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PUNCTATE SENSITIVITY OF THE BLUE-SENSITIVE MECHANISM

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Abstract—Thresholds were measured for a tiny, brief, violet flash on a long wavelength, B cone-isolating background in foveal locations spaced only 4 or 5′ of arc apart. Large spatial variations in B cone sensitivity were found just beyond the foveal tritanopic area even though thresholds for the same wavelength test flash hardly varied at all across these same retinal locations when the flash was detected by G cones. The relative constancy of G cone threshold suggests that these spatial variations are intrinsic to the blue-sensitive mechanism and cannot be explained by prereceptoral filtering. The spatial variations in B cone sensitivity are consistent with physiological evidence that B cones are scarce in the retina. In one observer, it was possible to discern discrete peaks in sensitivity spaced roughly 10′ of arc apart. A model is described which takes optical spread and eye movements into account to show that these peaks may represent individual B cones (or clumps of B cones).

INTRODUCTION

The mosaic of foveal cones is so fine that it usually leaves no trace in visual experience. Though coarser than some measures of visual acuity might suggest, it is too fine for even the tiniest optical probes to isolate a single cone in the intact eye. The following experiments attempt to fix the retinal locations of one particular cone type, the blue-sensitive cones or B cones, which is characterized by inferior resolving power and might accordingly form a relatively coarse receptoral mosaic.

The acuity of the blue-sensitive mechanism is markedly inferior to that of the red and green-sensitive mechanisms, even when correction is made for the chromatic aberration of the eye. Stiles (1949), isolating B cones† with a short wavelength checkerboard pattern seen against a long wavelength adapting field, reported an acuity for B cones of 2.9′ of arc. Daw and Enoch (1973) reported similar values for foveal B cone acuity, 3.75–5′ of arc. Brindley (1954) estimated the acuity of the B cones to be worse, providing a value of 7.5′ or arc. More recent investigations (see Stromeyer *et al.*, 1978) have yielded values close to Stiles' estimate, but even the most generous estimate of B cone acuity is roughly 6 times poorer than the resolution achieved by the R and G cones under optimal conditions. The poor acuity of the B cones is undoubtedly related to the striking failure of a juxtaposed pair of lights differing only in their amounts of B cone excitation to form a distinct contour (Tansley and Boynton, 1978).

The cause of this poor spatial resolution is less clear, and two explanations have emerged to account for it. One commonly accepted explanation is that B cones are sparsely represented in the retina, vastly outnumbered by the R and G cones. If B cone acuity were limited by the density of B cones in the fovea, the range of acuities in the literature implies that foveal B cones are spaced between 2.5 and 7.5′ of arc apart (Cornsweet *et al.*, 1980). Assuming that foveal cones (of all types) have a center-to-center separation of 0.5′ of arc, this would mean that less than 4% of the cones in the fovea are B cones. In the central fovea where B cone activity deteriorates the fraction would be still less than this.

However, it would be naive to infer scarcity of the B cones from poor acuity since, for example, acuity is poor under scotopic conditions yet rods are even more densely packed at an eccentricity of 20 deg than are foveal cones. Brindley (1954) reported observations in support to the notion that the poor resolution of B cones is due to a postreceptoral bottleneck rather than scarcity. He reasoned that if acuity were limited by B cone density there should exist sensitive spots in the retina corresponding to B cones with insensitive gaps between them. He slowly moved a 3′ violet spot seen against a green background from 40′ to 3 deg from the center of fixation. At no time did the spot appear to flash on and off as might be expected if the B cone density were low. Brindley's experiment is inconclusive, however, since he used a relatively large test spot in retinal locations where the B cone density is probably highest. Measures of B cone sensitivity as a function of eccentricity show a sensitive annular zone peaking at an eccentricity of about one degree and centered around fixation (Stiles, 1949; Brindley, 1954). The distribution of B cones in the baboon also shows the highest B cone density in this region with distances between B cones approaching the nominal

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† Throughout this paper, cones with peak sensitivities at 440, 535 and 565 nm will be designated as B, G and R cones respectively.

3′ dia of Brindley's test spot (Marc and Sperling, 1977, see Discussion). Optical spreading of the test spot would certainly increase its *effective* diameter well beyond this 3′ nominal dia, a problem exacerbated by Brindley's use of a broadband short wavelength filter for the test spot which could seriously blur it due to chromatic aberration in the eye. Furthermore, even if the steady test spot fell momentarily in a gap between B cones, the sluggish temporal response of the blue mechanism in conjunction with inevitable eye movements might maintain its unperturbed visibility.

Brindley's experiment, the only psychophysical investigation bearing on the question of B cone sparsity, yielded evidence against it. However, observations made by 7 observers in this laboratory indicated that an exceedingly dim and tiny steady violet spot (1.1′ of arc in diameter) seen against an intense yellow (584 nm) background to isolate B cones was only intermittently visible when presented to the fovea (outside the tritanopic area), in contradiction to the result obtained by Brindley. The intermittent visibility of the continuously exposed violet spot was surprisingly obvious, even in this informal situation.

It occurred over quite a wide range of test spot illuminances, and was not observed when the spot was visible to the other cone types; it appeared to be a property of the B cone system, and not of the visibility of near threshold lights generally. To determine whether this intermittent visibility is the consequence of local variations in B cone sensitivity, we have measured thresholds for a tiny and brief violet flash seen against a B cone-isolating long wavelength background. The test flash was presented to retinal locations within the fovea spaced from 4–5′ of arc apart in order to search for sensitive and insensitive spots corresponding to B cones and the gaps between them.

Mapping experiments such as this* are fraught with two major difficulties, both of which tend to obscure any existing local variations in retinal sensitivity. First, optical spreading due to diffraction and other aberrations in the eye place a lower bound on the size of the stimulus which can be used in the mapping, enlarging the size of the retinal location under test. Second, the problem of optical spread is compounded by the fact that the eye is continuously in motion. Even when an observer is attempting to fixate accurately, the root mean square deviation of the angle of regard in the horizontal and vertical directions is about 1.4–3.2′ of arc (Ditchburn, 1973; p. 98). Still, the spacing between B cones measured by Marc and Sperling in the baboon foveola, 6′ of arc, is two or three times as large as this, suggesting that a psychophysical mapping technique designed to minimize the degrading effect of eye movements and optical spread might be able to uncover local variations in B cone sensitivity resulting from their sparse distribution in the human fovea.

Method

All experiments used a standard two-channel Maxwellian view system shown in Fig. 1 with a 120 V,

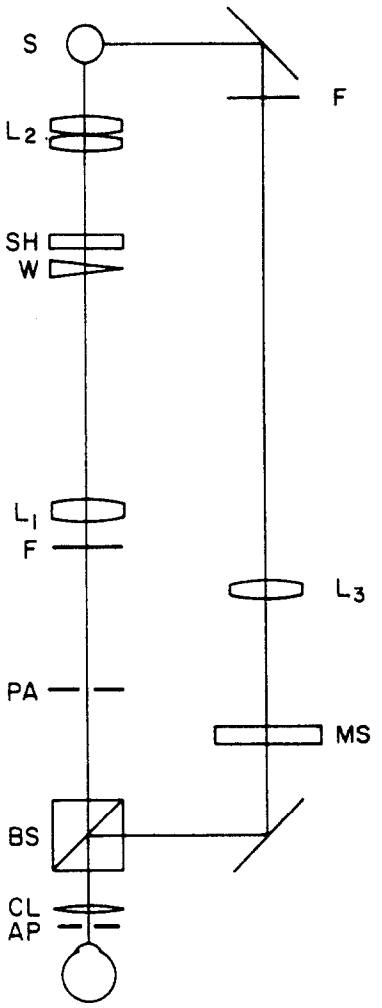

Fig. 1. Two-channel apparatus used in mapping experiments. Tungsten source, S, is imaged by lens pair, L_2, in test channel onto shutter, SH. Neutral density wedge, W, adjustable by observer, controls test flash intensity. Maxwellian lens, L_1, images filament in artificial pupil, AP. 100 μm precision aperture, PA, defining test spot lies between L_1 and observer. Background channel, combined with test channel by beam-splitter, BS, consists of single Maxwellian lens, L_3. A micrometer stage, MS, with horizontal and vertical adjustments held the aperture defining background and fixation crosshairs, and like the test aperture, lay between the lens and the eye. Wavelengths of test and background were determined by interference filters, F. Correcting lenses, CL, were sometimes used.

* Other investigators have used tiny test spots to search for local variations in the sensitivity of the cone mosaic. Hartridge (1950) argued that the rapid changes that can sometimes be observed in the hue of stars are due to fluctuations in the position of the star's image on the retina rather than to atmospheric effects. According to Hartridge, eye movements shift the tiny image across clusters of receptors of different types, signalling different color sensations. On this basis, he claimed to have found evidence for a total of seven different receptor types. Krauskopf (1964) showed that the use of color names for a tiny 580 nm flash varied with its retinal location, supporting the notion that there are spatially distinct cases of color receptors.

200 W Quartzline Lamp, S. One of the channels provided a chromatic adapting field while the other superimposed a tiny test flash on the background. All spectral filters were narrow band interference filters (bandwidth at half height less than 15 nm) except for a purple (Wratten 35) filter which passed light shorter than 470 nm and longer than 650 nm. All calibrations were done with an EG&G photometer model No. 450-1. A dental impression was used to fix the observer's head relative to the 2 mm artificial pupil, AP, of the system.

Since the purpose of the experiments was to map the sensitivity of very closely spaced foveal locations, optimal optical quality of the test flash was crucial. The test spot was formed by a 100 μ precision aperture, subtending a nominal visual angle of 1.1′ of arc. The aperture, PA, lay closer to the observer than the final Maxwellian lens, L_1, (which was 0.5 m from the eye) so that the only optical components between the eye and the aperture were a high quality beamsplitter, BS, and, in some experiments, correcting lenses, CL. The observer aligned his head horizontally and vertically to achieve the sharpest possible image of the test spot. The aperture defining the background (and the fixation target), at M.S., also lay between the final Maxwellian lens, L_3, in the background channel and the eye at a distance of 0.44 m. Optimal focus on the background thus required about 2.3 D accommodation. Since the test spot and background differed in wavelength, the relative distances of the apertures defining them had to be adjusted to compensate for the axial chromatic aberration of the eye. This was done by temporarily replacing the aperture defining the test spot with a high contrast square wave grating which the observer slid back and forth until it was in best focus when he was accommodated on the background field. The optical distances obtained in this manner agreed closely with those predicted from the eye's chromatic aberration (Bedford and Wyszecki, 1957).

In order to minimize retinal smear of the test spot due to eye movements, test flash durations were never longer than 50 msec. The median displacement of the visual axis over a 50 msec period of fixation is on the order of 15″ of arc according to Riggs, Armington, and Ratliff (1954). In the experiments reported here for observers D.R.W. and M.M.H. the fixation target was a set of fine crosshairs subtending about 15″ of arc superimposed on the 5 deg chromatic background. At the beginning of each session, the tiny test spot was centered on the crosshairs by the observer, as a method of zeroing its position relative to the center of fixation. The crosshairs and background were mounted on a two-dimensional micrometer stage, M.S., allowing them to be moved by the experimenter in a plane orthogonal to the observer's line of sight. The position of the fixation crosshairs thus determined the retinal location under test. This procedure was adopted instead of shifting the location of the test spot since that would have required translating the aperture defining the test through the violet beam striking it; any small non-uniformities in this beam would have produced differences in the radiance of the test spot as a function of its retinal location, contaminating our efforts to identify true retinal variations in sensitivity. For some of the retinal locations tested (those lying directly on the vertical and horizontal retinal meridians) the test flash was superimposed on the fine crosshairs. Control experiments using a tiny black speck as a fixation target failed to show any difference in thresholds with and without the crosshairs (which had a low contrast against the bright chromatic backgrounds) beneath the test spot.

In an effort to optimize accuracy of fixation, observers were provided with a switch which allowed them to present the test flash when they felt they were fixating accurately and were well accommodated, resulting in a low rate of flash presentation.

Threshold measurements were begun only after at least 2 min of adaptation to the chromatic background. Control experiments showed that threshold was stabilized at this point and, for observations made in the fovea at least, did not drift noticeably thereafter.

Results of three observers (right eyes) are presented: all were experienced psychophysical observers with normal color vision. Observers M.M.H. and A.L.N. were emmetropic while D.R.W. was slightly myopic and astigmatic. The specific methods and results for each observer will be discussed sequentially, first for experiments where the observer set thresholds by method of adjustment and then for experiments in which a double random staircase procedure was used with thresholds in multiple retinal locations measured simultaneously.

Observer D.R.W.

Thresholds were measured at 121 foveal locations spaced 5′ of arc apart, forming an 11 by 11 array 50′ on a side and centered on the line of sight. Three thresholds were set by method of adjustment at each location before testing a new location. New locations were chosen by the experimenter until thresholds had been measured at all 121 locations, creating a sensitivity map of the central fovea. It took four or five sessions to complete each of three different maps at these locations in the fovea, with about 30 locations being mapped in a given session. For a given map, roughly 10–20% of the locations were remapped in a second session to provide a crude estimate of between session variability. Correcting lenses were not used. The conditions for each of the three maps, which were done sequentially, are described below:

(1) A 420 nm test flash was presented against a 2.8 log td, 584 nm background intended to isolate B cones for the purpose of searching for sensitive and insensitive spots.

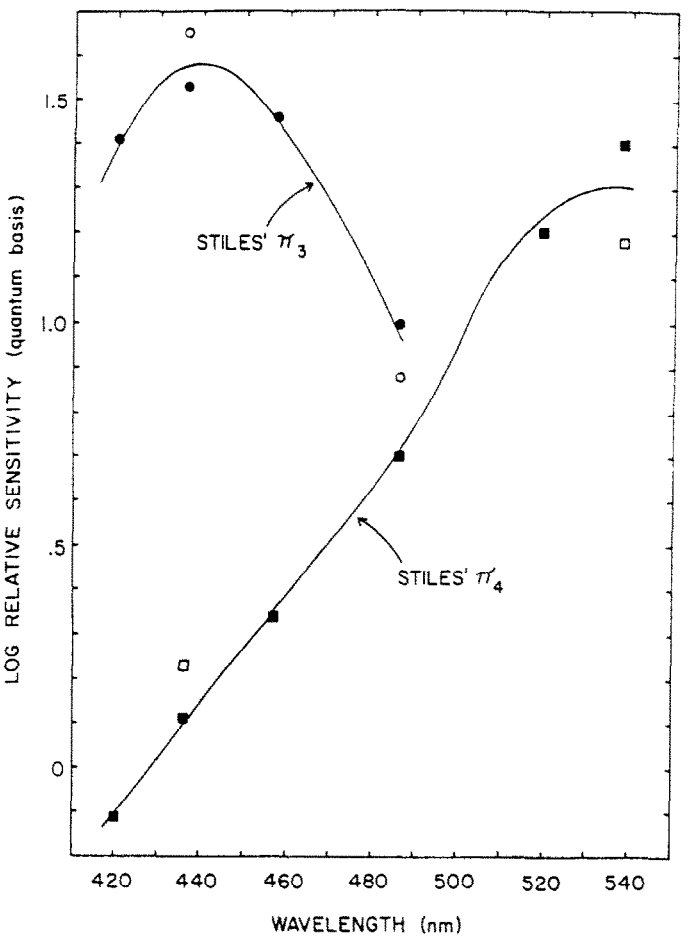

Fig. 2. Observer D.R.W: Solid circles show the log relative sensitivity (quantum basis for a 50 msec test flash at an eccentricity of 35′ presented against a 2.8 log td, 584 nm background. The data are fit with Stiles' π_3. Solid squares show the log relative sensitivity for the test flash presented against a 3.4 log td, Wratten 35 background fit with Stiles' π_4. Observer A.L.N: Open circles show log relative sensitivity to two wavelengths for a 25 msec, 15′ test flash at an eccentricity of 29 min presented against a 4.1 log td, 584 nm background.

(2) The same 420 nm test flash was presented against a 3.4 log td purple background (Wratten 35) intended to isolate G cones. This condition served as a control for prereceptoral filtering since the 420 nm test flash should be equally absorbed by any filter screening all the cones, whichever mechanism detects the test flash.

(3) A 538.5 nm test flash, also detected by G cones, was presented against the same purple background used in the second condition. This condition was used to assess the sensitivity of the G cones in the central fovea, uncontaminated by the filtering effects of macular pigment.

Results

Figure 2 demonstrates that the yellow and purple backgrounds isolated the blue and green mechanisms respectively. Solid circles and solid squares show the relative sensitivity (quantum basis) for 1.1′ test flashes of various wavelengths presented at an eccentricity of about 35′ against the 584 nm and purple backgrounds respectively. Filled circles are well fit by Stiles' π_3 mechanism; filled squares are fit by Stiles' π_4 mechanism. Short wavelength flashes presented on the yellow background always appeared blue and spatially diffuse whereas the same flashes seen against the purple background always appeared white and crisp, supporting the argument that detection was mediated by B and G cones respectively.

Figure 3 shows a sensitivity map generated from the threshold values obtained for the 420 nm test flash against the 584 nm background. This map, and others like it in this paper, were obtained by converting the mean log threshold values at each location to sensitivity values (−log threshold). These values and their SE for this and other maps can be found in Williams (1979). The resulting matrix was fit with a two-dimensional bicubic spline interpolating function (which fits the data with a surface that passes through each data point). This surface was then plotted in a three-dimensional format (Watkins, 1978). The hatch marks along the base of the figure represent the 5′ spacing of the test locations. Hatch marks along the vertical edges represent increments of 0.1 log units in sensitivity. The

center of fixation is at the small peak in the center of the plot, marked with a spot.

Several important features of this sensitivity map should be noted. First, there is a profoundly insensitive region of irregular shape in the center of the map corresponding to the B cone free area of the fovea (see Williams *et al.*, 1981a). Test flashes at locations throughout this region appeared white and sharply-defined whereas those falling in the more sensitive outlying regions appeared violet and diffuse, consistent with detection mediated by G cones and B cones respectively. There was no sign of B cone response within 10′ of the center of fixation. At the ragged edges of this central valley, sensitivity rises very rapidly; the far corner of the map, about 35′ from the foveal center, for example, is nearly 25 times more sensitive than the foveal center. The steepest gradient of sensitivity shows a factor of 10 increase in B cone sensitivity with an increase in eccentricity of only about 7 min arc.

A second feature of the map, more important for the present argument, is the uneven sensitivity outside the B cone free area at the edges of the map. In addition to large local variations in B cone sensitivity in these outlying regions, there is a marked asymmetry in B cone sensitivity between the near and far corners of the map. The inferior temporal corner averages roughly 0.8 log units more sensitive than the superior nasal corner. This asymmetry which extends at least 1 deg from the foveal center is a stable aspect of this observer's foveal sensitivity and has been checked repeatedly over the course of 2 yr. The stability of the more local variations in B cone sensitivity is less certain for this observer since only 20 of the 121 locations were mapped a second time in another session. However, the standard error of the mean

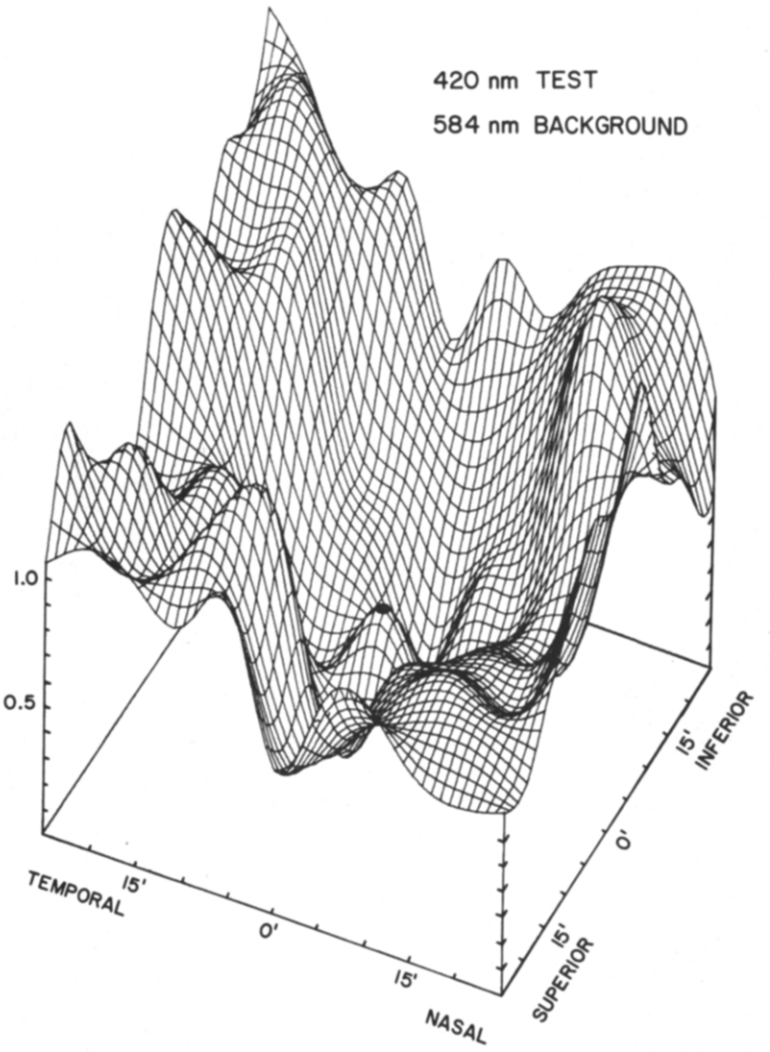

Fig. 3. Sensitivity map for D.R.W. using a 1.1′, 420 nm, 50 msec test flash in locations spaced 5′ of arc apart presented against a 2.8 log td 584 nm background. For this and other figures like it for D.R.W., the left corner of the plot represents the superior temporal fovea; the far corner represents the inferior temporal fovea; center of fixation is represented by black dot. Hatchmarks along base of plot indicate divisions of 5′ of arc. Hatchmarks along sides of plot indicate 0.1 log units in sensitivity. A value of 0.0 corresponds to 6.4 log quanta/flash.

based on variability between sessions for locations outside the B cone-free area averages 0.07 log units, which is small relative to the large local variations in sensitivity.

The unevenness of B cone sensitivity in this map suggests that B cones may be scarce there. However, these peaks and valleys might also be explained by local variations in the density of prereceptoral filters such as macular pigment or blood vessels, both of which would strongly absorb the 420 nm test light. Though the central fovea is free of any large blood vessels, Bird and Weale (1974) suggest that fine capillaries may run across it. Macular pigment is most prevalent in the fovea and small holes or irregularities in its distribution could produce sensitive and insensitive regions.

If B cones were well represented in the fovea and prereceptoral filtering were responsible for the local variations in sensitivity, then these variations should be reproducible when a different cone mechanism detects the same 420 nm test flash, since the filters would presumably screen all cone types alike. This was tested by repeating the threshold measurements under exactly the same conditions as before except that the test flash was presented against a purple adapting field which isolated the G cones rather than the B cones. Figure 4 shows the resulting sensitivity map. The map is much flatter than the map obtained under B cone isolation conditions, but the relatively small (0.25 log unit) peak at the center of fixation is as clearly evident in this map as it was in the previous one. Around this peak is an annular insensitive region roughly 25′ in diameter which in turn is surrounded by a plateau with fairly uniform sensitivity, quite unlike the peaks and valleys found in the corresponding regions B cone sensitivity map. This result demonstrates that the local variations in sensitivity under B cone isolation conditions are characteristic of the B cones themselves, and cannot be accounted for by prereceptoral filtering.

Prereceptoral filtering nonetheless distorts the maps obtained with the 420 nm test making it difficult to assess the true underlying receptor sensitivities. One way to determine the distribution of these prereceptoral filters, and of macular pigment in particular, is to compare the sensitivities of a given cone mechanism in different retinal locations for two test lights, one of a wavelength which is absorbed by macular pigment and one which is not. The difference in the log sensitivities for the two test flashes in different locations provides a measure of the distribution of the inert pigment. This technique has been exploited extensively to determine the density and absorption spectrum of macular pigment (e.g. Stiles 1953; Bone and Sparrock, 1971). It should be pointed out that this technique is only approximate since it depends on the assumption that the spectral sensitivity of the underlying cone mechanisms is independent of retinal location. This assumption is not entirely correct since photopigment density increases toward the center of

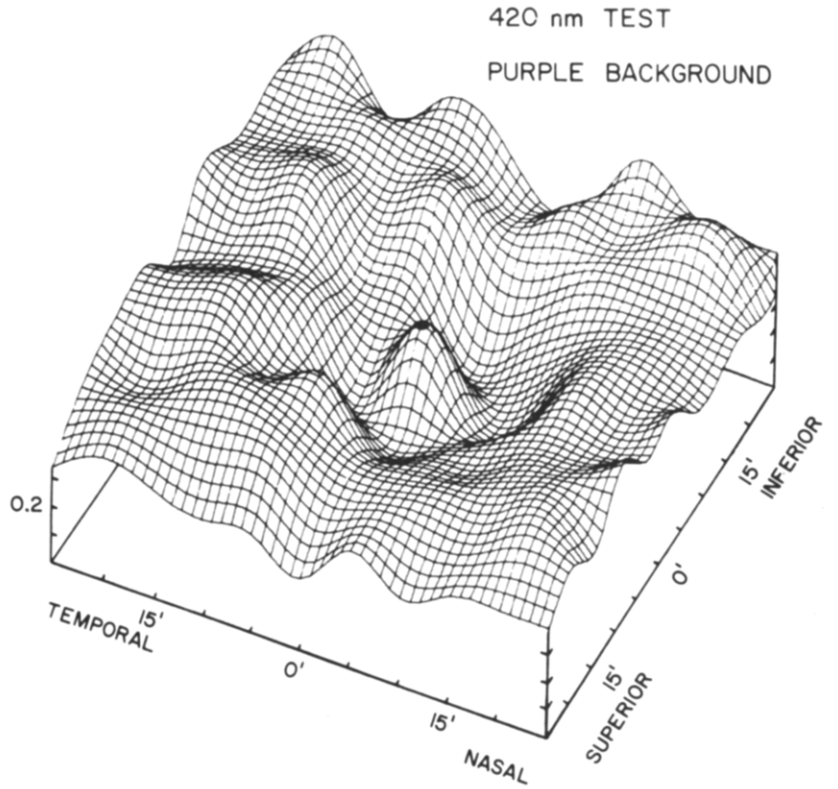

Fig. 4. Sensitivity map for D.R.W. using a 1.1′, 420 nm, 50 msec test flash presented against a 3.4 log td, purple (Wratten 35) background. A value of 0.0 corresponds to 6.1 log quanta/flash.

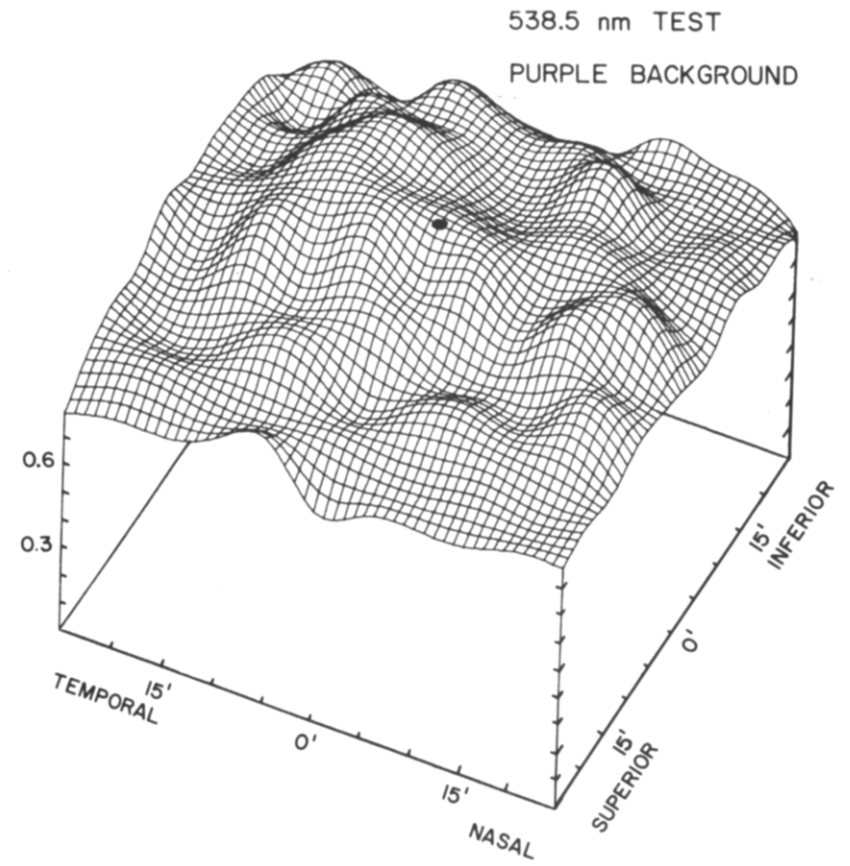

Fig. 5. Sensitivity map for D.R.W. using 538.5 nm 1.1′ 50 msec test flash against a 3.4 log td, purple (Wratten 35) background. A value of 0.0 corresponds to 4.4 log quanta/flash.

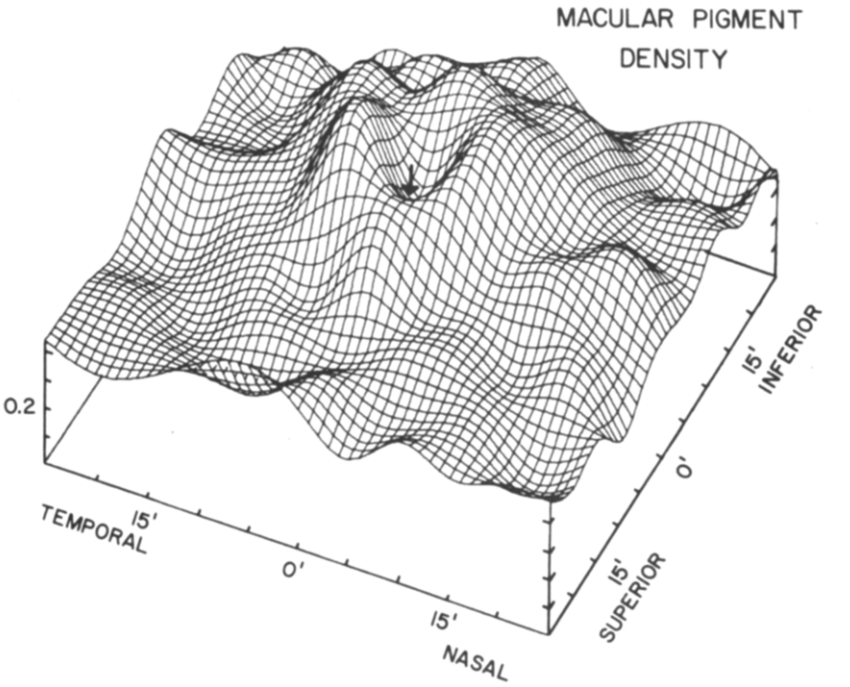

Fig. 6. Distribution of macular pigment density at 420 nm for D.R.W. calculated by subtracting log sensitivity values of Fig. 4 from those of Fig. 5 (G cone sensitivity with 420 nm test from G cone sensitivity with 538.5 nm test). Hatchmarks along side of figure represent density divisions of 0.1 log units.

the fovea (Baker *et al.*, 1979) slightly broadening the spectral sensitivities of the cones (Pokorny and Smith, 1976).

Figure 5 shows the foveal sensitivity map obtained with the purple, G cone isolating background and a 538.5 nm test flash, a light which is not appreciably absorbed by macular pigment (Wyszecki and Stiles, 1967, p. 207). This map, like the one obtained with the 420 nm test against the purple background, is also much flatter than the B cone sensitivity map; the small ripples in it are not beyond those expected from random error. Still, an overall slight gradient "is apparent": G cone sensitivity falls by about 0.3 log units toward the corners of the map. The map has been adjusted relative to the map obtained with the 420 nm test flash so that they have equal sensitivity at an eccentricity of 2.5 deg in the nasal retina where macular pigment is probably not very dense for this observer. (Some macular pigment is undoubtedly present at this eccentricity since Wald (1945) extracted small amounts of it in the eccentric retina. However, this observer's entopic Maxwell's spot does not extend beyond 1 deg from the foveal center). By subtracting point by point the G cone map obtained with the 420 nm test (which is absorbed by macular pigment) from the G cone map obtained with the 538.5 nm test (which is not absorbed by macular pigment), it is possible to derive the distribution of macular pigment across the central fovea of this observer, shown in Fig. 6. The general gradients in the density map agree closely with the detail of this observer's Maxwell's spot, supporting the notion not fully accepted (Walls and Mathews, 1952; Trezona, 1970) that macular pigment is responsible for the entoptic effect. The small dip in density at the center of fixation (which appears as a peak in the maps obtained with the 420 nm test) corresponds to a 3–6′ of arc brightening at the center of Maxwell's spot. Surrounding this punctate clearing is a 25′ in diameter dense annular region which is clearly visible as a dark ring in the entoptic effect.*

* This description of Maxwell's spot, and the corresponding macular pigment density map, agrees fairly well with the description of Maxwell's spot given by Holm (1922), who also reported a dense circular region with a small bright dot at the fixation point (see Walls and Matthews, 1952). Walls and Mathews provide extensive descriptions of the appearance of Maxwell's spot, showing that it varies substantially from person to person. They concluded that Maxwell's spot represents that area of the retina devoid of rods and B cones rather than the distribution of macular pigment. However, our measurements involved the detection of test flashes by only a single mechanism,.the G cones, rendering an explanation of Maxwell's spot based on the distribution of receptor types unviable. Our measurements also show that, in some observers at least, macular pigment is densest at the center of the fovea (neglecting the small dip at the very center). This contradicts the commonly held belief (see Wald, 1967; Polyak, p. 261; Thomson and Wright, 1947) that macular pigment is concentrated in the foveal slopes, being relatively absent in the floor of the fovea.

Figure 7 shows the result of correcting the B cone sensitivity map (Fig. 3) for the absorption of a macular pigment. This was done by simply adding the macular pigment density values point by point to the B cone log sensitivity values. Despite the correction for macular pigment, the peaks and valleys around the edge of the map persist as does the central insensitive area.

Observer M.M.H.

Though the data presented so far suggest that B cones may be sparsely distributed in the foveal regions surrounding the B cone free area, the reproducibility of these peaks and valleys was not assessed over long periods of time. This question has been investigated in more detail with observer M.M.H. over a period of more than 2 yr.

Method

The initial experiments on this observer were similar to those on D.R.W., mapping B cone sensitivity in closely spaced locations within the fovea. Correcting lenses were not used. B cones were isolated using a 4.36 log td 633 nm background (see Williams *et al.*, 1981a) and a 20 msec, 436 nm, 1.1′ of arc test flash. Forty-four foveal locations were tested spaced 4′ of arc apart forming an irregular shaped area in the superior temporal fovea. In the first set of mapping experiments, thresholds were determined using the ascending method of adjustment in a total of six sessions over the span of about 4 months. Only a subset (averaging about 15) of the 44 locations could be measured in each session as for D.R.W. Three thresholds were set at each location before proceeding to a new location. The observer was generally unaware of the exact location of the flash, nor was she aware whether a particular location had proven to be sensitive or insensitive in previous sessions. The threshold measurements were supplemented with five sessions in which the test flash was fixed in intensity near threshold and the percentage of 20 flashes seen for each location recorded. This procedure substantially confirmed the results obtained by method of adjustment.

Results

Figure 8 shows the B cone sensitivity map derived from the values given in Table 1 (upper numbers at each location). As for D.R.W., sensitivity rises rapidly away from the center of fixation (shown as a cross in the right foreground) indicating the edge of the B cone-free area. The most striking features of the map are the four discrete peaks in sensitivity. These peaks are location from 8–12 min apart and rise an average of 0.6 log units above the surrounding insensitive areas. The peaks could be reliably remapped from session to session; all of them were mapped in at least two sessions and one of them in a total of six sessions over a 4-month period. The average SEM based on variability between sessions was 0.12 log units. The

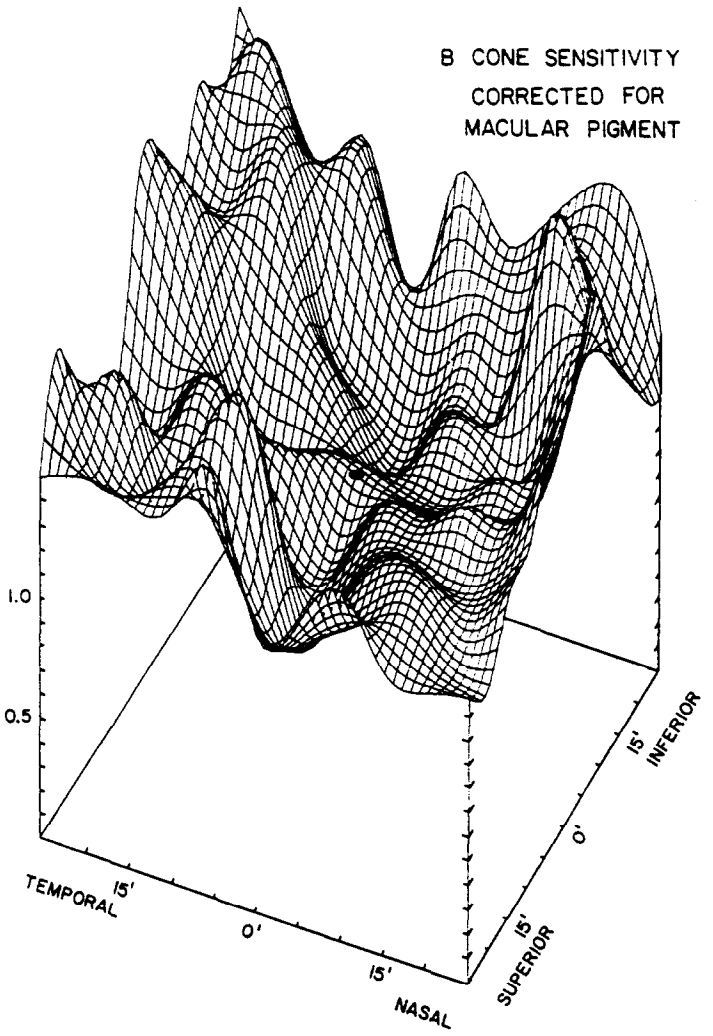

Fig. 7. B cone sensitivity map from Fig. 3 corrected for the absorption of the test flash by macular pigment. Map was obtained by adding macular pigment density shown in Fig. 6 to B cone sensitivity map of Fig. 3.

rounded peak on the left in the map (28–32′ superior to the fixation point) was sharply defined in both sessions devoted to it but shifted 4′ of arc during one of the sessions, resulting in a lower average height. The shift probably reflects a small temporary shift in fixation occurring during one of the sessions since the position of another peak mapped in each of these sessions did not shift.

A subset of the original locations was mapped with the same 436 nm test flash seen against a 3.4 log td purple (Wratten 35) background intended to isolate the green mechanism instead of the blue. As was the case for D.R.W., the peaks and valleys disappear under G cone isolation conditions showing that they are a property of the B cones alone and not due to prereceptoral filtering. Instead of the dramatic *increase* in sensitivity away from the center of fixation, there is a gradual and modest *decline* in sensitivity (roughly 0.4 log units from an eccentricity of 4′–36′ in the superior retina).

Two years after these original measurements were made, an attempt was made to remap the three peaks closest to the center of fixation (excluding the peak on the far left in Fig. 8), testing 21 of the original 44 locations. Many changes were made in the procedure. The wavelengths of test and background were changed to 420 and 584 nm (3 log td) respectively. The test duration was extended to 50 msec. A single threshold setting was made by descending method of adjustment at each location per session. To avoid observer bias, the neutral density wedge determining the test intensity was randomly offset by the experimenter between threshold settings. All 21 locations were tested in a given session with their order randomized; four sessions were run on four different days.

The lower numbers in Table 1 show the mean sensitivity values and, in parentheses, their SE based on variability between the four sessions. The average SEM for all 21 locations is 0.06 log units. The correlation coefficient between these sensitivity values and

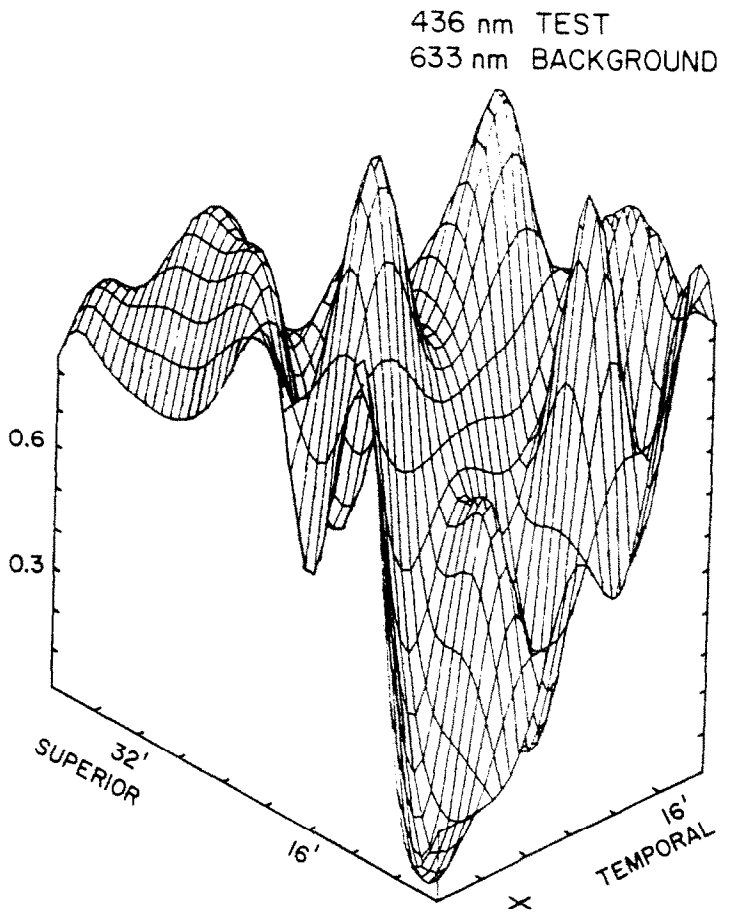

Fig. 8. Sensitivity map for M.M.H. using a 1.1', 436 nm, 20 msec test flash in retinal locations spaced 4' of arc apart against a 4.36 log td, 633 nm 5 deg background. Cross marks center of fixation; left corner of figure represents superior fovea; right corner represents temporal fovea. A value of 0.0 corresponds to 5.9 log quanta/flash.

Table 1. Upper numbers represent mean sensitivity values for M.M.H. used to generate map in Fig. 8, where a value of 0.0 equals 5.9 log quanta/flash. Lower numbers show mean sensitivity values for a subset of locations obtained in an attempt to replicate map made 2 yr earlier. A 420 nm 1.1' 50 msec test flash was presented against a 3 log td 584 nm background. A value of 0.0 represents 5.6 log quanta/flash. Numbers in parentheses show SEM based on variability between 3 thresholds set within a single session; those with asterisks show standard errors of mean based on variability between sessions.

Temporal 20'	16'	12'	8'	4'	0'	4'	
1.17 (0.05)	1.16 (0.05)	0.58 (0.04) 0.74 (0.04)*			0.19 (0.01)'		4'
1.24 (0.07)	0.55 (0.06) 0.85 (0.11)*	1.55 (0.17)* 1.415 (0.06)*	0.18 (0.05) 0.42 (0.10)*	0.86 (0.06)	0.12 (0.04)*	0.23 (0.11)	8'
1.16 (0.06)	1.26 (0.09)* 1.04 (0.09)*	0.9 (0.12)* 1.26 (0.07)*	0.82 (0.03) 0.70 (0.12)*	0.85 (0.11) 0.52 (0.12)*	0.68 (0.14)* 0.34 (0.08)*	1.28 0.23 (0.03)*	12'
	1.03 (0.06)* 1.14 (0.05)*	1.67 (0.06)* 1.15 (0.03)*	1.25 (0.04)* 1.28 (0.05)*	1.26 (0.17)* 1.42 (0.06)*	1.68 (0.04)* 1.43 (0.03)*	0.66 (0.06) 0.66 (0.02)*	16'
	1.21 (0.03) 1.44 (0.07)*	1.15 (0.04) 1.37 (0.05)*	1.23 (0.13) 1.37 (0.004)*	0.72 (0.06) 1.25 (0.07)*	0.85 (0.04)* 1.16 (0.06)*	1.15 (0.05)	20'
		0.81 (0.02)	1.03 (0.01)	0.69 (0.35)*	1.2 (0.06)*	1.07 (0.06)	24'
		0.83 (0.02)		1.03 (0.01)	1.29 (0.26)*	0.88 (0.10)	28'
				0.85 (0.03)*	1.28 (0.29)*	0.86 (0.17)	32'
					0.95 (0.13)*		36'
					0.82 (0.11) Superior		40'

those for the same 21 locations mapped under different conditions 2 yr earlier is +0.58. This value is much lower than would be expected from the across-session reproducibility of each set of data taken separately. Changes in the apparatus, method, or perhaps in the visual system could contribute to this low correlation which nonetheless is easily significant at the 0.01 level. Two of the 3 peaks are clearly visible in the same locations where they were found before. As before, the peaks rise on the average 0.6 log units above the surrounding areas. However, a major change is that the third and most eccentric peak, which lay in the original map 12′ temporal and 16′ superior relative to the fixation point, is no longer evident. Instead, sensitivity in the region where the peak should have been is moderate, increasing fairly gradually toward the edge of the map. There is no easy explanation for this discrepancy between the maps since it cannot be accounted for by random error. Since the other peaks appeared in their proper places, the disappearance of the third peak cannot be explained by a shift in the center of fixation between the two sets of measurements.

DOUBLE RANDOM STAIRCASE–RANDOM LOCATION PROCEDURE

The procedure described so far has the disadvantage that sensitivity at only a single location can be tested at a time. Furthermore, the method of adjustment can be vulnerable to observer bias and loses information about the total shape of the psychometric function at each location. To circumvent these difficulties, a microprocessor-controlled double random staircase procedure was used. The stimulus display, which lay in the center of a 4 deg, 2.6 log td, 584 nm background, is shown on the left in Fig. 9. The fixation display consisted of a grid of fine black lines forming a 3 × 3 array of fixation squares, with center to center separations of 4′ of arc. Only the three squares forming the center column were used. The test flash (420 nm, 50 msec, 1.1′ of arc) was located 12′ below the center of the nearest fixation square. By shifting her fixation from square to square, the observer could cause the test spot to fall at eccentricities of 12, 16 and 20′ in the superior fovea. These particular locations were chosen, without the knowledge of the observer, since they crossed a peak (at 16′ in the superior fovea) mapped previously with method of adjustment. This arrangement has distinct advantages over the crosshairs display used previously: the spatial relationship between the test flash and the fixation display was constant throughout the experiment keeping potential masking effects of the fixation display constant for all retinal locations tested.

Just to the right of the fixation array was a light-emitting diode superimposed on the background (not shown in Fig. 9) which displayed a number corresponding to the particular square to be fixated for the next presentation of the test flash. The fixation location was randomly determined by the microprocessor except that the experimenter could override the random assignment in order to obtain equal numbers of flashes at all locations at the end of a session. When the observer felt she was fixating the appropriate square accurately, she depressed a switch which delivered the test flash. The microprocessor would not allow the observer to present flashes faster than once every 4 sec, in order to avoid potential habituation effects. She then had a choice of response keys; a "yes" if the flash had been seen, and a "no" key if it had not.

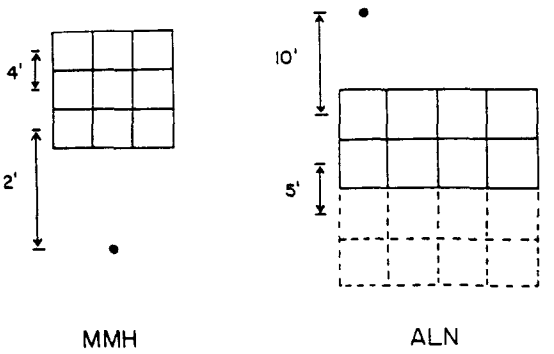

Fig. 9. Fixation displays used in double random staircase–random location procedure for M.M.H. on left and A.L.N. on right. Test flash is shown as a dot in each case. Only the central column of squares was used for M.M.H. Though only 8 squares were visible at a time for A.L.N., the display could be shifted (dotted line) to map an array of 16 retinal locations.

The microprocessor also drove a stepping motor connected to a circular neutral density wedge in the test channel, changing the intensity of the test flash with a 0.1 log unit step size. A simple staircase procedure was used in which the observer's previous response determined the intensity of the next flash delivered for that staircase. Two staircases were randomly interleaved for each of the three fixation locations to avoid response bias by the observer (Cornsweet, 1962). The pair of staircases at each location were started at intensities which bracketed the actual threshold value. The procedure was continued until at least 100 flashes had been presented at each fixation location.

The microprocessor recorded the total number of flashes presented and the number of "yes" responses at each flash intensity for each fixation location, allowing frequency of seeing functions to be plotted for each of the three retinal locations under test. The data for each location was fit with a cumulative normal probability function by probit analysis (Finney, 1962). The statistical package which performed this analysis can be found in Barr *et al.* (1976). A chi-square analysis showed that this function provided a good description of the data. The radiance giving the mean of the probability function, corresponding to 50% frequency of seeing, was chosen as threshold.

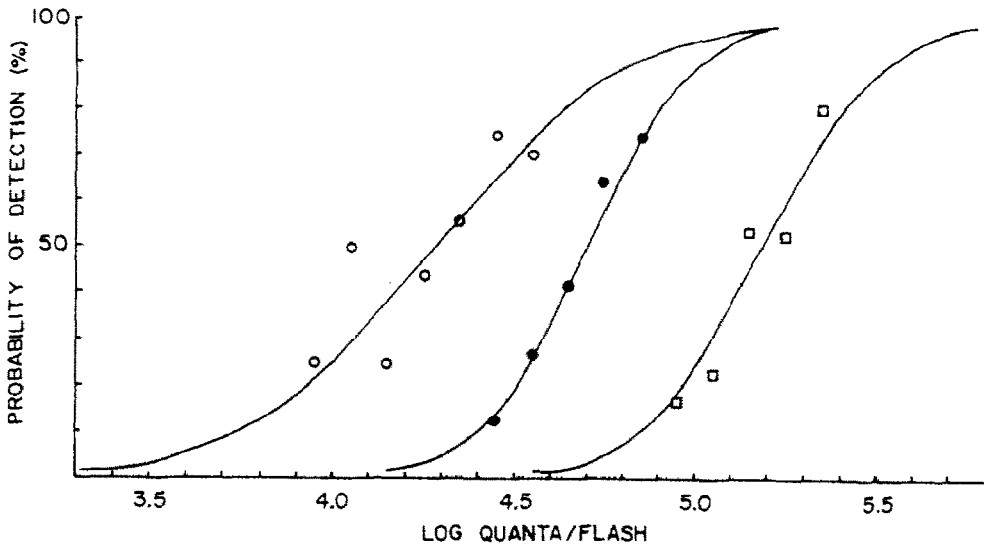

Fig. 10. Probability of detection (%) of a 1.1′, 420 nm test flash against a 2.6 log td, 4 deg, 584 nm background as a function of test flash radiance (log quanta/flash) for three retinal locations spaced 4′ apart on the superior vertical retinal meridian of M.M.H. Curves fit to the data were obtained by probit analysis. Only data points obtained from more than 6 flashes at a particular radiance are plotted. Open circles show the frequency of seeing curve for the sensitive spot at an eccentricity of 16′, bracketed on either side by relatively insensitive spots at 12′ (open squares) and 20′ (solid circles).

Results

Figure 10 shows the frequency of seeing data for the three retinal locations, 12′ (open squares), 16′ (open circles), and 20′ (solid circles) from the center of fixation. In agreement with the data collected using method of adjustment, the location at 16′ is much more sensitive than either the 12′ or 20′ locations. The threshold values are 5.18, 4.28 and 4.69 log quanta/flash for the 12, 16 and 20′ locations respectively (with SEM of 0.03, 0.05 and 0.03) compared with 5.26, 4.17 and 4.44 log quanta/flash for the same locations measured with method of adjustment about one month earlier. This procedure was repeated for three additional locations which crossed the point where the peak, found in the original measurements, had disappeared in the second set of measurements 2 yr later. In agreement with the more recent data, the peak was not evident.

These results establish that the B cone sensitivity peaks measured in this observer represent a fairly stable aspect of foveal organization. For example, the peak at 16′ in the superior fovea survived over 2 yr of testing, with two different test wavelengths, two different background wavelengths and retinal illuminances, three different psychophysical procedures for determining threshold, and two different fixation displays.

Observer A.L.N.

The double random staircase–random location method was used to map a 4 × 4 array of locations spaced 5′ apart in the inferior temporal fovea of A.L.N. A 1.1′, 25 msec, 436 nm test flash was presented against a 4 deg, 4.1 log td, 584 nm background. The stimulus display is shown at the right in Fig. 9. The 2 × 4 array of fixation squares could be moved to either of two locations (shown as solid and dotted lines in the figure) relative to the test spot in order to map a square array of 16 retinal locations. In a given session, only four of the eight visible fixation squares were used, either a single row of squares or a 2 × 2 array of squares with double random staircases at each fixation square. A session was completed when 50 flashes had been presented at each of the four test locations. All 16 locations were tested on each of 4 days with four sessions each day. The step size used for all staircases was 0.2 log units. Data from the first day of testing were discarded. The total number of flashes and the total number of "yes" responses at each intensity were summed over the last three days allowing frequency of seeing data to be plotted for each of the 16 retinal locations. Probit analysis was applied to the data (as described for M.M.H.); the resulting threshold values (50% frequency of seeing) were converted to log sensitivity by arbitrarily subtracting the log quanta/flash at threshold for each location from the threshold value at the test location closest to the fixation point.

Results

The upper numbers in Table 2 show the log sensitivity at each retinal location in the 4 × 4 matrix. Lower numbers in parentheses show SEM, which averaged 0.09 log units across all locations. Reliable differences in B cone sensitivity were found. As in the other two observers, sensitivity increases rapidly away from the center of fixation, corresponding to the absence of B cones in the foveal center. There is a

Table 2. Sensitivity values determined from frequency of seeing curves for A.L.N. for a 1.1′, 420 nm, 25 msec test flash presented against a 4.1 log td, 4 deg, 584 nm background. 0.0 equals 6.0 log quanta/flash. Numbers in parentheses represent the SEM.

0′		→ Temporal retina		
	↓ Inferior retina			
5′	0′	5′	10′	15′
10′	0.00 (0.25)	0.90 (0.07)	1.09 (0.08)	0.83 (0.14)
15′	0.79 (0.11)	1.57 (0.05)	1.40 (0.08)	1.22 (0.10)
20′	1.07 (0.13)	1.75 (0.05)	1.64 (0.08)	1.54 (0.07)
25′	1.11 (0.08)	1.45 (0.04)	1.49 (0.07)	1.50 (0.05)

reliable, but poorly defined peak near 5′ temporal, 20′ inferior in the retina with sensitivity declining slightly at eccentricities beyond the peak.

The four locations forming the diagonal through the location closest to the center of fixation were mapped a second time under G cone isolation conditions in two sessions, using a step size of 0.1 log units. The same test flash used in the B cone isolation conditions was presented against a 420 nm, 4.3 td background. The open squares in Fig. 2 demonstrate that this background did indeed isolate G cones. (The observer is somewhat more sensitive in the short wavelengths than Stiles' π_4 mechanism predicts but the same increased sensitivity is evident in measurements of the blue mechanism for this observer (open circles) suggesting that prereceptoral factors may account for the discrepancy.) The sensitivity values for the four locations along the diagonal starting with the location nearest fixation are 0.00, −0.04, −0.15, −0.17 showing a slight monotonic decrease in sensitivity with increasing eccentricity. This is quite unlike the dramatic rise in sensitivity observed under B cone isolation conditions showing that prereceptoral factors are not responsible.

There was a striking difference in the variability in detection of the test flash under B cone and G cone isolation conditions: B cone frequency of seeing curves were invariably shallower than their G cone counterparts. This difference is consistent with the notion that B cones are scarce since, due to eye movements, the small test flash would fall on or near a B cone only part of the time, falling between B cones the rest of the time. On this view one would expect the difference in slopes to disappear for test spots large enough to invariably include B cone or group of cones. However, one might aruge that B cones are well represented in these areas, attributing the difference in the slopes of the frequency of seeing curves to some intrinsic variability in the blue mechanism. If this hypothesis is correct, then increasing the size of the test spot is not likely to have an effect; the difference in the slopes of the frequency of seeing curves should persist.

Figure 11 shows the results of such a comparison for observer A.L.N. The 25 msec, 457 nm test flash was always centered on the most eccentric location in the map in Table 2 (15′ temporal, 25′ inferior). Frequency of seeing curves were obtained for small (1.1′) and large (15′) test flashes under B cone isolation (4.1 log td 584 nm background) and G cone isolation (4.3 td, 420 td, nm background) conditions. Each of the 4 frequency of seeing curves were obtained from 200 flashes presented in double random staircases in a single session. The step size for the small spot under B cone isolation conditions was 0.2 log units: in all other conditions it was 0.1 log units.

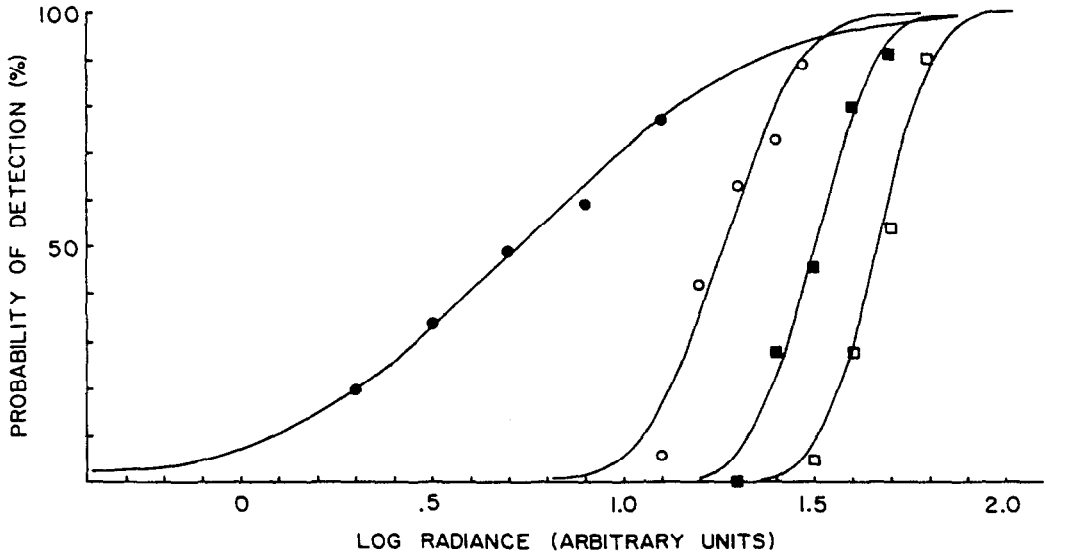

Fig. 11. Frequency of seeing curves for A.L.N. obtained with a 1.1′ test flash seen by B cones (solid circles), a 1.1′ test flash seen by G cones (open circles), and 15′ flash seen by B cones (solid squares), and a 15′ flash seen by G cones (open squares).

The left most curve in Fig. 11 (solid circles) shows the frequency of seeing curve for the small test flash under B cone isolation conditions; the open circles show the curve for the small test under G cone isolation conditions. Clearly, for the small test detected by B cones there is an abnormally wide range of uncertain vision. The standard deviation, sigma, of the cumulative normal probability function used to describe the frequency of seeing data, is a measure of the variability of detection of the test flash; large values of sigma correspond to shallow frequency of seeing curves. (The difference in log radiance between the 25% and the 75% points of the frequency of seeing curve is 1.349 times sigma.) For small spots, the value of sigma when the test is detected by B cones is 0.50 log units as opposed to 0.16 log units when it is detected by G cones. The curves fit through the solid squares and the open squares show the result when the large, 15′ test spot is detected by B and G cones respectively. The values of sigma for the large test under B and G cone isolation are nearly identical: 0.13 and 0.12 log units respectively. This result, which was also found in observers M.M.H. and D.R.W. shows that increasing the size of the test flash from 1.1′ to 15′ greatly reduces the variability in detection by the B cones, while hardly affecting that by the G cones at all. The simplest explanation of this difference is that the B cones, unlike their green-sensitive neighbors, are a small minority of the total cone population so that small spots stimulate them in a "hit or miss" fashion. This idea is developed further below.

DISCUSSION

The mapping techniques employed here proved to be very taxing for the observers, with meager information gained per person-hour. Setting thresholds by method of adjustment for the tiny violet test under B cone isolation conditions was particularly difficult due to the increased variability in detection (reflected by the shallow slopes of the frequency of seeing curves under these conditions). These flashes appeared both temporally and spatially diffuse; the observer was typically aware, if anything, of no more than the occurrence of some faint violet event, without clear contour or location and without distinct onset or offset. This was in marked contrast to the comparatively easy task of setting thresholds for the same wavelength test flash detected by G cones, in which case the flash near threshold appeared white and well defined.

All observers showed an abrupt rise in B cone sensitivity at an irregular distance roughly 15′ of arc from the center of fixation, presumably marking the edge of the B cone-free area. No hint of B cone response was found within this central zone supporting the conclusions of the previous paper (Williams *et al.*, 1981a).

In all three observers, the sensitivity of the B cones outside the B cone-free area is very uneven, revealing peaks and valleys in B cone sensitivity which in at least some cases are quite stable over long periods of time. These variations cannot be accounted for by an uneven distribution of some prereceptoral filter since they do not appear in maps of the same foveal area for the same wavelength test flash when it is detected by G cones. The peaks and valleys must be attributed to the blue-sensitive mechanism itself.

The stability of these variations in B cone sensitivity, particularly in the case of observer M.M.H. who was studied over a period of 2 yr, shows that, at least in some individuals, the center of fixation is a roughly constant retinal point. Had the center of fixation shifted by more than 1–2 min arc from session to session (or indeed from year to year) the steep gradients of B cone sensitivity would have produced much different patterns of sensitivity at the particular points where threshold was measured. The previously mentioned replicable sensitivity variation across the tiny clearing in D.R.W.'s macular pigment (Figs 4 and 6) also attests to the long term stability of fixation.

The most likely explanation for these local variations in sensitivity would seem to be that B cones are scarce in the retinal regions surrounding the central tritanopic area. The weight of the physiological evidence suggests that B cones are indeed scarce in the retina. First, the blue-sensitive pigment has proven stubbornly resistant to identification with retinal densitometry. Rushton (1962) failed to find evidence for the blue-sensitive pigment in the normal eye. Weale (1968) observed a light dependent change in fundal reflectance at short wavelengths which was absent in the central fovea, attributing it to B cones but other causes for it are not excluded. Alpern *et al.* (1971) appear to have detected a blue-sensitive pigment in a B cone monochromat, but the magnitude of the reflectance change due to B cone bleaching is not stated in their report. Unpublished measurements made by MacLeod with Rushton's densitometer do suggest an upper limit for the B cone signal in normals. After modifications of the densitometer which would have allowed detection of a 2% change in fundal reflectance in the violet, no sign of B cone bleaching could be found when bleaching of other cones was held constant. This difficulty in detecting the pigment with retinal densitometry means either that B cones are scarce or each B cone absorbs only a tiny fraction of the light that strikes it. Recent measurements suggests that the axial optical density of the blue-sensitive pigment in individual primate photoreceptors (Bowmaker *et al.*, 1979; see below) is 0.375 (assuming an outer segment length of 25 μ), which is about the same as that for the R and G cones. Since the blue-sensitive pigment is fairly concentrated in individual cones, the failure to find clear evidence for it with retinal densitometry must mean that B cones are scarce.

Evidence on the relative numbers of cone types from microspectrophotometry has consistently revealed fewer B cones than R or G cones. Marks

(1965) reported that in the goldfish there are only 10–20% as many B cones as R and G cones. In the early work of Marks *et al.* (1964) and Brown and Wald (1964) on primates, a total of 14 primate cones were measured, of which only 3 had peak sensitivities in the short end of the spectrum (445–455 nm). Bowmaker *et al.* (1979) have found a photolabile pigment with a peak absorptance at 420 nm in only 3 of 37 human cones and only 2 of 38 cones from Macaca fascicularis. They have not found a single short wavelength sensitive pigment in a sample of over 400 Rhesus cones.

The most direct physiological evidence for the scarcity of B cones in the primate comes from the work of Marc and Sperling (1977) (see also Sperling, 1978). They used the reduction of nitroblue tetrazolium chloride to stain B cones in the baboon retina during exposure to short wavelength light. Three to four per cent of cones in the central 1 deg of the fovea were B cones, corresponding to a mean angular distance between B cones of about 6′ of arc (uncorrected for shrinkage). B cone density increased to a maximum of 20% at an eccentricity of 1 deg, decreasing to 12–14% at 5 deg; nowhere in the retina was B cone density found to exceed that of either the R or G cones. Marc and Sperling point out that the distribution of B cones they found in the baboon agrees favorably with the distribution of ganglion cells with blue-sensitive receptive field centers calculated from the data of De Monasterio and Gouras (1975).

Our data for M.M.H. (the clearest case for the three observers investigated) show discrete peaks with a fairly even spacing of 8–12′ of arc, a spacing not much larger than the 6′ spacing reported by Marc and Sperling for the baboon foveola. We were not able to map enough of these peaks to make any certain statements about their arrangement, except that there is a suggestion that they might lie in an approximately rectangular array in this observer. These data support the conclusions of Marc and Sperling and extend them to man, with the proviso that, near the central fovea of at least some observers, the spacing is closer to 10′ than 6′ of arc. The data for D.R.W. and A.L.N. are not so clear, though they also show striking variations in sensitivity. The asymmetrical B cone sensitivity on opposite sides of the fixation point in D.R.W., for example, though not inconsistent with the scarcity of B cones, suggests that either B cones around the central tritanopic area are irregularly distributed, or that B cone sensitivity varies in different locations for other reasons as well. Poorer accuracy of fixation, poorer optical quality, and/or smaller B cone separation of the test flash might account for the failure to find such clear and discrete peaks as were found in M.M.H.

Punctate sensitivity model

When our results are considered in relation to estimates of the variability of the direction of gaze, it may seem surprising that such small scale spatial variation in sensitivity can be experimentally resolved at all. On the other hand, a quite contrary argument could also lead to scepticism about the identification of sensitive spots with individual B cones. Given that the average r.m.s. deviation in the direction of gaze sampled continuously over some period of time is only around 3.7′ of arc (Ditchburn, 1973; p.98) with horizontal and vertical standard deviations only 0.7 times this much,* one might intuitively expect that the mapping of tiny sensitive spots separated by almost 3 times this distance would be fairly easy, and that the peaks and troughs in sensitivity would be better defined than we have found them to be. The broad and shallow variations of sensitivity we have found might then suggest that the B cone sensitivity of the retina is truly continuous, rather than being characterized by tiny sensitive spots corresponding to single B cones separated by insensitive regions.

To decide between these opposing intuitions, we must consider quantitatively the influence of eye movements and image blur on our results. Are the differences in sensitivity between sensitive and insensitive spots consistent with truly punctate sensitivity as implied by the "single cone" hypothesis? And if so, are they also consistent with the competing hypothesis of continuous variation? The slopes of psychometric functions obtained with tiny test flashes detected by B cones are consistently very shallow; are the shapes of these functions consistent with the single cone hypothesis? How much does the statistical fluctuation in quantal absorption contribute to this large range of uncertain vision?

The effects of these factors were assessed using a Monte Carlo computer model as follows. The light distribution of the test flash was defined by the convolution of the 1.1′ test aperture with the point spread function of the eye (Vos *et al.*, 1976). An expression which adequately describes this radially symmetric light distribution is

$$I(d) = 0.234/(1 + 3d^{2.8})$$

where d is the distance in minutes of arc from the center of the light distribution and $I(d)$ is the local illuminance normalized such that the total volume beneath the distribution is unity.† B cones each with an effective light gathering area whose radius, r, was 0.25′ of arc were arranged in a rectangular array with an intercone distance of 10′ of arc (see Fig. 12). For a

* The horizontal or vertical standard deviation, not r_0, is what is tabulated in Ditchburn's Table 4.3. On page 380, Ditchburn equates the r.m.s. deviation with the horizontal or vertical standard deviation, but this is not correct unless the factor $\sqrt{2}$ is neglected.

† The true light distribution of the test flash used in the study can only be estimated. If a broader light distribution had been chosen in the model, the predicted frequency of seeing curves would have been steeper for a given value of the r.m.s. deviation in the direction of gaze and the differences in sensitivity between sensitive and insensitive spots would have been reduced.

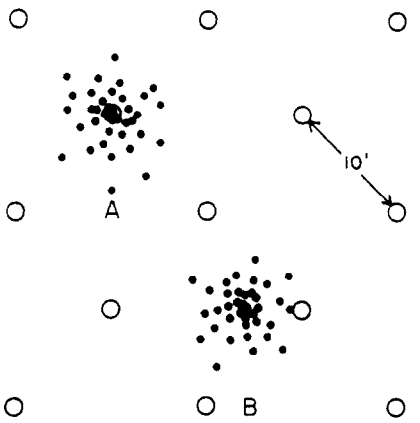

Fig. 12. Array of B cones in the punctate sensitivity model. B cones, shown as open circles, are spaced 10′ of arc apart in a rectangular array. In (A), the mean location from flash to flash of the center of the light distribution lies on a cone, whereas in (B) the mean location lies 4′ from the nearest cone. Dots represent the locations of individual test flashes which vary in accordance with the distribution of eye positions.

given location of the center of the light distribution relative to the receptor array, the number of quanta, N, caught by a given receptor at some distance from the center of the light distribution can be estimated by:

$$T\pi r^2 I(d)$$

where T is the total number of quanta delivered in the flash.* The separate quantum catches of each receptor were summed across all receptors to give the total quantum catch, consistent with evidence for the large summation area of B cones (Brindley, 1954; Wald, 1967; Williams *et al.*, 1981a, Fig. 3a).†

The model assumes two sources of noise or variability in the detection process: photon noise and variation in the quantum catch of the receptor array due to the variability in the location of the light distribution from flash to flash caused by eye movements. Thus the shallowness of the psychometric functions generated by the model, the predicted range of uncertain vision, will depend on the contributions of these two sources of noise.

The variability in quantal absorptions was incorporated into the model as follows: For a test flash at a given average intensity and location, the Poisson probability, P_n, that the actual quantum catch was equal to or exceeded the criterion number of quanta, n, required for detection given the average total quantum catch, a, of the receptor array for that flash location was computed with the Poisson expression (see Pirenne, 1956):

$$P_n = 1 - \sum_{x=0}^{n-1} \frac{e^{-a}a^x}{x!}.$$

A random number between 0 and 1 was then generated; if it exceeded the probability P_n then the flash was considered undetected, if it was equal to or less than P_n the flash was detected. The criterion number of quanta required for detection is difficult to estimate due to uncertainties about what fraction of light incident at the cornea is actually absorbed by photopigment. However, an examination of psychometric functions for large stimuli detected by B cones (whose slopes are presumably little affected by the local spatial variation in B cone sensitivity) can provide a lower limit on the number of quanta required for detection and, therefore, an upper limit on the contribution of photon noise to the range of uncertain seeing. For example, A.N.'s psychometric function for a 15′ test flash detected by B cones must require at least 10 quanta; if detection required fewer quanta than this, photon noise alone would produce a shallower curve than that observed.‡ A similar result was obtained on another observer (DRW). A criterion of 10 quanta was used in the model.

Eye movements were simulated by varying the location of the center of the light distribution in two dimensions from flash to flash such that the probability, P_i, of the center of the distribution falling at some location, (x_1,y_1) from its average location (x_0,y_0) was given by a bivariate gaussian distribution with

* The effects of preretinal absorption, absorption by macular pigment, and photopigment density are ignored by the model. Their only role, like the role of the effective light catching area of a single receptor, is to slide all the predicted psychometric functions uniformly along the log intensity axis without changing their shapes or relative positions.

† Since the light distribution of the test flash was small relative to the spacing of blue-sensitive cones in the model, the assumption of complete energy summation actually only requires summation between the four cones nearest the flash at the very most. A model based on the assumption that the receptors in the array are independent detectors produces similar results, the main difference being that sensitivity is reduced by 0.2 log units when the flash falls in a gap between receptors.

‡ This lower limit on the number of quanta required for detection is only valid provided the limits of spatial and temporal energy integration have not been exceeded, since Brindley (1963) has shown that for a given criterion for detection limited by a Poisson process the steepness of the psychometric function increases to some limiting slope as the number of detectors increases to infinity. The 50 msec, 15′ flashes used here probably do not greatly exceed these limits for B cones, if at all (see Brindley, 1954; Williams *et al.*, 1981a, Fig. 3a; Green, 1969; Kelly, 1974) making the 10 quantum lower limit on detection a reasonable one. It is worthwhile pointing out however, that even if the number of independent detectors beneath the flash were very large, A.N.'s frequency of seeing curve is still sufficiently steep to rule out detection on the basis of less than 4 quanta per detector. In this regard, the observed frequency of seeing curves are fairly similar to those of Marriott (1963) who claimed that cone detection requires at least 5 quanta. Even if detection required but 4 quanta per detector, other sources of noise which we attribute in our model to spatial variation in B cone sensitivity are sufficiently large to overwhelm the contribution from photon noise so that its impact on the slopes of the frequency of seeing curves is minimal.

zero covariance and an r.m.s. deviation, r_0. ($r_0 = \sqrt{2} *$ sigma, the standard deviation, in one direction).

$$P_i = \frac{1}{\pi r_0^2} \exp\left[\frac{-(x_1 - x_0)^2 - (y_1 - y_0)^2}{r_0^2}\right]$$

100 flashes were "presented" at each intensity level, which were graded in 0.1 log unit steps across the psychometric function. For each location and intensity, a deterministic computation yielded the expected number of absorbed quanta per presentation, a, and this value was used in the photon noise simulation described above.

Figure 13 shows psychometric functions predicted by the model; dashed lines correspond to frequency of seeing curves for different values of r_0, the r.m.s. deviation in eye position when the mean location of the center of the light distribution fell on a receptor; solid curves were obtained when the mean location of the light distribution was located 4′ from a receptor (see Fig. 12). These locations were chosen to determine whether the average sensitivity difference of 0.6 log units between a sensitive spot and a location 4′ of arc away found in M.M.H. is consistent with the punctate sensitivity model.

When the mean location of the light distribution is centered on a B cone, the position of the psychometric function along the log intensity axis shifts dramatically with the variability of eye position. As r_0 increases and flashes on the average fall further and further from the cone, sensitivity decreases and the psychometric function shifts to the right. When the mean location of the light distribution is in an insensitive region 4′ from the nearest cone, the psychometric functions, shown as solid lines, become slightly more shallow with increases in r_0 but hardly shift at all along the intensity axis. Thus as the variability of eye movements becomes greater the difference in sensitivity between sensitive and insensitive regions decreases until, for values of r_0 greater than about 0.5 times the spacing between cones, it makes little difference where the mean location of the test flash lies and the predicted curves are close to the curve labelled ∞ in Fig. 13.

In the model, the r.m.s. deviation in the direction of gaze which produces the 0.6 log unit sensitivity loss 4′ of arc from a sensitive spot is about 2.5′ of arc. This value is within the small range of values that have been measured during attempted continuous fixation (Ditchburn, 1973, p. 98). However, the value directly applicable to our experimental situation would be one based on samples taken just when the observer believes himself to be fixating accurately. We know of no estimates of this. Another peculiarity of our experimental situation is that it makes demands on long term stability of fixation; but only short term stability (over periods on the order of 1 min) has been measured. Our results imply that the long term stability of fixation can be impressively precise, with standard deviations not greater than a few minutes of arc. Over the 2 yr during which data on M.M.H. were collected, the image of her point of regard must usually have been included within a fixed group of less than 100 cones.

The punctate model generally predicts shallow slopes for the psychometric functions, particularly

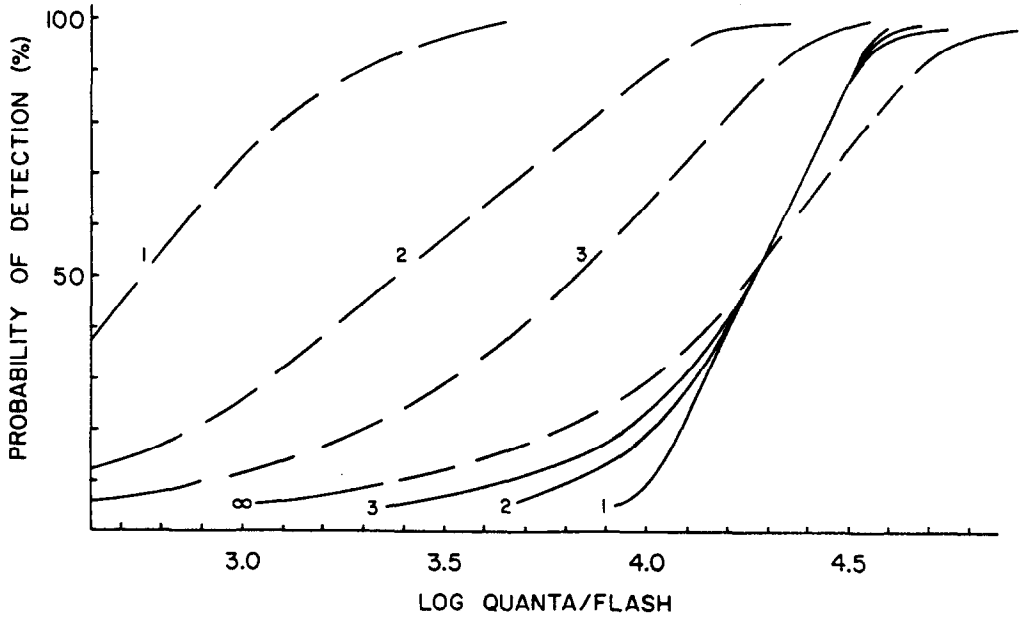

Fig. 13. Frequency of seeing predicted by the punctate sensitivity model as a function of the log number of quanta per flash. The criterion for detection was 10 quanta caught by the receptor array. Dashed curves represent psychometric functions for various values of the r.m.s. deviation in the direction of gaze, indicated next to each curve when the mean location of the test flash lay on a receptor. Solid curves represent psychometric functions when the mean location of the flash lay 4′ of arc away from a receptor.

when the mean location of the test is on a sensitive spot. This is borne out in the observed psychometric functions for M.M.H. (Fig. 10) and a value of r_0 of 2.5 predicts curves whose shapes are reasonably well fit by these data, though the data do not distinguish well in the tails of the curves where the predictions of the model for different values of r_0 differ most.

It is worth noting that the absolute blue cone sensitivity predicted by the punctuate sensitivity model using a criterion for detection of 10 quanta caught is consistent with the observed absolute sensitivity for M.M.H. For example, the threshold (probability of detection = 50%) obtained for the sensitive spot in Fig. 10 (open circles) was 4.28 log quanta/flash. Assuming a value of 2.5′ of arc for the r.m.s. deviation in the direction of gaze, the model predicted a threshold value of 3.66 quanta/flash (Fig. 13) which allows 0.6 log units of preretinal absorption, absorption by macular pigment (which is very small for this observer), and light loss within the photoreceptor. The agreement between the observed absolute sensitivity and that predicted by the model is remarkably good given the uncertainties about the light distribution of the test flash, the true distribution of eye movements, and the light-gathering area of a blue cone. High absolute sensitivity may be another property that blue cones share with rods. Barlow (1957) has pointed out that a receptor mechanism sensitive to the higher energy quanta at short wavelengths might be less susceptible than a long wavelength-sensitive mechanism to the noise producing effects of thermal decomposition, increasing its absolute sensitivity. Thus it may be reasonable to suppose that 10 quanta caught within the integration area of the blue mechanism is sufficient for detection.

The model's estimate of fixation variability needed to reconcile the observations with the punctate sensitivity hypothesis is so small as to discriminate heavily against the competing hypothesis that sensitive spots are only the peaks of a spatially continuous and gradual variation of retinal sensitivity. This hypothesis can only be correct if the accuracy of fixation is substantially better than indicated above. This seems unlikely but cannot be ruled out. The only viable alternative to the single cone hypothesis would be one in which the sensitive spots are isolated compact clusters of B cones. The successful prediction of variability in the detection of small B cone test flashes provides further support for the punctate sensitivity hypothesis, and indeed it is hard to account for the variability in any other way. This analysis therefore supports the identification of sensitive spots with single B cones (or clumps of them) that are separated by large stretches of retina lacking these receptors. It also shows why the locations of sensitive spots are difficult to demonstrate convincingly in some observers and perhaps in other retinal areas. The results of Marc and Sperling suggest that the spacing of B cones may often be less than 10′, and in any case the ability to fixate with a standard deviation of only about $\frac{1}{4}$ of the intercone distance may not be common. Greater variability, or smaller separations, rapidly reduce the expected differences in sensitivity to a point where they are difficult to demonstrate.

It is not clear to what extent the evidence for the scarcity of B cones in the central fovea reported here can be extrapolated to the eccentric retina; the scarcity of rods in the fovea certainly doesn't imply their scarcity in the eccentric retina. According to the careful histology of Osterberg (1935), the first "straggler" rods appear at a distance of 130 μ (″26 of arc) from the foveal center. But their density gradually increases until, at an eccentricity of 20 deg, they represent over 96% of the photoreceptors. However, the data of Marc and Sperling show that at an eccentricity of 10 deg in the baboon retina the B cone density is nearly the same as it is in the fovea. We tried some mapping experiments at this eccentricity but were hampered by habituation effects (and perhaps torsional eye movements). However, similar to the results found in the central fovea, frequency of seeing curves for observer D.R.W. were shallower when the test flash was detected by B cones than when it was detected by G cones, providing some support for the notion that B cones are sparse in the eccentric retina as well.

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