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FOVEAL TRITANOPIA*

DAVID R. WILLIAMS,† DONALD I. A. MACLEOD and MARY M. HAYHOE
Psychology Department, University of California, San Diego, La Jolla, CA 92093, U.S.A.

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Abstract—Measurements of sensitivity and color discrimination suggest that an area roughly 25′ in diameter in the central fovea lacks functioning blue-sensitive cones. Alternative explanations such as screening by macular pigment or Troxler fading are shown to be unable to account for the results. Evidence is presented that residual B cone-mediated color discrimination found in this and previous studies may be mediated by light scattered onto surrounding B cones. Scattered light can dramatically affect the color appearance of lights seen in the central fovea: a small fixated green field appears blue when surrounded by a dim, inconspicuous violet corona.

INTRODUCTION

Nearly everyone agrees that, under some conditions at least, color vision for small fields in the normal central fovea resembles congenital tritanopia; but here the agreement ends. There has been prolonged debate about the extent of this "foveal tritanopia" and the reasons for it. König and Köttgen [see König (1894)] first discovered foveal tritanopia, making two observations which they felt distinguished the central 1 degree of the fovea from the eccentric retina: (1) the central fovea was relatively insensitive to short wavelength light, and (2) color vision was impaired there. Small, fixated fields could be matched with a mixture of two, rather than the usual three, primaries. Color discrimination in the blue–green region of the spectrum was poor. König believed that a blue-absorbing photoproduct of rhodopsin was responsible for the short wavelength input to color vision and he therefore attributed his observations to the absence of rods in the fovea.

Willmer (1944), unaware of König's work, rediscovered the tritanopic confusions characteristic of small foveal fields, also blaming them on the absence of rods. Willmer and Wright (1945) extended Willmer's qualitative observations, confirming König's original results. Using a centrally fixated 20′ bipartite matching field, they found that only two primaries were required to match a third light, obtaining dichromatic coefficients in agreement with those obtained from congenital tritanopes (see Walraven, 1974). Color discrimination between two wavelengths, one in each half of a centrally fixated 20′ field, was impaired in the blue–green region of the spectrum. They reported the existence of two neutral points for small foveal fields, one at 578 nm and another near 410 nm, consistent with the idea that the normal central fovea, like the tritanope, lacks a short wavelength receptor response.‡

Shortly after Willmer's initial report, however, another interpretation emerged which proposed that foveal tritanopia was the result of a neural color vision loss central to the receptors. Hartridge (1945a, b) argued that tritanopia is characteristic of small fields in general and is not restricted to the central fovea. On this account, "small field tritanopia" is not due to the scarcity of some receptor in the fovea since the effect occurs outside the fovea as well. Thomson and Wright (1947) confirmed Hartridge's observations; they reported that with steady fixation dichromatic matches for a 15′ bipartite field could be made at eccentricities of 20 and 40′ of arc as well as at the foveal center.

It is generally agreed that these small field dichromatic matches are readily upset by lapses of fixation. Hartridge (1945b) clearly states that the slightest movements of the eye reinstate normal trichromatic vision. Konig (1894) mentions this with regard to central foveal matching fields and Willmer (1950a) states that foveal dichromatic matches could only be made after a brief lapse of time following fixation of the matching field. Bedford and Wyszecki (1957) and McCree (1960a, b) have emphasized the reduction in tritanopic effects when scanning instead of strict fixation is employed. These observations led Brindley (1970, p. 244) to suggest that foveal tritanopia may largely result from a Troxler fading effect rather than the absence of central foveal B cones. According to this view, steady fixation fades out signals from the poorly resolving B cones just as it fades out blurred or indistinctly seen stimuli in general, effectively eliminating the B cone contribution to the color match. To avoid a Troxler fading effect, he advised the use of flashed instead of continuously presented stimuli.

In light of the apparent similarity between color

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† Present address: Center for Visual Science, University of Rochester, Rochester, NY 14627, U.S.A.

‡ In this paper, the short, middle, and long wavelength sensitive receptors will be called the B, G and R cones respectively.

vision in the central fovea and outlying regions (for small steady fields at least), proponents of the receptor loss account of foveal tritanopia looked for support from the reduction in short wavelength sensitivity in the central fovea as compared with surrounding retinal regions. Willmer and Wright (1945) and Thomson and Wright (1947) reported reduced sensitivity to blue light for small centrally fixated fields using heterochromatic brightness matching. Similar results were reported by Sperling and Hsia (1957) measuring foveal spectral sensitivities at absolute threshold. However, as Hurvich (1969) has pointed out, an increasing density of blue-absorbing macular pigment toward the foveal center could account for a short wavelength sensitivity loss even in the presence of foveal B cones.

In general, whatever the alternative explanations invoked, recent opinion has usually rejected the claim that the central fovea is truly tritanopic. Walraven (1972) expresses this prevailing skeptcism and notes one exception: "Wald appears to be alone in his suggestion that the very center of the fovea lacks blue-sensitive cones." Wald (1967) supports his minority opinion with impressive evidence for foveal tritanopia that deals with many of the objections made to other claims. For example, by isolating each of the three color mechanisms with intense chromatic backgrounds, that kept the unwanted mechanisms insensitive, he showed a *selective* foveal loss in sensitivity of the B cones not evident in the R and G cones for the same wavelength targets and therefore not explained by macular pigment. Inasmuch as the macular pigment is a filter screening all the cones by an equal amount,* it should reduce the short wavelength sensitivity of all the cones by a constant factor. Wald reported that a B cone response could not be obtained from small, fixated, short wavelength test flashes presented against an intense long wavelength background, arguing that the central 7–8′ of the fovea lacked B cones. This region is so small, however, that even a point source could not be fixated well enough to fall invariably within it.

Although the influence of the variability of fixation and of scattering of light in such experiments has seldom been acknowledged, these factors could obscure the existence of a tritanopic area, and it seemed worth re-examining the question with that possibility in mind. This paper describes four sets of experiments which examine the nature of foveal tritanopia: (1) photopic recovery experiments which measure the sensitivity of foveal cones to violet tests of various spatial configurations viewed against long wavelength backgrounds; (2) color matching experiments to assess the effects of scattered light from the matching field on color discrimination in the very central fovea; (3) observations on the subjective transposition of blueness from a dim violet corona into a small foveally-fixated green field; and, (4) experiments on the stability of foveal dichromatic matches under light adaptation. These experiments reveal a central foveal region lacking a B cone response even when the contaminating effects of macular pigment are controlled for, and when transient stimuli are used to avoid Troxler fading effects. The tritanopic area, however, appears to be substantially larger than Wald's figure of 7–8′.

* The assumption that macular pigment lies predominantly in front of the outer segment layer, screening all the cone types by a constant factor is supported by histological measurements (Segal, 1950; Polyak, 1957, p. 260; Snodderly *et al.*, 1979). However, a relatively small selective screening effect of macular pigment (see Smith and Pokorny, 1975) cannot be ruled out.

GENERAL METHOD

The observers in all the experiments reported in this paper had normal color vision as tested with the Nagel Anomaloscope and the Ishihara Plates except D.I.A.M., who is deuteranomalous. Correcting lenses were used to correct refractive errors (always minor) in some of the observers. Right eyes were always tested. A dental impression was used to keep the observer in alignment with the 2 mm artificial pupil of the optical system, which was a standard Maxwellian view system with a General Electric 120 V, 200 W Quartz line Lamp.

Radiometric measurements were made with an EG&G photometer No. 450-1. In experiments in which continuous variation in wavelength was desired, a Schott interference wedge was used which was calibrated with the spectral lines of a mercury-cadmium lamp. It had a bandwidth at half height of about 13 nm but transmitted non-negligible light at wavelengths outside the passband, requiring the use of a Wratten 45 blocking filter. In some experiments, a 650 nm primary was produced with a Bausch and Lomb grating monochromator No. 33-86-02. All other spectral lights were produced with narrow band interference filters (bandwidth at half height less than or equal to 15 nm).

In order to facilitate accurate fixation in all experiments, observers were provided with a set of fine crosshairs (15″ of arc wide) and a switch to present test flashes only when they felt they were fixating accurately. In all experiments, the optical distances of field stops were adjusted to compensate for the axial chromatic aberration of the eye. Field stop sizes were changed to compensate for the magnification differences produced by lateral chromatic aberration.

PHOTOPIC RECOVERY EXPERIMENTS: CONTROL FOR PRERECEPTORAL SCREENING

The following experiments control for the absorption of light by macular pigment by measuring the sensitivity of B cones relative to that of the G cones in a given foveal location for a fixed wavelength test flash. The sensitivities of the B and G cones are determined by separating the two cone mechanisms during

recovery from an intense violet bleach that yields two-branched recovery curves (Auerbach and Wald, 1954; Du Croz and Rushton, 1966). The asymptotic values of these branches reveal the relative sensitivities of the G cones (upper branch) and B cones (lower branch) in a given location. If macular pigment alone accounts for the difference in short wavelength sensitivity between the central fovea and outlying regions, then it should affect both cone types alike and the ratio of B cone to G cone sensitivity for the fixed wavelength test flash should be independent of the location of the test flash. However, if, in addition, the B cone response is diminished or absent in the central fovea, then the ratio of B cone to G cone sensitivity should be smaller in the foveal center than outside it. Extensive comparisons of B and G cone sensitivities for a tiny test flash in closely spaced foveal locations are made in the following paper; the present experiments instead vary the diameter of a centrally fixated disc-shaped test flash and an eccentric one, to determine how B and G cone sensitivities vary in these two locations as a function of test field size. This approach has the advantage of averaging out the spatial non-uniformities in sensitivity characteristic of very small test flashes, particularly when they are detected by B cones (see following paper, Williams *et al.* (1981b)). Furthermore, the use of relatively larger test flashes lets any B cones in the central fovea take advantage of their ability to summate over larger areas.

Method

Three experienced observers were tested in these experiments. Each observer first preadapted to a 5 deg 633 nm background (4.93 log phot td for M.M.H., 4.36 log td for D.R.W. and D.I.A.M; 3.32 and 2.74 log scot td respectively) for 3 min. The background, intended to saturate rods and isolate B cones, stayed on continuously throughout the experiment. At the end of 3 min, the observer was exposed to a 436 nm, 3 deg bleaching light (3.34 log phot td) superimposed on the long wavelength background for 60 sec. Following the bleaching exposure, the observer tracked recovery by setting thresholds by method of adjustment for a 20 msec test flash.

Results and discussion

Figure 1 shows a typical recovery curve from a single run for observer M.M.H., using a 436 nm 1 deg test flash centered on the fixation crosshairs. The curve is two-branched; the upper branch asymptotes within roughly 90 sec (as we have demonstrated under conditions where the second branch starts later than it does in this particular curve) while the lower branch is nearly recovered within 6 min. Recovery curves for D.R.W. and D.I.A.M. were similarly two-branched except that both branches showed more rapid recovery. (This difference is due, at least in part, to the greater density of macular pigment in D.R.W. and D.I.A.M. than in M.M.H., measured in other experiments, which rendered the violet bleaching light less effective).

In order to determine the action spectrum of the mechanism responsible for each branch, the asymptotic values for each branch were determined for M.M.H. for the following test wavelengths: 420, 436, 457, 486, 538.5 and 584 nm. On the right side of

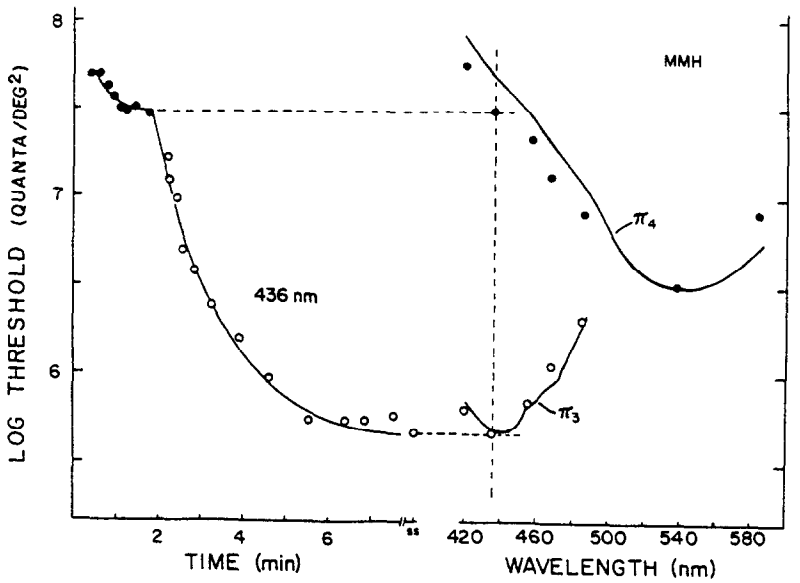

Fig. 1. (Left) A typical two-branched recovery curve for M.M.H. using a 436 nm, 1 deg, 20 msec test flash centrally fixated against a 4.93 log td, 633 nm, 5 deg background following a 3.34 log td, 436 nm, 3 deg, 60 sec bleaching exposure. On the right, the log threshold value in quanta/deg^2 for each of the branches is plotted as a function of the wavelength of the test flash, tracing out two spectral mechanisms. The spectral sensitivity of the upper branch of the recovery is fit with Stiles' π_4 (with arbitrary vertical position); that of the lower branch is fit with π_3.

Fig. 1. the fully recovered threshold radiances for each branch are plotted as a function of the test wavelength. Filled symbols correspond to the upper branch; unfilled symbols correspond to the lower branch. The asymptotic value of the upper branch was determined by fitting a template through the data by eye; the values for the lower branch correspond to test flash threshold against the 633 nm background without any violet bleach. The upper branch has a test sensitivity resembling Stiles' π_4 (with deviations that may result from this observer's almost complete lack of macular pigment, for which a D_{max} of 0.1 has been measured independently), whereas the test sensitivity of the lower branch is well fit by π_3 (Stiles, 1953) (the distinction between π_1 and π_3 is not important here). For the purposes of this paper, we assume that the upper branch of these recovery curves represents the recovery of the G cones and their associated neural processes while the lower branch represents recovery of the B cones, even though a small influence of cone–cone interaction is not ruled out. Reinforcing the conclusion that the lower branch corresponded to B cone recovery was the observation made by each observer that the test flash appeared white and well-defined on the upper branch of the curve, but turned violet and diffuse as soon as the lower branch intervened.

If the B cones are truly absent from the very center of the fovea, small fixated violet test flashes should fail to show the lower, B cone branch in these photopic recovery curves though larger flashes, which encroach upon B cones surrounding this B cone-free area would reveal the lower branch. Figure 2 shows for each observer how B and G cone thresholds determined from the recovery curves vary as a function of test flash diameter for centrally fixated, 436 nm circular test flashes. Filled symbols show the asymptotic values for the G cone branch; unfilled symbols show the values for the B cone branch. These values were determined from several runs at each test diameter except in the case of the larger diameter flashes in which single runs were sufficient. For all three observers, recovery curves for test flashes larger than or equal to about 19′ of arc were always two-branched. For the largest flashes used, 109′, the B cone threshold was roughly 100 times lower than G cone threshold. The difference between B cone and G cone thresholds gradually decreases with smaller test diameters until, for test diameters smaller than about 19′ of arc, the lower B cone branch of the recovery curve abruptly disappears. The threshold value in the steady state is not significantly lower than that found immediately after the rapid recovery of the G cones, indicating that B cone sensitivity relative to G cone sensitivity has been impaired by a factor of about 40 simply by a reduction in test flash area by a factor of 4 (from about 40′–20′ in dia). This result is inconsistent with the view that foveal tritanopia can be accounted for by the increasing density of macular pigment toward the foveal center. Test flashes smaller than about 19′ of arc appeared white with central fixation, supporting the contention that B cones failed to detect the flashes. However, occasional lapses of fixation produced a strong sensation of violet indicating that the test flash had fallen on blue-sensitive areas surrounding the insensitive region.

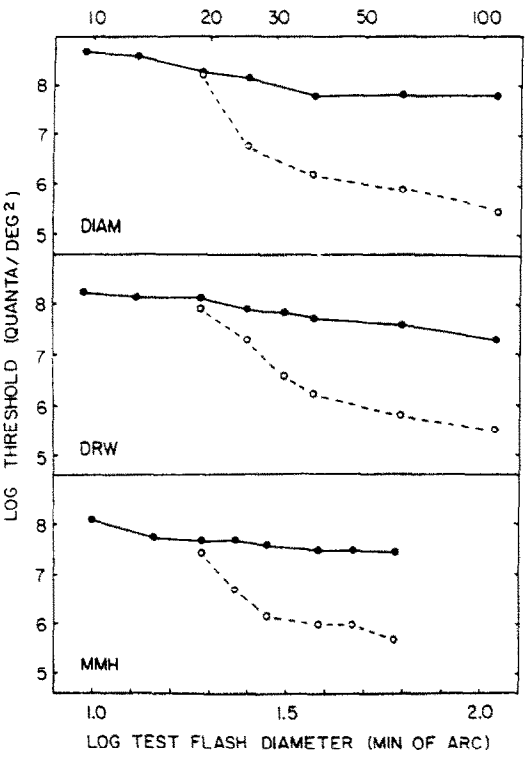

Fig. 2. The log threshold (quanta/deg^2) for the upper (filled symbols) and lower (unfilled symbols) branches of the recovery curves are plotted as a function of log test flash diameter in min of arc for three observers. The 436 nm test flash was centrally fixated in each case.

Comparison with parafoveal stimulation. Though this result clearly demonstrates that B cones fail to detect small, fixated violet flashes against long wavelength backgrounds, it does not rule out the possibility that this is a characteristic of small fields elsewhere on the retina rather than a unique feature of the central fovea. Figure 3a shows how B and G cone thresholds for observer D.I.A.M., determined in the same way as in Fig. 2, vary as a function of test flash diameter when the flash is located at an eccentricity of about 1 deg. Unlike the result with central fixation, recovery curves always show two branches, a result which was confirmed on the other two observers as well. Even for the smallest test flashes used (3.6′), the B cones are nearly a log unit more sensitive than the G cones at the same location and for 19′ flashes B cones are more than 100 times more sensitive.* This supports and

* The possibility that rods rather than B cones were responsible for the lower branch of the recovery curves for eccentric test flashes was excluded by noting that the rapid course of recovery of the lower branch was unaffected by preceding the violet bleach with a white bleach intense enough to keep the rods out of the picture.

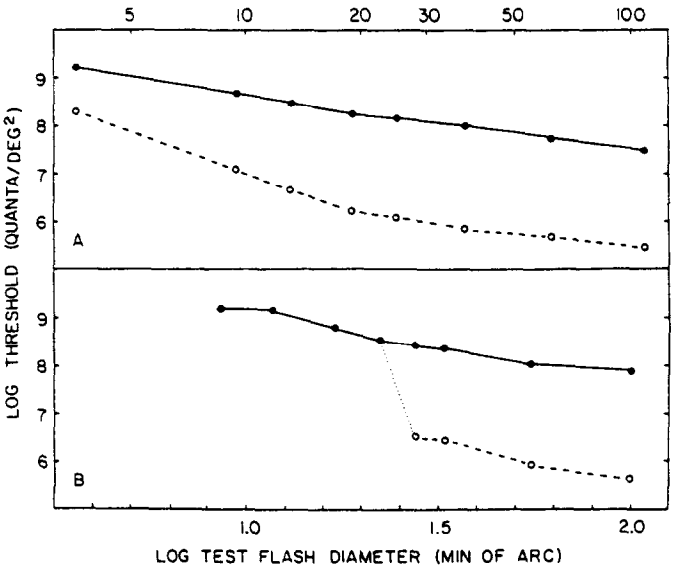

Fig. 3. (a) The log threshold (quanta/deg^2) for the upper (filled symbols) and lower (unfilled symbols) branches of recovery curves as a function of log test flash diameter in min of arc for observer D.I.A.M. when the test flash was located 1 deg from the center of fixation. (b) Log threshold for the branches of recovery curves for D.I.A.M. as a function of the log inner diameter of a 3 deg 436 nm centrally-fixated annular test flash. The observer adjusted the intensity of flash so that the central hole was just detectable.

extends the observations of Wald (1967). For tests at this eccentricity, B cone threshold declines somewhat faster than G cone threshold with increasing test diameter, in agreement with reports that the B cones have a larger summation area than that of the other cone types (Brindley, 1954; Wald, 1967). However, the relative gain in B cone sensitivity over G cone sensitivity with increasing test diameter is far less abrupt than the improvement seen when the diameter of a centrally fixated flash exceeds 19′ of arc. Thus, there exists a profound loss in B cone sensitivity in the central fovea which is not evident in outlying regions of the fovea and which cannot be accounted for by macular pigment.

Completion across the central fovea. If there does exist an anatomical B cone-free area, one might expect the brain to fill in across it, treating it as it does other retinal regions from which it lacks afferent input, such as the optic disc, the rod-free area, or scotomata of the visual cortex (Bender and Teuber, 1946a). Such a completion effect across the tritanopic area was demonstrated with a 3°, 436 nm, annular test flash with a variable inner diameter presented against the 633 nm background. For all three observers, when the inner diameter of the centrally fixated flash was small (say 20′ of arc) and the test flash radiance was such that the flash was detected only by B cones (that is, less than 100 times incremental threshold), the central hole disappeared; the annular flash looked like a uniform disc. However, if fixation was slightly shifted, or if the test radiance was increased above G cone threshold, the hole in the test flash immediately reappeared.

This sriking observation was examined more formally for observer D.I.A.M., using a procedure identical to that described for disc-shaped test flashes except that the observer's task was to adjust the radiance of a centrally-fixated annular flash (o.d. = 3°, variable i.d.) so that the central hole was just detectable (instead of setting threshold for the flash itself). Using this criterion, recovery curves similar to those obtained with disc-shaped test flashes were found. Figure 3b shows how the asymptotic values of the G and B branches of the recovery curves vary as a function of the inner diameter of the annular test flash. Annular flashes with inner diameters equal to or larger than 27.7′ of arc produced two-branched recovery curves; however, flashes with i.d.'s less than or equal to 22.4′ showed only a single G cone branch. Note that an increase in the test flash inner diameter of only about 5′ of arc caused B cone threshold for detection of the central hole to drop 2 log units. Though the B cones were easily capable of detecting the presence of the test flash, they were incapable of detecting the hole in the center of the flash when it was smaller than 22.4′, presumably because it fell within the B cone-free area.

How big is the tritanopic area? Sensitivity gradients and image quality. The only previous estimates of the diameter of the B cone-free area (König's 60′ estimate and Wald's value of 7–8′) differ widely. The estimate of the size of the B cone-free area using annular tests for D.I.A.M. is somewhat larger than the estimate from disc-shaped tests: the first hint of B cone activity is seen for disc-shaped targets with a diameter of about 19′ of arc whereas for annular targets it occurs

between about 22 and 28′ of arc. This difference might be expected if the gradient of B cone sensitivity is very steep at an eccentricity of about 10′ of arc. If the test is a disc then scattered light will fall outside the nominal area of the test onto retinal regions with a high B cone sensitivity. It may be that these surrounding B cones permit detection of the flash even though they are less intensely illuminated than the foveal center. The test diameter at which B cone activity first appears would therefore be underestimated. If the test is an annulus, however, the central hole must be large enough to include some number of B cones which fail to detect the test flash, signalling the presence of the hole. The presence of scattered light within the nominally "dark" hole would make the critical hole diameter an overestimate of the size of the B cone-free area.

The difference between annular and disc-shaped flashes suggests that scattered light from the test flash cannot be neglected. Another firmer indication that optical spread is a major factor in determining the pattern of results can be found in the way sensitivity improves with increasing disc diameter. The improvement as the edge of the disc moves to greater eccentricities may be very abrupt, reaching about 0.35 log units per min of arc increase in disc radius, observed for disc diameters in the 20′–25′ range; the gradient is steeper than this for D.I.A.M., shallower for D.R.W. (It is worth noting that this means threshold varies inversely as the 9th power of diameter in this range). The maximum gradient that is physically possible is the same as the steepest gradient of log illuminance in the retinal image, which is about 0.45 log units per min of arc, at a point outside the edge of the disc (Gubisch, 1967, Fig. 8), and this gradient is only attained if threshold is set by a fixed small retinal region located under the steepest image gradient; spatial summation can only reduce the sensitivity gradient. Since the observed gradients approach the limit, detection must have depended on receptors at or near the eccentricity that received the steepest image gradient (just outside the nominal edge of the disc) for disc diameters where the sensitivity gradient was steepest. This places the critical receptors at 11–16′ from the center of fixation. In agreement with this, the image quality estimates of Gubisch suggest that at the B cone threshold in our experiments, all discs less than 30′ in dia delivered a nearly constant illumination at an eccentricity of about 13′; at an eccentricity of 10′, the illumination from the 18′ disc exceeded that from the 30′ disc by a factor of 4–10, depending on the observer. The critical area for detection of these discs is therefore a ring of about 26′ dia; if the diameter were as small as 20′ or less the loss of sensitivity with decreasing disc diameter would have been much less pronounced than was observed. The region of spatial summation at threshold must be less than 4′ wide in the direction orthogonal to the disc contour. If this much summation is allowed for, the critical 26′ ring of receptive field centers could be picking up B cone signals as much as 2′ further in, suggesting a lower limit of 22′ for the diameter of the tritanopic area.

These experiments therefore give no evidence for detection of light by B cones within the central 25′ of the retina. All that can be said about the sensitivity of any B cones that may be present in that area is that they seem unable to significantly assist the 26′ ring of B cones even when given the advantage of much more intense stimulation. If the retinal gradient of sensitivity inside the boundary of the 25′ area is enough to offset the gradient of stimulus intensity at the edge of a disc of light, it must equal or exceed 0.45 log units per min of arc.

FOVEAL SUCCESSIVE COLOR MATCHING EXPERIMENTS

Though the photopic recovery experiments show that B cones isolated with intense long wavelength backgrounds cannot detect small, fixated stimuli on their own, they may be able to lend a hand in color discrimination, the job they seem to do best. The use of a color matching procedure to assess the color discrimination of hypothetical B cones in the central fovea has the added advantage that it does not employ an intense adapting field, like those used in the photopic recovery experiments, which could conceivably prevent B cones from expressing themselves.

As pointed out in the introduction, a difficulty with the use of steady bipartite fields to assess foveal tritanopia is that these fields are subject to Troxler fading effects which could obliterate the distinction between the small half fields, even in the presence of B cones. The use of transient stimuli instead of steady ones overcomes the Troxler fading objection. Ingling *et al.* (1970) found a decrease in the ability to use color names selectively in the blue–green region of the spectrum for 3′ fixated flashes, 0.5 or 1.5 log units above threshold. Their results are consistent with a strong tendency toward foveal tritanopia not explained by Troxler fading. Still their data suggest that some residual B cone discrimination persists, leading them to conclude that though B cones may be scarce, they are not entirely absent from the central fovea. However, at least two factors in their experiment may have contributed to produce this residual B cone discrimination in the central fovea, neither of which require that B cones actually reside there. First, eye movements inevitably occur, even when observers are trying to fixate accurately (Ditchburn, 1973, p. 95), which could have resulted in occasional trials in which the test flash fell outside a central region devoid of cones. Second, the problem of eye movements is compounded by the fact that the *effective* size of the test flash will be substantially larger than the nominal size of the test flash due to optical spreading (Gubisch, 1967). This would increase the percentage of flashes on which B cone discrimination could be mediated by receptors outside the central fovea. In this context, it is interesting to note that Krauskopf and Srebro

(1965) and Weitzman and Kinney (1959), also using a color naming technique, failed to find a residual B cone discrimination for small fixated flashes. Ruddock and Burton (1972) also failed to find residual B cone discrimination at the center of the fovea, finding that tritanopic matches could be made for a fixated 16′ bipartite field, flashed for 40 msec to avoid Troxler fading. However, this observation is also consistent with the view that small field tritanopia is the result of poor spatial resolution.

In the following experiments, a successive color matching procedure was employed in which a disc-shaped matching light was replaced by a second coextensive light for a brief period of time. By making matches between successively presented stimuli in this manner, the problem of Troxler fading can be avoided. Furthermore, this procedure has the advantage that, instead of splitting a given sized matching field in half as in the case of the typical bipartite field, the retinal area under each matching light is effectively doubled. This provides hypothetical B cones at the center of the fovea with double the area over which to summate their responses, in addition to providing a larger stimulus, easier for the coarse B cone discrimination mechanism to resolve. The matching field was surrounded with a violet annulus to desensitize the retinal regions surrounding the location of the matching field to any scattered light, reducing the probability that eccentric B cones outside the central fovea might mediate the discrimination.

Method

Figure 4 shows the stimulus configuration used. The matching lights were two coextensive monochromatic fields subtending either 14.5′ or 9.3′ of arc. One of the lights was a 140 td 436 nm standard, produced with an interference filter whose bandwidth at half height was 10 nm. When the observer felt he was fixating accurately, he depressed a button which, without interruption, replaced the standard light with a second light whose wavelength and intensity were adjusted by the observer. The second matching light was presented for 200 msec, allowing any central B cones the full benefit of temporal integration, after which it was replaced by the standard. The observer's task was to adjust the wavelength and intensity of the substituted field in an attempt to find a perfect match between the two fields. There exist pairs of wavelengths in the short wavelength end of the spectrum which, with a suitable-adjustment in intensity only, are equivalent for the R and G cones, differing only for the B cones. The particular wavelength chosen as the standard in this experiment, 436 nm, has the advantage that its tritanopic equivalent, about 482 nm as measured here, is about equally absorbed by macular pigment. (Wyszecki and Stiles, 1967, p. 217). This minimized the spatial inhomogeneities caused by Maxwell's spot when the two lights were exchanged. Though roughly equivalent for macular pigment, this particular tritanopic pair differ in their effects on the B cones by about a factor of 22, making their exchange a potent stimulus for any B cones in the central fovea. Observers attempted to make matches between the two lights both when the matching field was presented in an otherwise dark field and when it was surrounded by a 1.5 deg annulus of the same wavelength and retinal illuminance as the standard matching light.

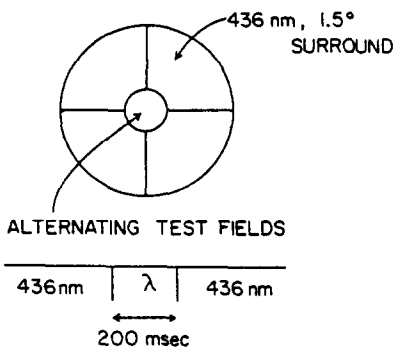

Fig. 4. Stimulus configuration used in successive matching experiments. A 436 nm 140 td standard could be replaced at the observer's command by a second light of variable wavelength and intensity for 200 msec. In some conditions, the matching field (which was either 14.5 or 9.3′ of arc) was surrounded by a contiguous, 436 nm annulus with an outer diameter of 1.5 deg, with crosshairs superimposed.

Eight observers were tested, all with normal color vision. Three of the observers (D.S., C.G. and M.J.M.) were ignorant of the intent of the experiment; the latter two were inexperienced in psychophysical procedures.

Results

Table 1 shows the matching field diameter, the wavelength of the test light matching the standard 436 nm light, and the SEM matching wavelength based on 5 matches for each of the eight observers when the matching field was surrounded by the 436 nm annulus. Seven of the 8 observers were able to match the 436 nm standard by making suitable adjustments in the wavelength and intensity of the substituted test light. Four of these observers found an acceptable match when the field size was 14.5′; two were unable to make an acceptable match at this field size (other than a physical match) but were able to make matches with the next smaller field size tried, 9.3′. With the two lights matched with central fixation, these 6 observers all reported a striking difference in their color appearance of the two lights, and were unable to reset a match, when the matching field fell anywhere in the eccentric fovea. A seventh observer, J.W., could not make a match when the field was centrally fixated but, by shifting the crosshairs with respect to the matching field, a nearby retinal region was found centered on 9′ inferior and 3′ nasal to the center of fixation which was clearly tritanopic

Table 1. The matching field diameter, and mean wavelength of the substituted test light which matched the 436 nm standard in the presence of a 140 td 436 nm surround, and the SEM matching wavelength based on variability between 5 settings

Observer	Matching field diameter (min)	Mean wavelength matching 436 nm standard (nm)	Standard error of mean (nm)
J.W.	14.5	484	0.3
D.S.	14.5	479	2.0
C.G.	14.5	482	0.5
D.R.W.	14.5	486	0.7
M.M.H.	14.5	481	0.2
A.L.N.	9.3	477	2.2
R.M.B.	9.3	484	—
M.J.M.	9.3	no match	—

with a 14.5′ field. There was a suggestion that this observer's Maxwell's spot is also displaced in the same direction from the center of fixation, suggesting that he fixates eccentrically and that approximate radial symmetry of the fovea is preserved.

For these 7 observers, the wavelength of the substituted light which matched the 436 nm standard was well-defined; the standard error of the mean based on variability between 5 settings averaged about 1 nm, showing that the ability to match the two monochromatic lights was not the result of poor color discrimination in general. The average wavelength which matched the 436 nm standard for these observers was 482 nm, somewhat shorter than the 489 nm expected from estimates of tritanopic pairs in the literature (Walraven, 1974). The increased density of photopigment (up to perhaps 0.7) at the very center of the fovea, where our measurements were made, would be expected to shift the matching wavelength in this direction due to self-screening effects, and is enough to account for the difference (Pokorny and Smith, 1975).

The eighth observer (M.J.M.) was unable to make a match when the matching field was centrally fixated or in nearby locations, even for the smaller, 9.3′ field. The observer was inexperienced and it is possible that she could not accurately fixate the matching field from exchange to exchange. However, even this observer reported that the color difference between the matching lights was minimized with central fixation (at a wavelength of 484 nm), increasing when the matching field was displaced from the fixation crosshairs. With the wavelength and intensity of the substituted field adjusted to minimize the color difference, this observer still detected 84% of the exchanges with central fixation (see Fig. 5). This suggests that if M.J.M. has a B cone-free area at all it is smaller than that found in the other observers.

All of the seven observers who could make tritanopic matches in the presence of the surround equiluminous with the standard matching light reported that it was impossible to make a match when the surround was not present, even for the smaller, 9.3′ matching field. The substituted light always appeared greener than the standard, though the color difference was still more pronounced with eccentric fixation. The hypothesis proposed here to account for this residual B cone response is that it is caused by scattered light falling outside the tritanopic area onto surrounding B cones. Optical spreading would deliver about 1–2% of the peak illuminance to a ring of cones 25′ in dia, i.e. 5′ away from the nominal border of the 14.5′, 140 td test field (Gubisch, 1967). This would be well above threshold there. For the 9.3′ test field, accurately fixated, potentially usable stimulation would extend beyond 20′, but whether it would extend to 25′ is not clear. This scattered light hypothesis receives support from observations made by two observers (M.M.H. and D.R.W.) that reducing the radiances of the exchanged matching lights, which reduces the amount of scattered light falling on these eccentric B cones markedly impairs discrimination of the tritanopic pair. The proposed effect of the violet surround in eliminating this residual B cone response is that it light adapts B cones surrounding the tritanopic area, rendering them insensitive to scattered light from the matching field. Alternatively, however, the violet annulus might handicap B cones at the very center of the fovea either by light adaptation due to eye movements and scattered light or by lateral neural interactions, preventing these hypothetical central B cones from signalling the difference between the tritanopic pair. The following experiments investigate the effects of surrounds on small centrally fixated fields in order to determine whether scattered light falling outside the nominal area of the test field can actually mediate discrimination of tritanopic lights at the center of the fovea.

Effect of surround retinal illuminance on foveal tritanopia. It is unlikely that B cones at the foveal center were being light-adapted by the annulus in view of the following experiment which shows that the surround retinal illuminance required to render the central fovea tritanopic is a very small fraction of the retinal illuminances of the matching fields themselves. Figure 5 shows how the probability of detecting a color difference between the tritanopic pair of lights depends on the retinal illuminance of the 436 nm surround for three observers. Five tritanopic matches were set by

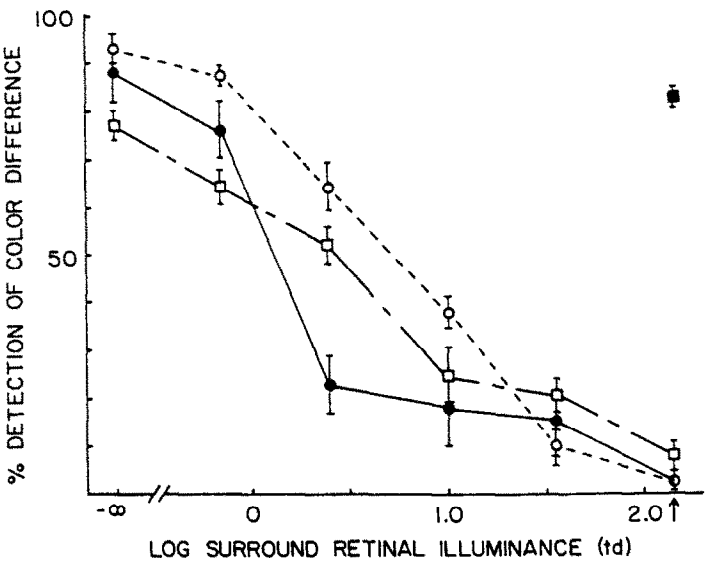

Fig. 5. Probability of detecting a color difference (%) between an exchanged pair of centrally fixated tritanopic lights 9.3′ in dia. for observers M.M.H. (filled circles), D.S. (unfilled squares), and D.R.W. (unfilled circles), as a function of the log retinal illuminance of a 1.5 deg, 436 nm surround. Error bars represent ±1 SEM based on variability between 4 blocks of 25 exchanges at each surround retinal illuminance. Arrow on abscissa marks the condition in which the surround was equiluminous with the 436 nm standard matching light. Filled square shows the percentage of 100 exchanges in which a color difference was detected with an equiluminous surround by M.J.M. The intensity and wavelength of the substituted light in the matching field was adjusted to *minimize* the color difference in this case since no perfect match could be made.

each observer with the 9.3′ matching field and in the presence of the 140 td 1.5 deg surround, equiluminous with the standard matching light. The mean of these matches was then used for six levels of the surround retinal illuminance ranging from no surround to equiluminous. The observer, fixating the matching field, presented exchanges of the tritanopic pair in blocks of 25. The retinal illuminance level of the surround was randomly varied between blocks until 100 exchanges had been presented at each surround retinal illuminance. After each exchange, the observer indicated whether or not he had detected a color difference during the exchange. Small movements of the head on the bite bar occasionally produced relative displacements of the matching fields, which could have interfered with the judgment of a color difference between them. Exchanges for which this was a difficulty were not counted. Of the three observers, D.S. was naive as to the purpose of the experiment.

For all three observers, the ability to detect a color difference between the tritanopic pair is very good, though not perfect, without a surround. With a surround equiluminous with the 436 nm standard (indicated by the arrow on the abscissa in Fig. 5) the probability of discriminating between the tritanopic pair of lights falls nearly to zero. Those few occasions in which a color difference was detected could easily have resulted from lapses of fixation.* Surround retinal illuminances between about 1% (for M.M.H., filled circles) and 4% (for D.R.W., unfilled circles) of the retinal illuminance of the matching field are capable of reducing the probability of detection to 50%.† These weak surrounds are unlikely to be exerting their effects on B cones at the very center of the fovea, but may be intense enough to prevent discrimination of the tritanopic pair by impairing the detection of scattered light from the matching field by B cones outside the central fovea.

* The three observers detected a color difference approximately 5% of the time with this 14.5′ field. Ditchburn, (1975, p. 95) summarizing the literature, estimates the root mean squared deviation of the line of sight, r_0, over short periods of time to be about 3.7′ of arc. Assuming that eye movements during fixation are distributed according to a bivariate normal distribution, the probability, P, that the test flash will fall at or beyond some distance, r, from its edge is given by

$$P = e^{-r^2/r_0^2}.$$

We assume for simplicity that the B-cone free area is a circular region, centered on the line of sight and that the surround around the matching field completely limits the effective area of the field to its nominal area. Given a value of P of 0.05, and a value of r_0 of 3.7, the distance from the edge of the test flash to the edge of the B cone free area, D, equals 6.4′ of arc. Thus the B cone-free area could be as big as 27′ of arc, a result perfectly consistent with the estimates from the photopic recovery experiments.

† Burton and Ruddock (1972, see below) found that, under some conditions at least, changes in surround retinal illuminance can shift foveal tritanopic matches. Observations made under the conditions used here did not show any shifts beyond experimental error. In any case, since the tritanopic pair was determined with the most intense surround used, any shift would tend to increase color discrimination at lower surround illuminances, making dim surrounds appear less effective in reducing the effects of scattered light than they actually are.

LOCATION OF CONES INFLUENCED BY SURROUND

Further evidence for this scattered light hypothesis comes from an experiment in which the degree of foveal tritanopia produced by a thin violet ring equiluminous with and immediately surrounding the matching field was compared with that produced by a pedestal of violet light which was coextensive with the matching field. The total area and flux of the ring equalled that of the pedestal, giving them the same light adapting potential, so that they differed only in the foveal regions which they most strongly light adapted. If the effect of violet annuli in producing foveal tritanopia is due to light adapting effects on B cones *within* the central fovea and beneath the matching field, then the violet ring should be less effective than the violet pedestal which falls directly on these hypothetical central B cones. However, if the effectiveness of these annuli is due to light adaptation of B cones *outside* the central B cone-free fovea beyond the nominal area of the matching field, then the violet ring should prove somewhat more effective than the pedestal.

Another condition was employed to test the possibility that the effect of the annuli is due to a kind of perceptual interference, depending only on their spatial configuration surrounding the matching field, and not on their light adapting effects on B cones. In this condition, a thin blue–green ring which was the tritanopic equivalent of the violet ring surrounded the matching field. This blue–green ring had the same spatial configuration as the violet ring; in fact, they were identical as far as the R and G cones were concerned. However, the blue–green ring was at least 22 times less effective in light adapting B cones.

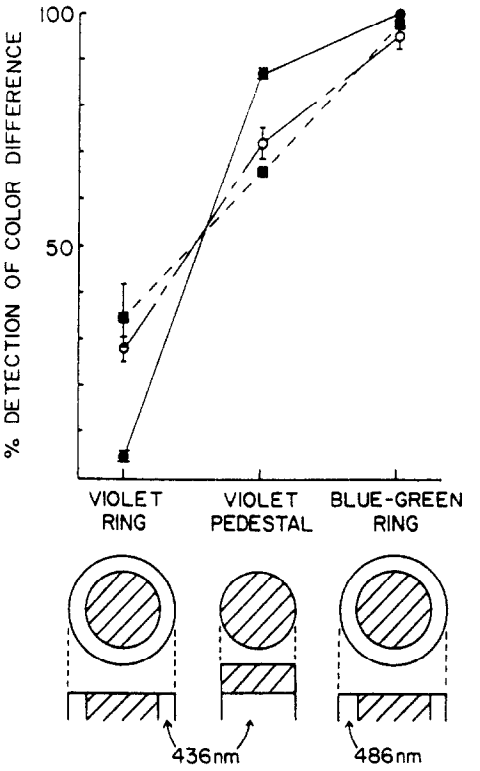

Fig. 6. Probability of detecting a color difference between a tritanopic pair of lights exchanged in a centrally fixated 9.3′ field for observers A.L.N. (filled circles), D.R.W. (unfilled circles), and R.M.B. (filled squares) under three conditions; (from left to right): when the matching field was surrounded with an equiluminous 436 nm ring (i.d. 9.3′; o.d. 13′); when the matching field was superimposed on a coextensive 436 nm pedestal with an area and flux equal to that of the ring in the first condition; and when the matching field was surrounded by a 486 nm ring which was the same size as the 436 nm ring and was roughly its tritanopic equivalent. Error bars represent ±1 SEM based on variability between 2 blocks of 50 exchanges for each condition.

Method

The matching field was 9.3′ in dia and, as in the previous matching experiments, consisted of a 140 td, 436 nm standard which could be replaced by a second tritanopically equivalent light for 200 msec. The rings used in two of the three conditions (see bottom of Fig. 6) were contiguous with the matching field, having an o.d. of 13′. The equiluminous ring was composed of either 436 or 486 nm light. The 436 nm pedestal beneath the matching field in the second condition was the same size as the matching field, 9.3′. The observer presented 2 blocks of 50 exchanges each for each of the three conditions in random order, indicating whether he could detect a color difference between the lights at each exchange. Three observers were run (A.L.N., R.M.B. and D.R.W.); the first two were naive as to the purpose of the experiment.

Results

Figure 6 shows the probability of detecting the tritanopic exchange for each of the three conditions for each observer. For all observers, the violet ring less than 2′ of arc thick was far more effective than the violet pedestal in reducing the percentage of exchanges in which a color difference was detectable, providing strong support for the scattered light hypothesis. Furthermore, the violet ring was also more effective than the blue–green ring, suggesting that the violet ring's effectiveness is due to light adapting effects on eccentric B cones rather than some noncolor-specific spatial interaction.

These results were supplemented with observations comparing the effectiveness of a 1.5 deg violet annulus with an annulus doubled in retinal illuminance but halved in area by removing two of its quadrants (forming a windmill surround with two light vanes). The two types of surround should have a comparable overall light adapting potential at the center of the fovea since they have the same total flux, but if the scattered light hypothesis is correct, the windmill surround should prove less effective in eliminating B

cone color discrimination since its two dark vanes should be ineffective in light adapting scattered light-sensitive B cones beneath the surround. Consistent with the scattered light hypothesis, the windmill vanes proved less effective than the full annulus in revealing foveal tritanopia for three observers.

SUBJECTIVE TRANSPOSITION OF COLOR FROM A SCATTERED LIGHT CORONA

These experiments show that B cones just outside the tritanopic area use scattered light to mediate color discrimination between lights which nominally fall in a region devoid of a B cone response. The importance of this scattered light is particularly intriguing since it is not subjectively obvious. The 436 nm standard appears uniformly violet and its exchanged tritanopic equivalent appears distinctly blue–green (provided the fields are fairly intense and are not surrounded by the violet annulus) even though the scattered light which we propose is responsible for these color appearances is not clearly visible. This suggests that some mechanism exists which gathers signals from B cones surrounding the tritanopic area and then attributes them not to the spatial regions from which they originate but to the test spot itself, as if the signals were transposed from the retinal regions underlying the scattered light halo to the central region underlying the nominal area of the test field.

This remarkable prediction of the scattered light hypothesis can be tested by adding a dim corona of violet light around a small green test field in an attempt to mimic the effects of light actually scattered by a shorter wavelength test field. If the scattered light hypothesis is correct, the color appearance of the test field should be strongly affected by the presence of this artificial scattered light, so that the test field, which ordinarily appears green in the dark, might appear uniformly blue when surrounded by the dim violet corona.

Such an effect is fairly easy to demonstrate with colored papers or slide projectors, but is subject to the objection that chromatic aberration of the eye could optically mix the violet corona with the green test field. The problem of optical mixing can be minimized in Maxwellian view where the optical distances of the corona and test field can be adjusted to compensate for chromatic aberration. The effect has been demonstrated on 5 observers in Maxwellian view as follows. A 519 nm test field 19′ of arc in dia was surrounded by a thin dim 436 nm corona contiguous with the edge of the test field. The inner edge of the corona was sharply focused while the outer edge was defocused by roughly 3 D (2 mm artificial pupil) so as to mimic the distribution to be expected from real scattered light. The test field viewed in the dark appeared green but the addition of the dim violet corona immediately and dramatically changed the appearance of the field to blue. The radiance of the corona could be adjusted so that it was not visible even though its strong effect of inducing a uniform sensation of blueness into the center of the field remained. The effect does not require that the corona and test be tritanopically equivalent or equiluminous, distinguishing it from small field tritanopia. Furthermore, the effect is quite robust when both the corona and test are presented as a brief flash, showing that the spreading or assimilation of blueness into the test field is not caused by Troxler fading.*

The transposition of blueness from the corona to the test field provides a firm basis for our suggestion that scattered light can mediate the discrimination of tritanopically equivalent lights, which nominally fall within a retinal area lacking a B cone response. But the corona effect does not show that stimulation of surrounding B cones by scattered light is the *only* source of blueness for central foveal stimuli. It is possible that central foveal R and G cones alone could generate blueness at those short wavelengths where G cone excitation exceeds R cone excitation. Observations of Alpern and Krantz (in preparation) on a subject with unilaterally acquired tritanopia demonstrate that this can happen.

The corona effect may help to account for the report by Hurvich and Jameson (1957) that the crossover point of the red–green opponent function at unique blue does not shift toward shorter wavelengths when the field size is reduced from 2 deg to 10′ of arc, as might be expected if the B cone input to the red–green mechanism were absent at the foveal center. The red–green opponent mechanism at the very center of the fovea may receive a B cone input, not from B cones lying in the foveal center, but from B cones in the surrounding fovea outside a B cone-free area.

STABILITY OF FOVEAL COLOR MATCHES TO LIGHT ADAPTATION

Though the evidence presented so far suggests that, for most observers at least, a central region in the fovea lacks a B cone response, there remains one fly in the ointment. Burton and Ruddock (1972; see also Ruddock & Burton, 1972) proposed that the central fovea may not entirely lack B cones and that foveal

* Transposition of blueness revealed by the corona effect is similar to the Von Bezold spreading effect which has also been called assimilation (e.g. Helson and Rohles, 1959). However, it is distinguished from these effects by the fact that the blueness is *removed* from the retinal region beneath the corona and transposed to the test field; that is, the corona itself is not visible. In assimilation effects, colors are neurally mixed from two adjacent regions both of which are spatially clearly defined. In this sense, the corona effect more nearly resembles an effect reported by Hartridge (1950, p. 101) in which a grating composed of blue and yellow bars appears black and white when the spatial frequency is sufficiently high, the signals from the blue bars being transposed to the yellow bars, to produce white bars alternated with black ones.

tritanopia may be the result of the convergence of all three spectral classes of cones into only two independent color channels. They argue that if foveal tritanopia were imposed at some stage central to the receptors, small field color matches in the central fovea might not be stable with light adaptation. However, if foveal tritanopia is simply the result of the absence of B cones, and if this receptor loss leaves the central fovea with only two spectral classes of receptor, small field dichromatic color matches will be matches for these two classes and should remain unperturbed at light levels below those causing appreciable pigment bleaching. Burton and Ruddock report that dichromatic matches with a centrally fixated 16′ bipartite field are not stable with light adaptation. Specifically, the ratio of the amounts of a 460 nm and a 650 nm primary mixed to match a 510 nm standard increased with increasing retinal illuminance of a 460 nm annulus surrounding the test fields. They argue that this is inconsistent with the absence of B cones from the central fovea.

One ambiguity in the interpretation of these results is that, though the disruption of small field dichromatic matches with light adaptation requires that the matches are determined by cones with more than two spectral sensitivities, it does not imply that B cones contribute to the match. Even in the absence of B cones, retinal inhomogeneities in the central fovea could create variations in the spectral sensitivities of the remaining R and G cones, effectively producing more than two classes of receptor. Macular pigment density can change rapidly across the central fovea (see following paper) creating differences in the spectral sensitivities of differently located cones which house the same photopigment. In addition, cone morphology changes toward the foveal center (Polyak, 1957); the increase in outer segment length and the associated increase in axial pigment density produces variations in R and G cone action spectra (Pokorny and Smith, 1976). Changing wave guide characteristics of cones across the fovea might also produce such variations. Thus the tritanopic match must vary with retinal eccentricity, and an adapting light can alter the match by bringing (for instance) the most central cones into greater prominence. The spatial inhomogeneity hypothesis gains credibility in light of Burton and Ruddock's observation that an annular surround created larger shifts in the match than a uniform background.

If the perturbations in color matches reported by Burton and Ruddock are due to B cone involvement, then the effect should disappear under conditions in which the B cones are prevented from detecting the matching field. This was tested by determining whether the effect persists in a temporary state of artificial tritanopia produced by exposure to an intense violet light (Brindley, 1953).

Method

The experimental conditions were similar to those employed by Burton and Ruddock except that the light levels used were fixed at about 1 log unit below the highest intensity they used. Figure 7 shows the stimulus configuration. The left half of the 14.5′ bipartite field consisted of a 60 td 519 nm standard; the right side consisted of a mixture of a 460 nm and a 650 nm primary. Three observers (D.R.W., D.S. and M.J.M., the last two being naive) adjusted the radiances of the two primaries to match the 519 nm standard, either in the dark or in the presence of a 457 nm annulus (o.d. 2 deg) surrounding and contiguous with the matching field. Matches made in the presence of the surround were alternated with those made without the surround until at least five matches had been made in each condition.

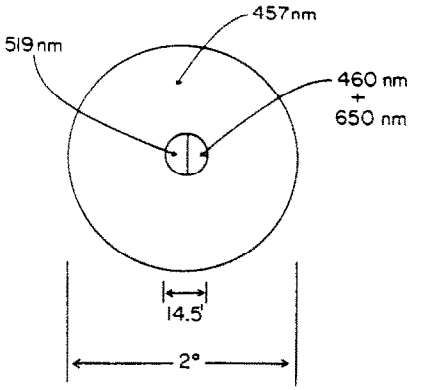

Fig. 7. Stimulus configuration used to investigate stability of small field foveal matches as a function of the retinal illuminance of a 2 deg, 457 nm surround. The left half of a 14.5′ bipartite matching field contained a 60 td 519 nm standard; the right half contained a mixture of a 460 nm and a 650 nm primary. Observers adjusted the radiances of the two primaries to match the 519 standard in the presence and the absence of the surround.

For observer M.J.M., this procedure was repeated under the condition of artificial tritanopia. Prior to each match, the observer adapted to a 15 deg, 3.36 log td, 436 nm field for 30 sec. Though this light strongly light adapted the B cones, it represented only about a 2% bleach for the R and G cones, small enough to prevent self-screening from altering the match for these cones. The tritanopia-inducing effect of the violet adapting light was confirmed as follows. The matching field was enlarged to 20′, which for this observer was sufficient to permit full trichromatic discrimination. Following exposure to the violet adapting light, the observer could not detect a difference between the tritanopically equivalent violet and green half fields for about 75 sec, even with the help of scanning eye movements. All matches with the 14.5′ field were made within 60 sec of the offset of the violet adapting light.

Results

The effect of the surround on foveal color matches under the conditions used here was not consistent across the 3 observers. Two of the observers, D.S. and

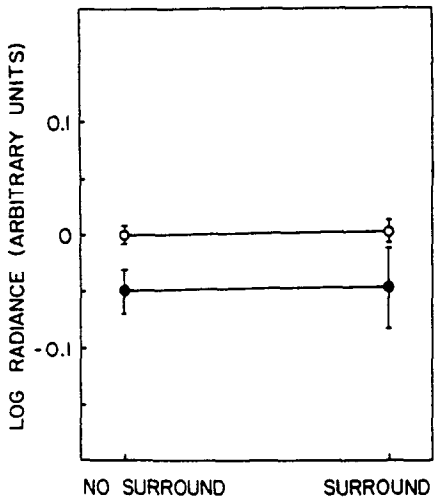

Fig. 8. Log radiance (arbitrary units) of the 460 nm primary (unfilled circles) and the 650 nm primary (filled circles) required to match the 519 nm standard in an otherwise dark field (no surround) and in the presence of a 300 td 457 nm surround. Observer D.R.W. Error bars are plus and minus one standard error of the mean based on variability between 5 matches made in a single session.

D.R.W., failed to show a shift in the match within the limits of experimental error, whereas the third observer, M.J.M., showed a clear shift in the same direction as that reported by Burton and Ruddock. (Burton and Ruddock also found substantial observer variation).

Figure 8 shows the results from one session for one of the observers (D.R.W.) who failed to show an effect of the surround on the match. Unfilled circles show the amount of the 460 nm primary and filled circles show the amount of the 650 nm primary required to match the 519 nm standard with and without a 300 td, 457 nm surround. The amounts of the primaries in the match are the same with and without the surround. Interestingly enough, this same invariance of the match was also found when the matching field was placed at an eccentricity of 30′ from the center of fixation, an area which is rich in B cone sensitivity for this observer, using Troxler fading to enable tritanopic matching. This shows that, under these conditions at least, the presence of B cones does not by itself produce the shift reported by Burton and Ruddock.

Figure 9a shows the amount of the two primaries required to match the standard (mean of four sessions) with and without a 90 td annulus for M.J.M., the observer who showed a clear shift in the match. The amount of the 460 nm primary (unfilled circles) increases while the amount of the 650 primary (filled circles) decreases when the matching field is surrounded by the annulus, in agreement with Burton and Ruddock's report that the ratio of the 460 to the 650 nm primary increased with more intense surround adaptation. This observer reported that matches made with the surround were unacceptable without the surround and vice versa.

Figure 9b shows the effects of the surround on the match for M.J.M. when the eye is in a state of artificial tritanopia, preventing the B cones from participating. The data show that the effect of the surround in perturbing the match persists even when the B cones are knocked out of the picture. Whatever is responsible for the instability of these matches, it is not the B cones, so the effect is not evidence that B

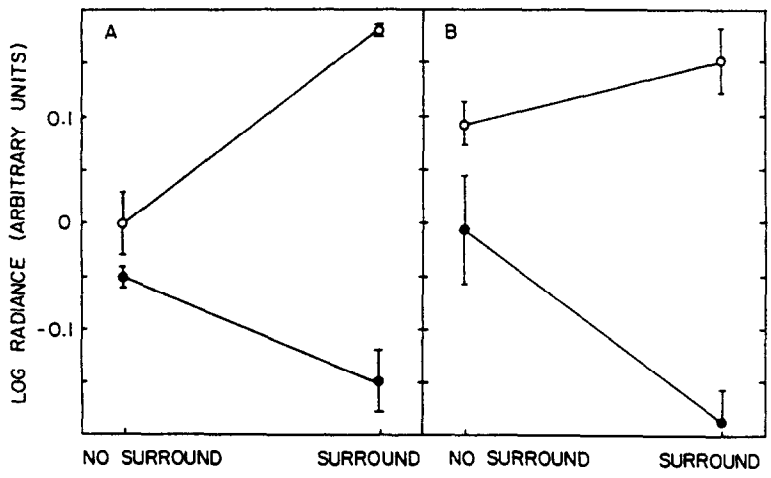

Fig. 9. (a) Log radiance (arbitrary units) of the 460 nm primary (unfilled circles) and the 650 nm primary (filled circles) require to match the 519 nm standard in an otherwise dark field (no surround) and in the presence of a 90 td, 457 nm surround. Observer M.J.M. Error bars are ±1 SEM based on variability between 3 sessions. (b) Amounts of the two primaries required to match the standard with and without the 90 td surround following a 30 sec exposure to a 15 deg, 3.36 log td, 436 nm light intended to induce artificial tritanopia for M.J.M. The observer was exposed to the adapting light prior to each match; all matches were made within 60 sec following the offset of the adapting light.

cones are present in the central fovea. Foveal inhomogeneity remains a possible explanation for it.*

Discussion and conclusions

The experiments reported here support the conclusions that a region in the central fovea lacks functioning B cones. With an intense long wavelength adapting field intended to isolate B cones, a central region 20–25′ of arc in diameter failed to show any B cone response to violet increments for three observers even though the B cones were about 100 times more sensitive than the G cones for stimuli of the same size outside the central fovea. Macular pigment is not responsible for this sensitivity loss since it lies in front of G and B cones alike, yet the foveal sensitivity loss was confined to the B cones. The use of test flashes too brief to allow Troxler fading effects confirms that they cannot account for this selective sensitivity loss unique to the foveal center. Outlying regions of the fovea which are subject to small field tritanopia with steady matching fields show a healthy B cone response to transient stimuli, suggesting that Troxler fading may account for the tritanopic effects observed there.

The estimate of the size of the B cone-free area derived from the photopic recovery experiments (20–25′ of arc) is consistent with the matching experiments and agrees well with that obtained by mapping the central fovea with a tiny violet test flash against a long wavelength background for the same observers (see following paper). This estimate is larger than the 7–8′ dia B cone-free area reported by Wald (1967). But there is little or no conflict of *evidence* between the two studies. Admirable though Wald's paper is, it conspicuously fails to substantiate the claim that B cone function is absent "only within a central area subtending 7–8 min arc." The claim is based on the observation that "for a few subjects, a trace of blue receptor function remains" when the test field is nominally 7.5′ in dia. The data illustrating this (Fig. 3, subject R.H.) show a threshold 100 times greater than for the next larger field size, which is 62′. The intense small stimulus would therefore deliver potentially useful stimulation for B cones over a region receiving as little as 1% of the peak illumination, a region of dia perhaps 17′. When fixational variability is considered in addition it becomes hard to maintain that these data are inconsistent with a tritanopic area subtending 20′. Nowhere in the paper is there a comparison of B cone thresholds for two different field sizes less than 30′, which is what is needed to allow an assessment of the role of optical spread; but the most relevant data do show that it must have been of critical importance.† Such small differences as do exist between Wald's data and ours can plausibly be attributed to procedural differences. Our use of a set of fine crosshairs and self-initiated test flashes with experienced psychophysical observers may have provided superior accuracy of fixation. Furthermore, our use of a smaller artificial pupil size than Wald (2 mm instead of 3.5 mm) and correction for chromatic aberration of the eye may have helped confine light from the test flashes within the area lacking a B cone response. The data from the successive color matching experiments, in which two of the eight observers could not make a tritanopic match with a 14.5′ field, and another would not accept matches with any field size tried, suggests that individual differences of some kind (including optical quality and fixation variability) are important. The low density of B cones surrounding the tritanopic area (see following paper, Williams *et al.* (1981b)) makes estimates of the diameter of the tritanopic area less meaningful since the distances between these surrounding B cones (roughly 10′ of arc in one observer) are not very much smaller than the size of the tritanopic area itself. Thus the tritanopic area probably corresponds to the absence of a very small number of B cones. This B cone-free area may correspond to the "foveal bouquet of cones" which Polyak (1957, p. 269) describes as an irregularly circular island, perhaps 20′ of arc in dia containing the thinnest cones of practically uniform diameter.

The tritanopic area is considerably smaller than the rod-free area, though investigators in the past have often suggested either that they were the same thing, equating rods and B cones (König, 1894; Willmer, 1944) or claiming that they were coextensive (Walls and Mathews, 1952). Histological estimates of the size

* The nature of the shift for M.J.M., however, also shows that variations in macular pigment density alone cannot account for the effect. The 457 nm surround would preferentially light adapt R and G cones which were relatively unshielded by macular pigment, reducing the overall sensitivity to the 460 nm primary. However, since neither the 519 nm standard nor the 650 nm primary is subject to absorption by macular pigment, shielded and unshielded cones would have identical relative sensitivities to them, leaving their amounts in the match unaltered. The data for M.J.M., on the other hand, show a significant decrease in the amount of the 650 nm primary in the match when the surround is present, in addition to an increase in the amount of the 460 nm primary required. Additional factors such as the variation in pigment density or wave guide properties of foveal cones must be invoked to entirely account for the effect.

† In one case (Fig. 5, subject C.C.) no B cone response could be obtained with a 7.5′ field at 20 times the threshold intensity for a 15′ field. Since the 20-fold more intense smaller stimulus must have produced a retinal illuminance greater than the large one over a region of 12′–13′ dia this result suggests that B cone function was effectively absent over a field at least as large as that. In another case (Fig. 12) there is only a questionable B cone response to a 15.5′ field, at 50 times the threshold intensity for a 31.5′ field; the intensity profiles of the two fields would have crossed at 22′ to 23′, suggesting a lack of B cone function within a region of about that size. Responses of B cones to this field size in other observers could similarly be due to detection by remote B cones.

of the rod-free area vary substantially;* still, the most conservative estimates are larger than the 20′–25′ dia of the tritanopic area.

The instability of small field, centrally fixated, tritanopic matches with light adaptation found in some observers does not imply that the central fovea contains B cones, as Burton and Ruddock suggested, since the instability persists under conditions of artificial tritanopia in which B cones are temporarily prevented from contributing to the match. A more likely explanation of this instability is that it is due to variations in the spectral sensitivities of the remaining classes of cones in a region lacking functional B cones.

The completion effect, in which the central hole in a fixated violet annulus detected only by B cones is filled in with a uniform sensation of violet, provides dramatic support for the postulate of a B cone-free area. Since the central fovea contains no B cones to signal the absence of light in the center of the annulus, the brain can do no better than to assume that it is seeing a uniform disc.

The successive color matching experiments show that the central fovea fails to detect an exchange of lights which differ by a factor of about 22 for B cones, provided that B cones outside the nominal area of the matching field are prevented from mediating the discrimination via scattered light. The ability of these cones surrounding the B cone-free area to mediate discrimination of stimuli nominally falling in the very center of the fovea was demonstrated by the corona effect and may be related to the completion effect discussed earlier, since in both cases signals from eccentric B cones seem to determine the color appearance of the visual field at the line of sight. These effects are similar to the averaging of B cone signals described by Boynton *et al.* (1977). The effect of scattered light is particularly intriguing since the scatter is not subjectively obvious to the observer; it is as though the visual system compensates for the poor acuity of the B cones and for the poor optical quality of the image available to them (due to chromatic aberration in the eye) attributing the resulting spatially diffuse B cone signals to the appropriate areas of the visual field. This may be what makes the presence of a tritanopic area in central vision functionally tolerable; by the same token, it makes the experimental detection of the tritanopic area difficult.

* Osterberg (1935) found the first rods at a distance of 130 μ from the center of the fovea, corresponding to a rod-free area of 260 μ or 52′ of arc. Polyak (1957; p. 266) provides a much larger value for its diameter, 500–600 μ, corresponding to 1.67–2.0 deg. Rochon-Duvigneaud (1943) claimed the rod-free area was only 30–40′ in dia, but even this value is much larger than our estimate of the B cone-free area. Mapping experiments performed on the eye of D.R.W. suggested a rod-free area of 100′, closest to that reported by Polyak.

REFERENCES

Auerbach E. and Wald G. (1954) The participation of cones in human light and dark adaptation. *Am. J. Ophthal.* **39**, 22–40.

Bedford, R. E. and Wyszecki G. W. (1957) Axial chromatic aberration of the human eye. *J. opt. Soc. Am.* **47**, 564.

Bender M. B. and Teuber H. L. (1946a) Phenomena of extinction and completion in visual perception. *Archs Neurol. Psychiat.* **55**, 627.

Boynton R. M., Hayhoe M. M. and MacLeod D. I. A. (1977) The gap effect: Chromatic and achromatic visual discrimination as affected by field separation. *Optica Acta* **24**, 159–177.

Brindley G. S. (1953) The effects on color vision of adaptation to very bright lights. *J. Physiol., Lond.* **122**, 332–350.

Brindley G. S. (1954) The summation areas of human colour-receptive mechanisms at increment threshold. *J. Physiol.* **124**, 400–408.

Brindley G. S. (1970) *Physiology of the retina and visual pathway* (2nd edn). Arnold, London.

Burton G. J. and Ruddock K. H. (1972) A lateral light adaptation effect in human vision. *Vision Res.* **12**, 347–352.

Ditchburn R. W. (1973) *Eye Movements and Visual Perception.* Clarendon Presss, Oxford.

Du Croz J. J. and Rushton W. A. H. (1966) The separation of cone mechanisms in dark adaptation. *J. Physiol.* **183**, 481–496.

Gubisch R. W. (1967) Optical performance of the human eye. *J. opt. Soc. Am.* **57**, 407–415.

Hartridge H. (1945a) Color vision of the fovea centralis. *Nature* **155**, 391–392.

Hartridge H. (1945b) The change from trichromatic to dichromatic vision in the human retina. *Nature* **155**, 657–662.

Hartridge H. (1950) *Recent Advances in the Physiology of Vision.* Blakiston, Philadelphia.

Helson H. and Rohles F. H. (1959) A quantitative study of reversal of classical lightness-contrast. *Am. J. Psychol.* **72**, 530–538.

Hurvich L. (1969) Is the central fixation area of the fovea blue-blind? *Proc. Int. Color Meeting "Color 69"* **1**, 49–57.

Hurvich L. M. and Jameson D. (1957) Further development of a quantified opponent-colours theory. In *Visual problems of color* (Symposium Teddington, 1957), Vol 2, pp. 691–723.

Ingling C. R., Scheibner H. M. O. and Boynton R. M. (1970) Color naming of small foveal fields. *Vision Res.* **10**, 501–511.

König A. (1894) Über den menschlichen Sehpurpur und seine Bedeutung für das Sehen. *S. B. Akad. Wiss. Berlin*, 577–598.

Krauskopf J. and Srebro R. (1965) Spectral sensitivity of color mechanisms: derivation from fluctuations of color appearance near threshold. *Science* **150**, 1477–1479.

McCree K. J. (1960a) Color confusion produced by voluntary fixation. *Optica Acta* **7**, 281–290.

McCree K. J. (1960b) Small field tritanopia and the effects of voluntary fixation. *Optica Acta* **7**, 317–323.

Osterberg G. (1935) Topography of the layer of rods and cones in the human retina. *Acta ophthal.* **13**, *Supplel.* 6.

Pokorny J. and Smith V. C. (1976) Effect of field size on red–green color mixture equations. *J. opt. Soc. Am.* **66**, 705–708.

Polyak S. (1957) *The Vertebrate Visual System.* Univ. Chicago Press, Chicago.

Rochon-Duvigneaud A. (1943) Les Yeux et la Vision des Vertebres. Masson, Paris.

Ruddock K. H. and Burton G. J. (1972) The organization of human color vision at the central fovea. *Vision Res.* **12**, 1763–1769.

Segal J. (1950) Localisation du pigment maculair de la retine. *C.R. Séanc Soc. Biol.* **144**, 1630–1631.
Smith V. C. and Pokorny J. (1975) Spectral sensitivity of the foveal cone photopigments between 400 and 500 nm. *Vision Res.* **15**, 161–171.
Snodderly D. M., Auran J. and Delori F. C. (1979) Localization of the macular pigment. Presented at 1979 meeting of the Association for Research in Vision and Ophthalmology, Sarasota, FL.
Sperling H. G. and Hsia Y. (1957) Some comparisons among spectral sensitivity data obtained in different retinal locations and with two sizes of foveal stimulus. *J. opt. Soc. Am.* **47**, 707–713.
Stiles W. S. (1949) Increment thresholds and the mechanisms of colour vision. *Documenta ophth.* **5–6**, 452–554.
Stiles W. S. (1953) Further studies of visual mechanisms by the two color threshold technique. *Coloquio sobre problemas opticas de la vision.* Union internationale de physique pure et appliquee, Madrid, pp. 65–103.
Thomson L. C. and Wright W. D. (1947) The colour sensitivity of the retina within the central fovea of man. *J. Physiol.* **105**, 316–331.
Van der Horst G. J. C. (1969) Fourier analysis and color discrimination. *J. opt. Soc. Am.* **59**, 1670–1676.
Walls G. L. and Mathews R. (1952) New means of studying color blindness and normal foveal color vision. *Univ. Calif. Publs Psychol.* **7**, 1–172.
Wald G. (1967) Blue blindness in the normal fovea. *J. opt. Soc. Am.* **57**, 1289–1301.
Walraven P. L. (1972) Color Vision. *Ann. Rev. Psychol.* **23**, 347–374.
Walraven P. L. (1974) A closer look at the tritanopic convergence point. *Vision Res.* **14**, 1339–1343.
Weitzman D. O. and Kinney J. A. S. (1969) Effect of stimulus size, duration, and retinal location upon the appearance of color. *J. opt. Soc. Am.* **59**, 640–643.
Williams D. R., MacLeod D. I. A. and Hayhoe M. M. (1981) Punctate sensitivity of foveal blue-sensitive cones. *Vision Res.* **21**, 1357–1375.
Willmer E. N. (1944) Colour of small objects. *Nature, Lond.* **153**, 774–775.
Willmer E. N. (1950) The monochromatism of the central fovea in the red–green-blind subjects. *J. Physiol.* **110**, 377–385.
Willmer E. N. and Wright W. D. (1945) Colour sensitivity of the fovea centralis. *Nature* **156**, 119–121.
Wyszecki G. and Stiles W. S. (1967) *Color Science*. Wiley, New York.