for all wavelengths.

² In the case of 577 paired with the 538.5 nm green, the two clusters overlap so that there is one relatively broad range of bleaching and background ratios which yielded borderless afterimages. This overlap is not surprising in light of the fact that the two wavelengths used are less than 40 nm apart. Since the spectral sensitivity curves of the two underlying channels are normalized at the reference wavelength (538.5 nm), the curves will be very close together at wavelengths near the reference. If the ranges over which borderless afterimages can be obtained are large enough, overlap will occur. The elongated cluster was arbitrarily split in half to obtain two pairs of mean bleaching and background ratios yielding borderless afterimages.

and vice versa. This pattern of results would be expected if the sensitivity regulation processes responsible for these afterimages proceed independently in two spectrally selective channels: to obtain a borderless afterimage, the bleaching hemifields must be equal for one or the other of these channels, making that one uniformly sensitive, while the backgrounds are equated for the remaining channel so that only the uniformly sensitive channel is stimulated by the exchange. The upper arm of the horseshoe-shaped scatterplot is defined by bleaching ratios which must be equated for one channel (which we can arbitrarily designate Channel A). The background ratios corresponding to the bleaching ratios in the same arm must be equated for a different channel (B) which, due to the larger ratios of the long-wavelength background to the green, must be less red-sensitive than Channel A. The lower arm of the horseshoe is defined by bleaching ratios corresponding to the relatively green-sensitive Channel B and by background ratios corresponding to the relatively red-sensitive Channel A.³ The clusters of Fig. 4 deviate slightly from the symmetry predicted by the hypothesis of two independent channels. These deviations could mean that the two channels are not completely independent, but as we have no firm estimate of session-to-session variability we cannot be sure that they are not due to experimental error.

Obviously the simplest hypothesis about the two unspecified Channels A and B is that they are simply the *r* and *g* cones, respectively, but before considering

³ Due to self-screening, bleaching slightly alters the spectral sensitivities of the *r* and *g* cone pigments. The effects of self-screening cannot be determined precisely without questionable assumptions, but fortunately they are slight in these experiments so that no corrections for self-screening have had to be made. The appropriate corrections, however, have been approximately calculated on the assumption that the observed spectral sensitivities of the two channels are those of pigments with optical densities of 0.5 at the wavelengths of maximum absorption. Photosensitivities and regeneration times were taken from Hollins and Alpern (1973) with the assumption that the quantum basis photosensitivities are equal at λ_{max} . The corrections for the test spectral sensitivity are time-dependent, and one minute of recovery from the bleach at the time of testing was taken as representative. Calculations thus suggested that the only significant effect of bleaching on test sensitivity was to lower the relative sensitivity of the *r* cones in the red; this underestimation was greatest at 639 nm where it was still only 0.024 log units.

The calculated effects of bleaching on sensitivity to the bleaching light were to reduce the sensitivity of the *g* cones by 0.03 log units at 620 nm and also at 639 nm, while *r* cone sensitivity was reduced by 0.064 log units and 0.073 log units respectively. If corrections were made for these effects the main result would be to improve, very slightly, the correspondence between bleach and test sensitivities.

Another interesting expected consequence of self-screening is that when the fraction of bleached pigment (in, say the *g* cones) is nonuniform across the bipartite field, the spectral sensitivity becomes different in the two halves of the field, so that in theory two adjustments should be insufficient to produce a borderless afterimage. But the difference in spectral sensitivity is only (in the worst case) about 0.024 log units, and apparently this was not enough to be obvious to the observer.

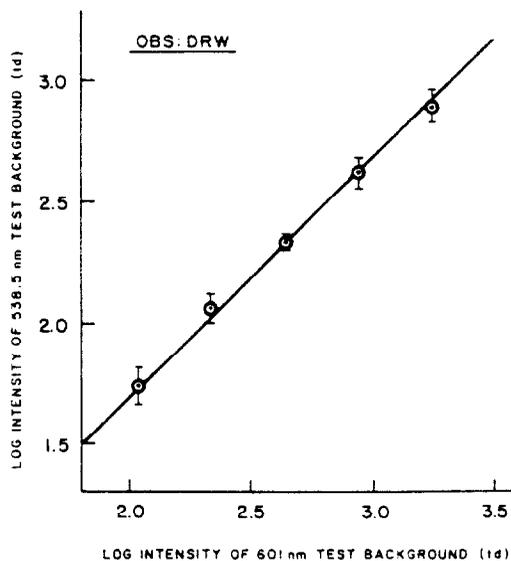


Fig. 5. Log retinal illuminance of the substituted 538.5 nm background yielding borderless afterimages for a fixed bleaching ratio as a function of the log retinal illuminance of the 601 nm background. Each point is the mean of five trials. Error bars in this and later figures equal ± 2 times standard error of the mean based on within-session variability.

this possible identification in more detail, it is important to show that the appearance of a revived afterimage depends not on the absolute radiance of the substituted background but on the ratio of the radiances of the exchanged backgrounds. Only then will the derived spectral sensitivities be generalizable across different absolute radiances. To check this point, DRW found borderless afterimages for a fixed bleaching ratio at five different retinal illuminances of a 601 nm background upon which the afterimage was originally faded. Figure 5 shows the mean log retinal illuminance of the 538.5 nm green background which yielded borderless afterimages for five bleaching exposures at each retinal illuminance of the 601 nm background over a range of 1.2 log units. A line of unit slope on the log-log plot fits the data well, showing that the ratio of background radiances required for a borderless afterimage was invariant over the entire range tested. Checks done by fading the afterimage on the green background and substituting the red showed that the critical red-to-green ratio was the same to within experimental error.

II. SPECTRAL SENSITIVITIES COMPARED WITH COLOR DEFECTIVES

Although the background substitution technique has revealed two channels (A and B) underlying dark adaptation, it remains to be seen whether these channels correspond to the *r* and *g* photopigments or to some complex interaction between them. In Fig. 6, the open symbols replot the data of Fig. 4 to show the spectral sensitivities of the two "channels". The circles show for each bleaching wavelength used the mean radiance of the long-wavelength field relative to the 538.5 nm bleaching field where a borderless afterimage was recorded. Squares show similarly, for

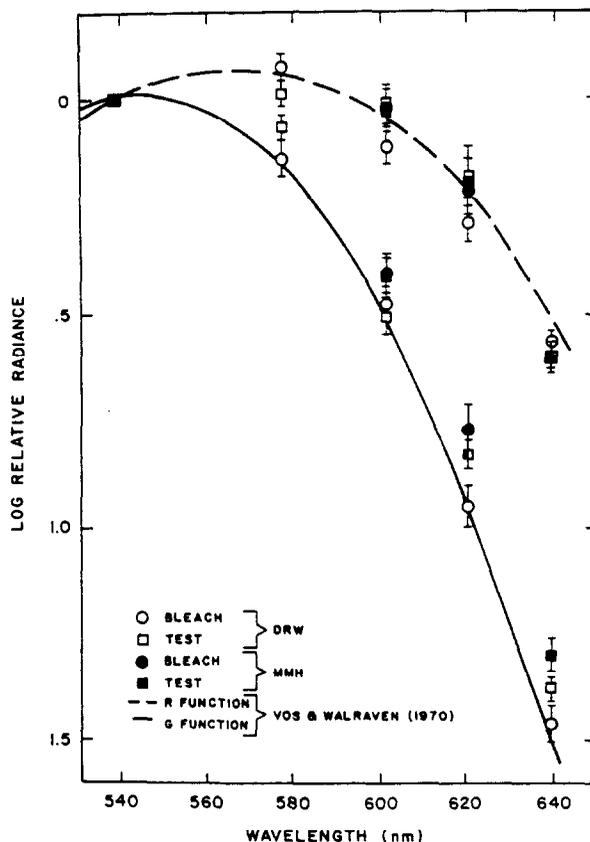


Fig. 6. Circles represent mean bleaching ratios which produced borderless afterimages for a particular long wavelength; squares represent the corresponding mean test background ratios. Open symbols, observer DRW; solid symbols, MMH. Dotted and solid curves are the r and g functions from Vos and Walraven (1970) normalized to the reference 538.5 nm green light. Error bars = ± 2 times SEM. Ordinate is in radiance units, on a log scale, increasing downwards.

each background wavelength, the radiance required to produce a borderless afterimage relative to the radiance of the 538.5 nm background. The circles show the vertical coordinates of the clusters in Fig. 4, while the squares show the horizontal coordinates. Each of the two limbs of Fig. 4 generates circles for one channel, squares for the other. Solid symbols are for another observer.

The curves in Fig. 6 are Vos and Walraven's r and g functions (1970) derived from dichromatic color-matching data and normalized at the standard wavelength. Since protanopes and deuteranopes have only one pigment sensitive enough to lights longer than 530 nm to contribute to color matches between lights in this range, they can match spectral lights using radiance adjustments only. The matches made by protanopes and deuteranopes in this range are thought to reflect the spectral sensitivity of g cones and r cones, respectively. The agreement between the Vos and Walraven r function and the background substitution data is good for both DRW and MMH. However, the background substitution technique produced a green-sensitive channel which is slightly more sensitive in the long end of the spectrum than Vos and Walraven's g function.

In order to gauge whether this slight difference between the two sets of data is due to calibration

error or represents a real difference caused by a failure of independence between the r and g cones during dark adaptation, color defectives made color matches on the same apparatus used in the background substitution technique.

Method

Two deuteranopes and two protanopes, screened using the Ishihara plates, the Farnsworth-Munsell 100-Hue Test, and the Nagel anomaloscope, varied the radiance of the green (538.5) half of the bipartite field until it appeared indistinguishable from the long wavelength half. Ten matches were made by each dichromat for five wavelengths (577, 587, 601, 620 and 639 nm), each paired with the reference green light. The luminances of the hemifields were roughly the same as those used during the test condition of the background substitution technique.

Results and discussion

Figure 7 shows the mean hemifield radiances which were perfect matches for each of the color defectives (solid symbols) compared with both the background substitution data for DRW (open symbols) and the Vos and Walraven r and g functions (curves). Both the protanope and the deuteranope data are slightly more red-sensitive than the Vos and Walraven g and r functions, respectively. The small discrepancies could be due to observer variation among dichromats (Alpern

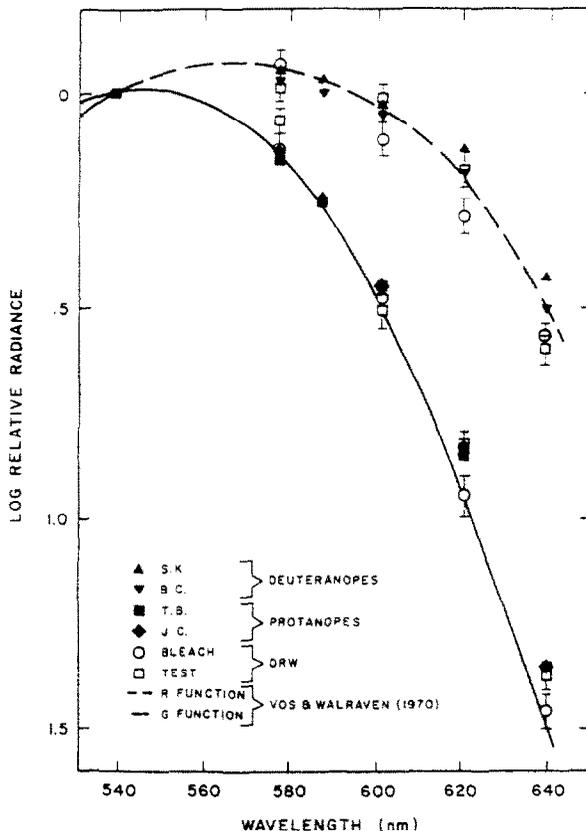


Fig. 7. Color-matching data from two deuteranopes (solid triangles) and two protanopes (solid squares and diamonds) compared with the background substitution data of DRW (open circles and squares) and the r and g functions (curves) of Vos and Walraven (1970). Error bars (± 2 times SEM) are about as large as the symbols for dichromats.

and Wake, 1977), or to the dependence of pigment density and spectral sensitivity on field size (Pokorny and Smith, 1976), together with calibration error. The protanopic sensitivity curve (solid squares and diamonds) agrees well with the data derived from the background substitution technique. The deuteranopic sensitivity curve (triangles) is slightly more red-sensitive than the data from background substitution. In general, the color defective data agree reasonably well with that derived by the new technique; hence, if interactions do occur between the r and g cones during dark adaptation, those interactions are too small to reveal themselves clearly under the conditions of these experiments.

III. SPECTRAL SENSITIVITIES DERIVED FROM MONOCHROMATIC MATCHING IN THE NORMAL EYE

Given the individual differences that exist between dichromats (Alpern and Wake, 1977), it was desirable to compare the channels tapped by the background substitution technique with the spectral sensitivities derived by a different technique in the eye of the same observer. The second technique chosen for comparison was the artificial red-green blindness (Fedorow and Fedorowa, 1928; Brindley, 1953) induced by adaptation to very bright lights. Following adaptation to a blue-green or a red light, lights from the long

wavelength portion of the spectrum can be matched using radiance adjustments only; matches following blue-green adaptation are presumably equal for the r cones, while matches made following red adaptation are presumably equal for g cones. The spectral sensitivities reported by Fedorow and Fedorowa and by Brindley agree better than do π mechanisms with estimates of the cone spectral sensitivities based on evidence from color defectives, as MacLeod and Hayhoe (1974b) have pointed out.

Method

Observer DRW fixated a 483 nm bleaching light ($10^{5.4}$ td) for 60 sec. As soon as possible following the bleach, a perfect match was made between two halves of the bipartite field (30–60 td). The radiance of the 538.5 nm green reference light was adjusted until it looked identical to a long-wavelength light (577, 587, 601, 620 or 639 nm). This temporary red-green blindness lasted approximately 30 sec allowing time for several matches to be made. Matches were made following four bleaching exposures for each of the 5 pairs of wavelengths.

This same procedure was then repeated using a 681 nm adapting light ($10^{5.5}$ td) viewed for 60 sec.

Results and discussion

Figure 8 compares the spectral sensitivities derived from monochromatic matching (solid symbols) with the data from the background substitution technique

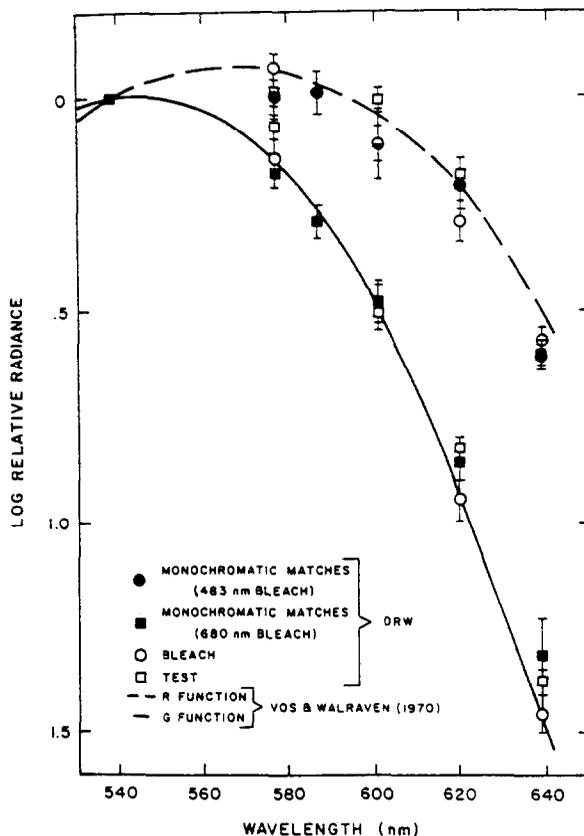


Fig. 8. Artificial red-green blindness following adaptation to a very bright 483 nm light (solid circles) and a 680 nm light (solid squares) compared with background substitution data (open symbols) on the same observer (DRW). Curves are the r and g functions of Vos and Walraven (1970). Error bars = ± 2 times SEM.

(DRW, open symbols).⁴ The agreement between the data derived from two different techniques, and between both these and the dichromatic data, suggests that the two spectrally selective channels revealed by the background substitution technique may indeed be simply the r and g cones.

GENERAL DISCUSSION

The conditions under which interchangeable backgrounds were found agree fairly well with the predictions of the independence hypothesis. This does not of course prove that the independence hypothesis is correct; but the demonstrated sensitivity of the background substitution technique, together with the fairly close correspondence between the "cone" spectral sensitivities derived from it and those derived from congenital or artificial dichromacy, shows that any interactions under the particular conditions of these experiments are slight in their effects. Sensitivity regulation following intense bleaching seems to occur predominantly before signals from r and g cones come together.

⁴ The monochromatic matching data were not corrected for the effects of self-screening. Calculations (assuming optical densities of 0.5) suggested that no data point would be altered by as much as 0.1 log units since the adaptation lights did not bleach as much of the photopigment being investigated as of the pigment purposely rendered insensitive.

The technique allows estimation of the fundamental spectral sensitivities of the r and g cones, but unfortunately its precision here is limited. In our experiments, the conditions for a borderless afterimage, though defined with great precision (with regard to background intensity) in any one trial, fluctuated slightly from trial to trial, yielding the variability represented by the dispersion of the clusters in Fig. 4. The sources of this trial-to-trial variation have not been identified. Another source of uncertainty is the unknown pigment density and the extent of the resulting self-screening effects.

In view of these uncertainties, the agreement between the spectral sensitivities derived by the afterimage technique with those of protanopes and deuteranopes (Fig. 7) is as good as could be expected. When data from observers of the same type are averaged, the differences between normal and protanopic data are slight (± 0.04 log units in relative sensitivity) and show no clearly systematic dependence on wavelength. Normal and deuteranopic data agree to ± 0.05 log units; the afterimage sensitivities may be systematically lower in the red, but only by amounts that could be reasonably ascribed to observer variation. Among Alpern and Wake's deuteranopes (1977), the standard deviation of relative sensitivity to red and green was 0.07 log units. The afterimage spectral sensitivities do not agree so well with those of the Stiles' Π mechanisms. In the case of Π_3 , the agreement is quite satisfactory (± 0.02 log units). But Π_4 is clearly

too sensitive at long wavelengths: by 0.06 log units at 601 nm, 0.16 log units at 620 nm and 0.23 log units at 639 nm. These differences are too large to be plausibly ascribed to measurement error or observer variation; besides, crude measures of the Π_4 field sensitivity for DRW and MMH (17, 200 msec flash) give an even worse fit than Stiles' Π_4 to the afterimage data, with deviations (in sensitivity relative to 538 nm) reaching 0.39 log units at 639 nm. Any of the following three factors could be responsible for the difference between the Stiles spectral sensitivities and the sensitivities attributed here to cones. First, horizontal cell interactions might perhaps be implicated in steady-state light adaptation but not in dark adaptation (Green *et al.*, 1975; Naka and Rushton, 1965). Second, the exponential nonlinearity relating sensitivity during dark adaptation to the level of bleached pigment may aid isolation of a single cone type by allowing the sensitivity of "unwanted" cones to be depressed further than under steady-state levels where Weber's Law prevails (Du Croz and Rushton, 1966). Third, the experiments on normal vision that have yielded results consistent with those from dichromats have so far used null, or matching, methods rather than threshold measurements. Suppose that there are multiple sites of sensitivity regulation: peripheral sites, that preserve cone-cone independence because signals from different cone types are still fairly well segregated, and also more "central" sites, at which cone-cone interaction may occur due to the convergence of input from different cones onto individual cells at the more central stage. If this sort of organization is assumed, and Pugh and Mollon (1979) give convincing evidence for it, the difference between matching and thresholds might be important for the following reason. When stimuli that are contiguous (in space or time) are exactly matched, they form no spatial or temporal transient (e.g. no border in a bipartite field) that could strongly excite central neurons. Already at the bipolar level the preference for spatio-temporal transients is strong (Shantz and Naka, 1976), and retinal ganglion cells and lateral geniculate cells are progressively more efficient in filtering out uniform or steady input (Marrocco, 1972). To the extent that central neurons are quiescent across the invisible border between matched fields, any differential excitability of the central neurons within the matching field cannot affect the match. Threshold sensitivity, on the other hand, depends on the capacity of the test flash to excite successively all levels of the visual system. Hence cone-cone interactions due to alterations of sensitivity at relatively central sites might become apparent in threshold measurements but not in matching. More experiments will be needed to decide which of these three factors (if any) are important.

Previous studies of chromatic preadaptation have often yielded results inconsistent with cone-cone independence, even in some cases where matching rather than thresholds was employed. Color matching after asymmetric adaptation to colored lights (Wright, 1934; Walters, 1942; MacAdam, 1956) has yielded spectral sensitivities that cannot plausibly be associated with cones, and although cone-cone independence in the sense considered here was not explicitly tested in these studies, the reported results suggest

that it fails. Moreover, studies of both thresholds and color appearance have shown clearly that sensitivity for stimuli applied to the blue-sensitive cones does not recover independently of the states of other cones during dark adaptation (Stiles, 1978; Mollon and Polden, 1976; Pugh and Mollon, 1979). Instead, the offset of an adapting field that stimulates the *r* and *y* cones is found to decrease substantially the effectiveness of the blue-sensitive cones. Mollon and Polden report one aspect of this phenomenon of "transient tritanopia" which may help reconcile the interactions implicit in it, and in the color matching data, with the background substitution data presented here: transient tritanopia is absent when the adapting field is very bright. Since the experiments of Wright, Walters and MacAdam used relatively low adapting intensities, it may be that use of very bright bleaching exposures, as in our experiments, is a necessary condition for obtaining cone-cone independence. To understand why this might be so, the multiple site concept again proves helpful. Virsu and Laurinen (1977) and Loomis (1978) suggest that relatively dim and prolonged adapting exposures can alter sensitivity at a site which is preceded by a compressive nonlinearity. Very bright bleaching lights should have similar effects at such a site, due to saturation of the preceding nonlinear stage, and indeed such bleaching lights tend to look quite similar, as this would suggest (Cornsweet, 1962). Perhaps, then, the two bright hemifields used for bleaching in our experiments were similar in their effects on those sites, more central than the cones, which are responsible for interactions in dark adaptation. With the "central" sites thus made uniformly sensitive, the relative sensitivity of the two hemifields may depend only on the independently recovering sensitivities of the cones.

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