A STUDY OF SENSITIVITY GRADIENTS AND SPATIAL SUMMATION IN THE NORMAL

RETINA BY STATIC CHROMATIC PERIMETRY WITH PHOTOMETRICALLY-EQUATED

STIMULI UNDER FULLY-PHOTOPIC AND FULLY-SCOTOPIC CONDITIONS

by

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Abstract

A study was conducted to investigate the sensitivity and
spatial summation properties of the normal retina under fully-
photopic and fully-scotopic conditions, using photometrically-
equated chromatic stimuli of four sizes. Fully-photopic
adaptation yielded equivalent sensitivity gradients extra-foveally
but different foveal thresholds for the red, green and blue
stimuli. The extra-foveal scotopic sensitivity gradients were
similar in form but different in height for the chromatic stimuli,
while all stimuli excepting the smaller red ones yielded "relative
scotomata" at the fovea. Spatial summation was shown to increase
with eccentricity and decrease with increasing stimulus size under
fully-photopic but not under fully-scotopic conditions, but was
found in general to be greater under scotopic adaptation.

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The author would like to extend her thanks to the people who contributed so much to the development of this thesis:

INTRODUCTION

Determination of Retinal Sensitivity Gradients by Perimetric Methods

Static Perimetry. Light-sense perimetry, the investigation of the sensitivity of the visual system to light in specific locations in the visual field, can be done using static or kinetic presentation of stimuli. According to Traquair's (1927) representation of the visual field as a three-dimensional 'hill', kinetic perimetry (in which a constant-luminance target is moved centrally until it is seen) represents the process of obtaining horizontal bearings (isopters), while static perimetry (in which a stimulus is presented at one retinal point and increased in luminance until it is seen) represents the process of obtaining vertical soundings (profiles) (Aulhorn & Harms, 1972). Static perimetry yields more precise, definable information in a shorter period of time than does the kinetic method. For an experimental investigation, it is important that factors which could influence the outcome variable be controlled or at least precisely specified. In kinetic perimetry, the moving stimulus complicates interpretation of the data obtained as thresholds, because temporal and spatial summation are implicated in a complex, interactive manner. In static perimetry, invariant stimulus duration controls for temporal summation effects (Aulhorn & Harms, 1972), so that spatial summation can be studied independently using a range of stimulus sizes. Kinetic perimetry is also limited in the kind of information obtainable. For example, the 'depth' or relative loss of a scotoma could not be precisely specified (Sloan, 1961) nor could the 'relative central scotoma' reported for

short-wavelength stimuli (Verriest & Israel, 1956a, 1956b) be demon-
strated, with kinetic perimetry. Static perimetry is, by contrast, a
precise method yielding objectively-specified threshold values for any
part of the visual field. The threshold values so obtained can be com-
pared among stimuli of different chromaticities, sizes, and eccentricities.

Chromatic Perimetry. Most perimetric research has been done with
achromatic stimuli, where objective specification of stimulus size,
duration, colour-temperature, and luminance are required. Chromatic
perimetry did receive some early research attention (for example,
Ferree & Rand, 1919; Wentworth, 1930). However, in much of the early
work objective specification of stimulus conditions was deficient, so
that the criticism was made that chromatic perimetry did not give
additional information to that already yielded by achromatic perimetry
(Dubois-Poulsen, 1952). With the advent of the Goldmann (Goldmann,
1945a, 1945b) and Tübinger (Harms, 1960) hemispheric perimeters, peri-
metry in general began to develop as a precise method in which experi-
mental conditions could be objectively specified and thus meaningful
psychophysical data could be obtained. As a result chromatic perimetry
regained respectability as a useful, precise method, and has been
investigated extensively by Verriest and his associates (Verriest &
Israel, 1965a, 1965b; François, Verriest, & Israel, 1966; Verriest &
Kandemir, 1974; Verriest & Uvijls, 1977a, 1977b) as well as by others
(e.g., Nolte, 1962; Hansen, 1974; Carlow, Flynn, & Shipley, 1976).

Static perimetry with chromatic stimuli can yield two types of
thresholds, the achromatic and the chromatic. The achromatic threshold
is defined by the ΔL required for the subject to detect the stimulus,

whether or not he perceives its colour. The chromatic threshold, which
is generally higher than the achromatic at extra-foveal locations, is
defined by the ΔL required for the subject to perceive (and report)
the colour of the stimulus. For a number of reasons, it was the
achromatic threshold which was of interest in the present investigation.
The chromatic threshold shows greater variability than does the achro-
matic (Aulhorn & Harms, 1972). This is to be expected, as it depends
on psychological variables, such as how long the subject waits to be
certain of the hue and how many choices he has (i.e., how many possible
colours). The complexity of the subject's task in chromatic threshold
determination would thus necessitate an extended training period.
Also, because hue differences can be detected with no luminance dif-
ference, determining a chromatic threshold against a background of
different chromaticity may actually represent hue-difference threshold
determination (Aulhorn & Harms, 1972). Since the achromatic threshold
determination presents a simple task to the subject, and retinal
gradients of achromatic thresholds indicate the relative light-sensi-
tivity across the retina, achromatic thresholds were determined in the
present investigation.

Objective specification of stimuli becomes a far more complex
problem, both theoretically and practically, with the change from
achromatic to chromatic perimetry. The specifications necessary for
achromatic stimuli—size, colour-temperature, and duration—must be
standardized if increment thresholds obtained at different retinal
locations for achromatic stimuli are to be directly compared. Such
precise specification is relatively easy to obtain, and much information

has been gained concerning the sensitivity of the visual system to achromatic stimuli as a function of retinal location, stimulus size, background luminance, and subject age (e.g., Lakowski & Aspinall, 1969; Verriest & Uvijls, 1977a; Aulhorn & Harms, 1972). However, if stimuli are to differ in chromaticity, a decision must be made on how such stimuli are to be equated. Two methods are possible, each implying different assumptions about what the obtained thresholds represent. Increment thresholds to stimuli of varied chromaticity can be considered equal in terms of radiant energy or of luminance.

Radiometric equivalence of chromatic stimuli in perimetry has been advocated as the appropriate method by many researchers (e.g., Ferree & Rand, 1919; Dubois-Poulsen, 1952; Aulhorn & Harms, 1972). It is suggested that such physical energy specification of stimuli is more appropriate than photometric specification because the spectral sensitivity of the fovea (i.e., V_λ) is not representative of the spectral sensitivity over the entire retina (Aulhorn & Harms, 1972). However, with radiometric equalization, the one standard with which perimetric data can be compared is lost: the invariant foveal threshold. Radiometric equivalence of chromatic stimuli results in high foveal thresholds for blue and red stimuli relative to that for green (and 'white'-- achromatic) stimuli; this merely reflects V_λ. Once outside the fovea, different thresholds for the chromatic stimuli then reflect not only differences between foveal and extra-foveal sensitivity, but also the relative luminous efficiency which is known to characterize the fovea. This confounding influence can be illustrated by referring to Figure 1, which shows Nolte's results using monochromatic stimuli specified
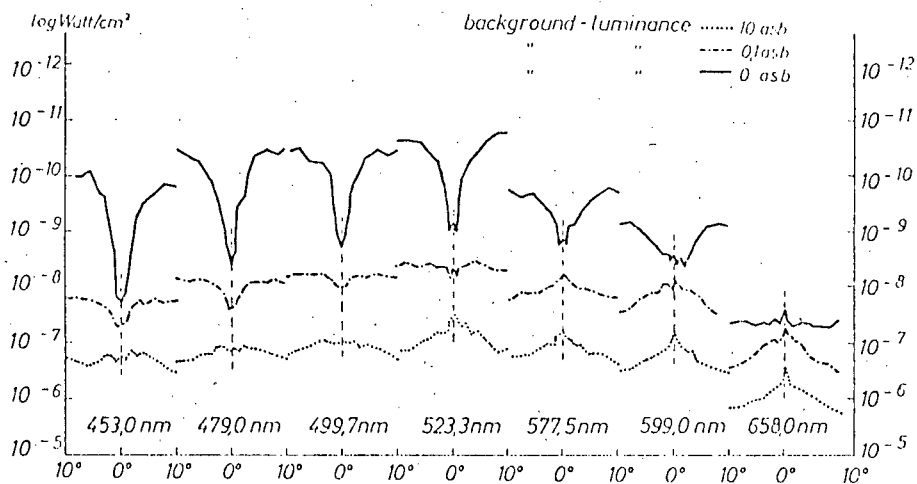
Achromatic thresholds in the central and paracentral regions of 0° meridian of retina. Coordinates: as in Fig. 16. Upper curves obtained with complete dark adaptation, middle curves with adaptation to 0.1 asb background luminance and lower curves with adaptation to 10 asb background luminance (according to Nolte)

Figure 1   (from Aulhorn and Harms, 1972)

radiometrically. A curve could be drawn through the foveal threshold

points for the seven selected wavelengths; this curve in general form

reflects V_λ. Since V_λ is well established, if its influence were

removed (by photometrically equating the stimuli), the foveal thresholds

would then coincide, and perimetry would delineate the changes in sen-

sitivity as a function of retinal position for stimuli of varied

chromaticity.

A number of investigators have specified their stimuli and made

their measurements photometrically (e.g., Verriest & Israel, 1965a,

1965b; Ronchi, 1972), but photometric equivalence was not employed.

With the initial modifications of the Goldmann perimeter used in the

present investigation, photometric-equivalence was achieved and the

first chromatic perimetric results based on photometrically-equated

stimuli were reported (Lakowski, Wright, & Oliver, 1976, 1977). With

such equivalence, the stimuli are equated at the fovea, so that a

standard is established to which extra-foveal sensitivity can be com-

pared.

Once photometric specification has been decided upon, it remains

to be decided how the stimuli to be presented under scotopic conditions

are to be equated: in terms of V_λ or V'_λ (the scotopic luminous effi-

ciency curve). The use of V_λ to equate all stimuli at the fovea has

the major advantage that photopic and scotopic adaptation results can

be more directly compared if both are based on the same luminous

efficiency curve. The fact that all equating has been done in terms of

V_λ and therefore of the fovea must be considered when interpreting

results obtained in this manner.

Adaptation. Increment thresholds are influenced by the ambient luminance in a complex manner, presumably due to differential contributions of the rod and cone systems at scotopic, mesopic, and photopic levels. Photopic vision has generally been considered to begin at 10 cd.m.$^{-2}$ (LeGrand, 1957), although this value depends on the stimulus size. Adaptation luminance of 10 cd.m.$^{-2}$ has been widely used in perimetric studies (e.g., Verriest & Israel, 1965a, 1965b; Lakowski & Aspinall, 1969; Carlow et al., 1976). However, the original work of Goldmann (1945c), on which the specifications for the widely-used Goldmann perimeter are based, proposed the use of 40-45 asb (12.7 - 14.3 cd.m^{-2}) as the adaptation luminance. This value was chosen to fall in the middle of the range of luminances found in doctors' examining rooms (Goldmann, 1945c). At these adaptation luminances (10, 12.7, or 14.3 cd.m.$^{-2}$), both rod and cone systems are active (Aguilar & Stiles, 1954), so that it is difficult to draw conclusions concerning the function of either.

If an attempt is made to study these two systems separately, it is necessary to consider whether the two systems are to be dealt with as completely separate or as a continuum from scotopic to photopic. There is no clear-cut solution to this problem. Sufficiently high adaptation luminance can achieve rod saturation (Aguilar & Stiles, 1945) so that fully photopic thresholds can be assumed to be rod-free thresholds. However, fully scotopic conditions do not guarantee that thresholds obtained under such conditions are cone-free thresholds. "Fully scotopic" refers to the condition wherein the threshold--that is, the absolute threshold--changes minimally over time. This occurs

only when the retina is fully dark-adapted. Thresholds obtained under

such conditions would presumably be cone thresholds in any retinal

location which had no rods--that is, in the foveola. One would expect

then that beyond the 54-minute-of-arc extent of the foveola (Moses,

1975), any fully scotopic thresholds would reflect rod sensitivity.

Data reported by Sloan (1950) support this (see Figure 2). Using

dark-adaptation methods, she found that for an achromatic (Illuminant

'C') stimulus subtending one degree of visual angle, rod thresholds

were lower than cone thresholds at all points tested except the fovea.

The eccentricities investigated ranged from 50° nasal and 90° temporal

to 3.5^{o} from the fovea, in the horizontal meridian. As was expected,

no rod component was seen in the dark-adaptation curve obtained at the

fovea. These results would seem to indicate, then, that for an

achromatic stimulus of 1° (or, presumably, smaller), thresholds obtained

under fully-scotopic conditions may be assumed to be cone-free thres-

holds to at least within 3.5^{o} and probably closer to the foveal centre.

Foveal thresholds obtained under these conditions would appear to be

cone thresholds. Whether these results would be duplicated with

stimuli of selected chromaticity is not known. This discussion will,

therefore, be restricted to references to fully photopic and fully

scotopic conditions; the former can be considered to refer specifically

to rod-free functioning, while the latter must be interpreted in a

more restricted sense.

(a) Specific review of relevant research. Fully-photopic

perimetry requires saturation of the rod mechanism, which occurs with

a retinal illumination of 2,000 to 5,000 scotopic trolands, corresponding
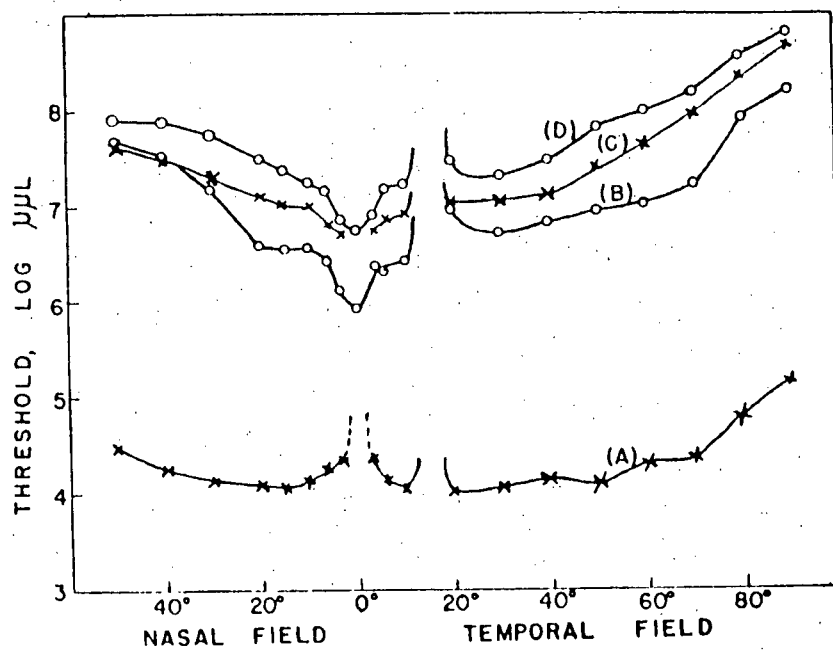
(Sloan). Retinal threshold gradients for the horizontal meridian. (A) Rods: dark adaptation. Cones: dark adaptation. (C) Rods: adaptation to 0.7 ml. (D) Cones: adaptation to 0.7 ml.

Figure 2   From Sloan, 1950, p. 1081.

to 120 to 300 cd.m.$^{-2}$ with a natural pupil (Aguilar & Stiles 1954).

1. Verriest and Kandemir

There has been no data reported for sensitivity gradients estab-

lished under conditions of complete rod saturation. Verriest and

Kandemir (1974) did obtain foveal thresholds for monochromatic stimuli

against a background of 132 cd.m.$^{-2}$ (Illuminant 'A'), just within the

lower limit of rod-saturation found by Aguilar and Stiles (1954).

They used five 116' stimuli ranging from 500 to 600 nm, and thus did

not obtain any results with a stimulus in the blue portion of the spec-

trum. Their results are shown in Figure 3. They found that the foveal

threshold value, expressed in radiometric units, was lowest for green

stimuli (λ = 528, 553 nm), higher for red (λ = 600 nm), and still

higher for blue-green (λ = 500 nm). The relative values of these

thresholds reflect the relative spectral luminous efficiency of the

fovea. According to the CIE standard photopic relative spectral

luminous efficiency function (V_λ), the foveal sensitivity to these

wavelengths follows the same relative pattern: highest sensitivity

to the green, lower to the red, and still lower to blue-green. This

would seem to indicate that the relative spectral sensitivity of the

fovea under fully-photopic conditions is similar in form to that

specified by the CIE V_λ function. This is interesting in view of the

fact that the V_λ curve was obtained under conditions in which the

retinal illumination never reached 100 trolands (LeGrand, 1968), indi-

cating an adaptation luminance of about 10 cd.m.$^{-2}$. The small size

of stimulus used to determine V_λ (2°; Wyzecki & Stiles, 1967) was

presumed to restrict the measurements to cones. This is supported by
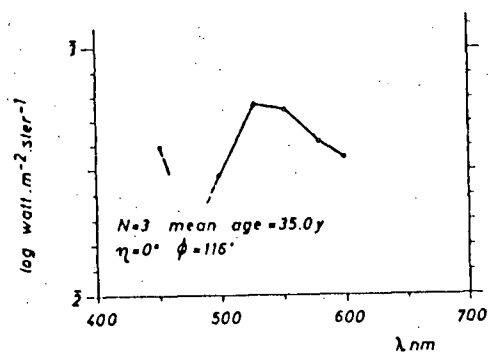
Figure 3   Mean foveal thresholds (log sensitivity
vs. wavelength).   Adaptation= 132 cd.m.$^{-2}$, stimulus
size = 116', achromatic stimulus (C.I.E. Illuminant A)
From Verriest and Kandemir, 1974, p. 5.

the similarity of the relative values of Verriest and Kandemir's

thresholds obtained with sufficient luminance to approach rod satura-

tion. If the relative spectral sensitivity of the fovea is truly

independent of adaptation, one would expect that (provided all other

variables are held constant) foveal thresholds for a given wavelength

would not vary with adaptation luminance. Unfortunately, the above

proviso is seldom met, so that comparison, for example, between

Verriest and Kandemir's data and the V_λ date can only be in relative,

descriptive terms. Nonetheless, if V_λ does hold under 'fully' photopic

adaptation, it would be expected that photometric-equating of chromatic

stimuli in terms of V_λ would yield equivalent foveal thresholds at

fully photopic conditions.

One further aspect of Verriest and Kandemir's investigation war-

rants mention: they used a light source with the spectral distribu-

tion of Illuminant 'A' to achieve the adaptation of 132 cd.m.$^{-2}$.

The low energy of this source in the shorter wavelengths may have meant

that not all response systems of the eye were under fully-photopic

conditions.

2. Sloan

Sensitivity gradients for achromatic stimuli under fully scotopic

conditions (dark adaptation) have been reported by Sloan (1939, 1947,

1950). She used a 1° square, CIE Illuminant 'C' stimulus which was

presented for one second. Her investigation took the form of dark

adaptation curve determinations, and thus involved ascending and des-

cending stimulus presentations. Figure 4 shows the sensitivity gradient

for a normal eye determined in this way; Figure 5 shows curves for the
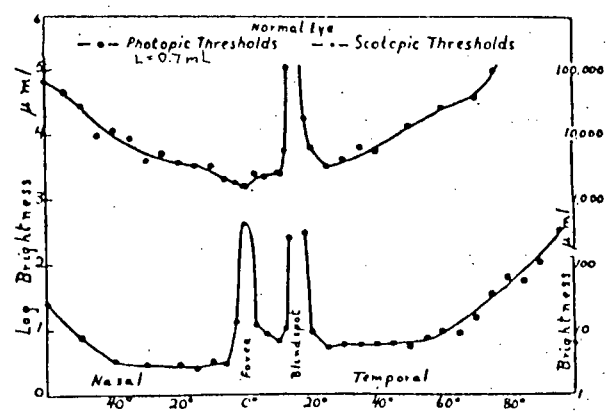
Photopic and scotopic thresholds in the horizontal meridian of a normal eye.

Figure 4 From Sloan, 1939, p. 240.
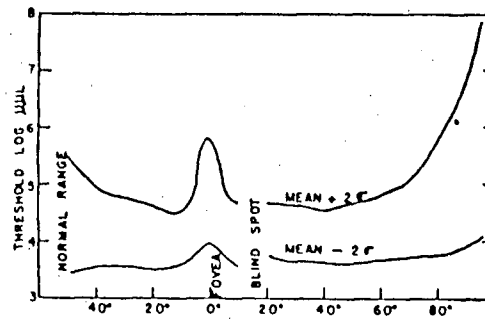
Figure 5   From Sloan, 1947, p. 708.

mean gradient (N = 101) plus or minus 2 standard deviations.

Several points can be made about these results. First, it is apparent that the scotopic sensitivity to this stimulus is highest in the mid-periphery, falling off rapidly at the fovea and more slowly in the periphery. This relative drop at the fovea has been referred to as a relative central scotoma. When using this term, it is important to keep in mind that is does not imply a loss of sensitivity at the fovea; the fovea simply does not show as large a gain in sensitivity as other retinal locations under scotopic conditions.

The second notable aspect of Sloan's data is the wide variability in sensitivity indicated by Figure 5. The reasons for this wide variability are not easily identified. The fact that the data is based on subjects from 14 to 70 years of age is likely a contributing factor, as age has been shown to influence retinal sensitivity (Lakowski & Aspinall, 1969; Verriest & Uvijls, 1977a). As well as the age factor, whether or not the variability reflects actual variation in the normal light sense is obscured by the lack of precise control of fixation under fully scotopic conditions. Provided there is some light illuminating the subject's eye, the experimenter can monitor fixation continuously throughout the testing and disregard responses made when fixation was not maintained. If, however, conditions of complete dark-adaptation prevail, unless an infra-red light-sensitive fixation monitor is used, the experimenter must rely on the subject's subjective impression that he is fixating precisely.

Sloan, as well as others who have reported scotopic sensitivity gradients, did not monitor fixation, but relied on the subject's report

that he was fixating. Thus, it is not possible to tell whether the variation she observed was due entirely to variance in the light-sense or was partially the result of losses of fixation. The large foveal variation is particularly suspect in this regard. If, indeed, the foveal sensitivity is greatly and sharply reduced from that of adjacent areas, any small shift of fixation would yield a much higher sensitivity. This may be seen in Figure 6. If the foveal threshold is actually at the value $\underline{a}$, a fixation shift of 2^O would yield a 'foveal' threshold of $\underline{b}$, which might be as much as 0.5 to 1.0 log unit lower (more sensitive) than $\underline{a}$. As the literature to date indicates that such a foveal "relative scotoma" does exist (Sloan, 1939, 1947, 1950; Nolte, 1962; Wentworth, 1930), control of foveal fixation would appear to be an exceedingly important aspect of scotopic threshold determination.

Returning to Sloan's work, it is important to note that for foveal fixation, she used a 6° diameter pattern of four radium-painted dots, into the centre of which the 1^O square stimulus was projected. The possibility of fixation shifts cannot be ruled out as a factor in the wide variability in the foveal thresholds determined. More importantly, the actual value of the foveal threshold cannot be specified with any certainty. There appears to be a natural tendency under scotopic conditions, to shift fixation until the stimulus image falls on a more sensitive paracentral area of the retina. It is obvious that the only solution to this problem would be to directly monitor fixation throughout scotopic threshold determination. Unfortunately, this presents considerable methodological problems, and has not been done in any of
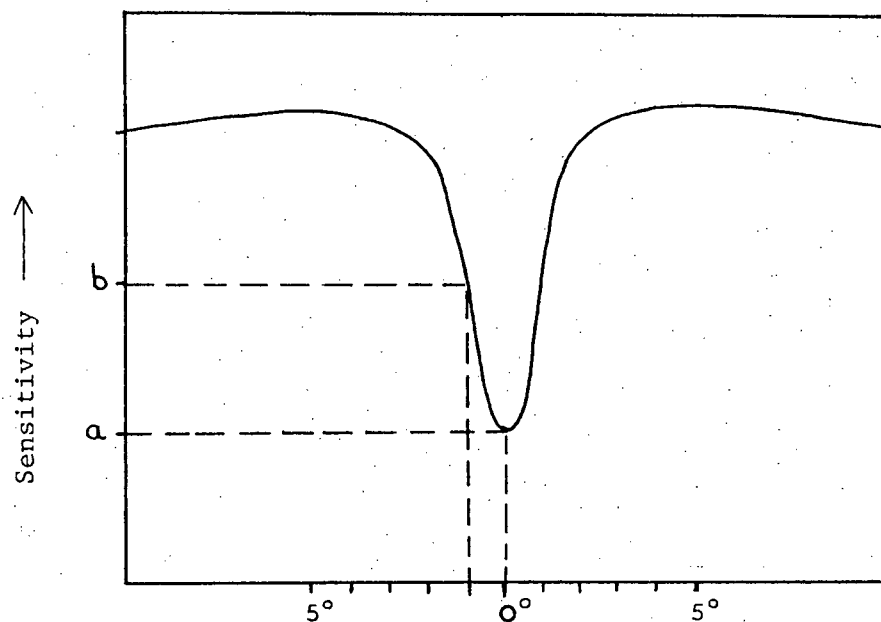
Figure 6 Hypothetical graph of retinal sensitivity
vs. eccentricity under fully-scotopic conditions.
Refer to text for explanation.

the scotopic perimetric studies reported thus far.

Aside from the highly variable foveal thresholds, Sloan's data also indicate considerable variation in the threshold obtained right across the 0°-180° meridian, this variability being greatest in the far periphery, and decreasing as eccentricity decreases. Aulhorn and Harms (1972) report similar results, except that their minimum variation was found at 0° as opposed to the large variation at 0° found by Sloan. As was pointed out, the foveal thresholds under scotopic conditions are very unreliable, so that this difference between the two studies is difficult to interpret. Aulhorn and Harms found this same variability pattern under other adaptation conditions (wherein fixation was presumably monitored), except that the magnitude of the variations tended to decrease as adaptation luminance was increased from 0 to 100 apostilbs. Using dark adaptation methods, Lakowski, Drance, & Goldthwaite (1976) also found smaller variations in foveal as opposed to peripheral thresholds.

3. Wentworth

Wentworth (1930) obtained scotopic sensitivity gradients on the 0°-180° meridian for various $1^o16'$ monochromatic stimuli (λ = 672.5, 581.5, 522, and 468 nm). Her data is all based on one subject, and a foveal fixation device fitted precisely to this subject was used. This consisted of a pattern of four radium-painted dots so positioned as to fall within the subject's blind spot only when she was fixating correctly. Foveal threshold data was collected only when these four dots disappeared from her view. For other retinal points, a similar pattern of four dots of radium-paint subtending 2° was used which

would disappear (due to the 'relative central scotoma') when fixation

was correct.

Wentworth's results are reported in radiometric units. It would

be expected, then, that the foveal sensitivities would be in the order

of 581.5 (yellow) > 522 (green) > 468 (blue) > 672.5 (red), as this

is the order of spectral efficiencies for these wavelengths as specified

by V_λ (Stiles & Wyszecki, 1967). This was not found; the foveal sensi-

tivity order was green > blue > yellow > red. This is rather surprising,

particularly as the blue and green foveal sensitivities were almost

identical, in spite of the fact that V_λ gives a ratio of 1:9 (468:522

nm) for the relative spectral efficiencies of these wavelengths. The

fact that the stimulus used subtended $1^\circ 16'$ of visual angle implies

that the 'foveal' threshold may not be strictly a rod-free threshold,

and the order of foveal spectral sensitivities obtained might reflect

V_λ' rather than V_λ. The results appear to support this: the relative

spectral efficiencies of these wavelengths according to V_λ' are green >

blue > yellow > red, the same order as was obtained for sensitivities.

It would seem that Wentworth's foveal thresholds can be interpreted

as rod thresholds, assuming the rods present within 68' of the foveal

centre are more sensitive than the cones under fully scotopic condi-

tions. It is also important to note that the monochromatic stimuli

used were produced by a spectroscope with a constant slit width (1.05

mm). This would result in different amounts of energy reaching the

eye for different wavelengths, as more short-wavelength energy would

be sampled by a given slit-width than long-wavelength energy. This

would then represent yet another variable influencing the thresholds

obtained for the different chromatic stimuli.

Considering now the entire sensitivity gradients obtained by Wentworth (see Figure 7) wherein sensitivity is plotted as a function of eccentricity, shows that at all retinal points tested, the highest sensitivity was to the green and the lowest was to the red stimulus. The foveal relative sensitivity order (green > blue > yellow > red) is not precisely reflected peripherally, where the order is green > yellow > blue > red. The apparent reversal of the yellow and blue in the order of sensitivities between the central and peripheral field may not be significant, as the magnitude of the difference at the fovea is small (.46 log units) as compared to that in the periphery (Figure 7). For all stimuli, a similar trend to that found for an achromatic stimulus (Sloan, 1939) is seen: maximal sensitivity in the mid-periphery, falling off rapidly at the fovea, and more slowly in the far periphery. The separation of the gradients for the different chromatic stimuli presumably reflects differences in the dark-adapted retina's sensitivity to stimuli of different spectral composition. Whether these peripheral spectral sensitivity differences are the same as those of the fovea is obscured by the fact that the stimuli were not photometrically equated.

As with Sloan's data, it must be kept in mind that the validity of Wentworth's results depends on whether fixation was correctly maintained during all measurements. Although her techniques for ensuring fixation would seem more accurate than any others thus far reported, Wentworth still relied on a subjective impression of stable fixation rather than an objective measure.
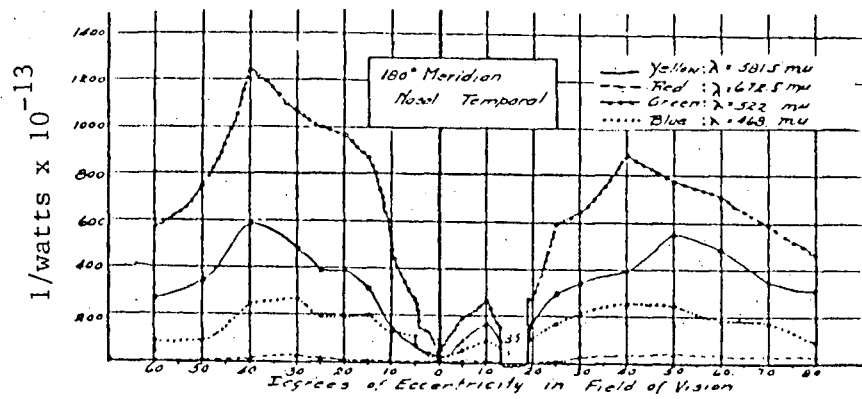
Figure 7 Achromatic sensitivity to spectrum lights under dark adaptation. From Wentworth, 1930, p. 21.

4. Nolte

In 1962 Nolte used the Tübinger perimeter to obtain scotopic

sensitivity gradients on the 0°-180° meridian to monochromatic

stimuli subtending 30' of visual angle. His data are based on three

subjects, using stimuli of seven wavelengths from 453 to 658 nm.

Figure 8 shows the 10° nasal-0°-10° temporal segments of the gradients

he obtained. Once again, radiometric specification of stimuli has been

used, and the relative values of the foveal thresholds reflect the

form of the V_{λ} curve, with the foveal sensitivity to λ = 523.5 nm

being highest and that to λ = 658 nm the lowest.

Nolte compared his results to Wentworth's (Figure 9). The major

discrepancies between the two sets of data are as follows. First,

Wentworth's sensitivity gradients are all higher than Nolte's and this

increased sensitivity is not uniform across the retina, being greatest

in the periphery and smallest in the central and paracentral areas.

This presumably reflects the difference in size of stimuli used;

Wentworth's stimuli were approximately 2½ (2.53) times as large as

Nolte's. The increased sensitivity to the larger stimuli reflects

the spatial summation capacity of the retina, and the greater increase

seen in the periphery indicates a higher capacity for spatial summa-

tion there. The second major difference between Wentworth's and

Nolte's results is in the foveal sensitivity to long wavelengths.

While Wentworth found a relatively lower sensitivity in the fovea to

all stimuli including the red one (λ = 672.5 nm), Nolte did not find

this foveal 'dip' at the longest wavelength used (λ = 658 nm), though

he did find one for λ = 599 nm. It seems unlikely that the stimulus
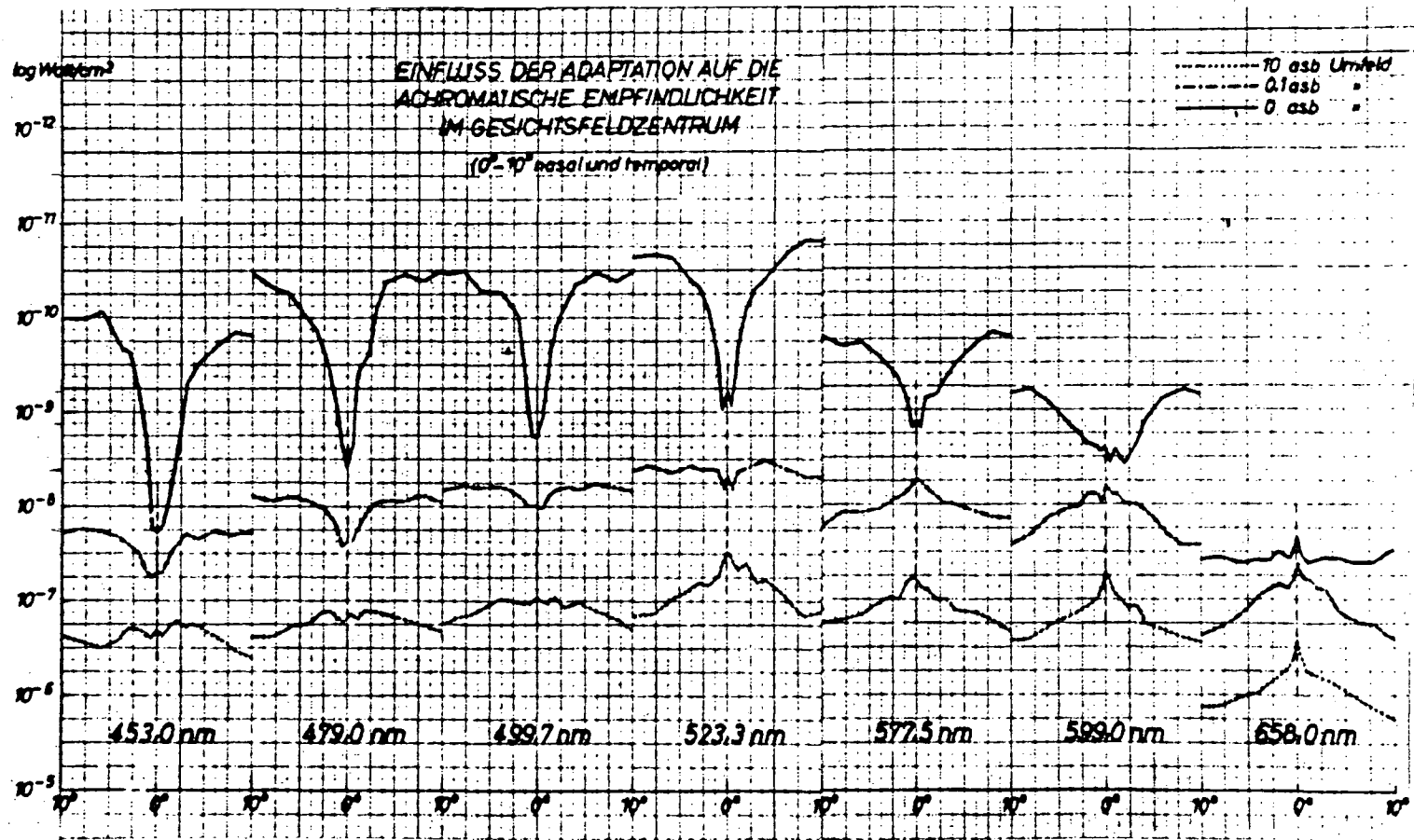
Figure 8   Fully-scotopic sensitivity gradients from 10° nasal to 10° temporal, for monochromatic stimuli.   From Nolte, 1962.
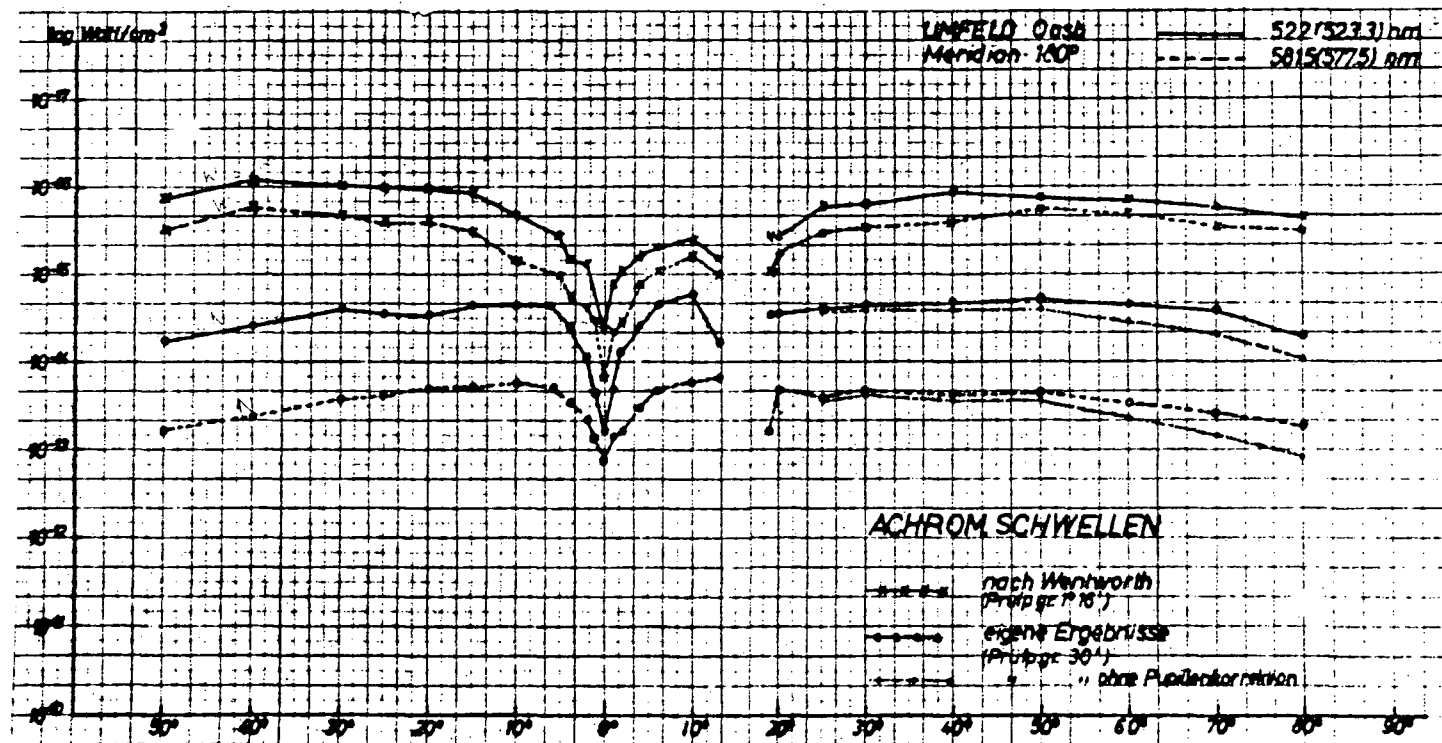
Figure 9   Fully-scotopic sensitivity gradients obtained by Wentworth (1930) and Nolte (1962). From Nolte, 1962.

size was an important factor here. Wentworth's stimulus ($1^{o}16'$) most

likely stimulated rods as well as cones, so that, if anything, one

would expect greater sensitivity than if cones alone were stimulated.

However, the low scotopic spectral luminous efficiency of this wave-

length (.0001) makes it unlikely that the rods would contribute much

in any case. It is quite possible that control of foveal fixation is

an important factor in this discrepancy. Nolte used an achromatic

pattern consisting of a circle having four partial radii pointing to

the centre, wherein the stimulus was presented. With such a fixation

devise, shifts of fixation are quite possible and cannot be monitored.

The possibility, therefore, exists that foveal sensitivity to this

stimulus was not assessed accurately.

Subject Variables. Luminance thresholds determined by static

perimetry have been shown to be influenced by a number of subject-

related variables. Refraction abnormalities are known to raise thres-

holds within 25° of the fovea (Aulhorn & Harms, 1972). It is necessary,

then, that normal sensitivity gradients be obtained with emmetropes.

There is, of course, a practical limit to this criterion. An emme-

tropic eye is defined by Adler as "one in which the retina coincides

with the posterior principal focus of the optical system when the

muscular activity controlling focusing is at a physiologic minimum"

(Moses, 1975, p. 298). The precisely emmetropic eye according to this

definition is a non-existant phenomenon clinically (Newell & Ernest,

1974); for practical purposes an eye may be considered emmetropic if

it is assessed by objective refractive methods at 20/20 Snellen

acuity with a correction of less than $\pm.5$ diopters (Drance, Note 1).

Colour vision deficiencies influence increment thresholds for some chromatic stimuli. Verriest and Israel (1965b) and Verriest and Uvijls (1977b) have shown that protan, deutan, and tritan defects are associated with increment sensitivity losses for the long, middle (around 500 nm), and short wavelengths, respectively. In addition, for all colour vision defects, it was found that foveal sensitivity was reduced for all stimuli and the 'relative central scotoma' for the short wavelengths was also reduced (Verriest & Israel, 1965b; Verriest & Uvijls, 1977b). Lakowski et al. (1977) presented contradictory evidence: a protanope showed, in addition to reduced sensitivity to a red stimulus, increased (relative to the normal) sensitivity to a blue stimulus.

The effect of age on perimetric sensitivity gradients has been investigated by Lakowski and Aspinall (1969) and by Verriest and Uvijls (1977a). While the latter used monochromatic stimuli, Lakowski and Aspinall used an achromatic target. In both cases, age was shown to influence sensitivity, but different age categories were used in each case. Lakowksi and Aspinall's age groups of 13-15 and 17-25 years of age showed the highest sensitivity both centrally and peripherally, sensitivity being lower in both younger and older age groups. It is important to note that these subjects were not classified as emmetropic. Though the 13-15 and 17-25 year age groups had a mean visual acuity of 20/20 Snellen, the older age groups had lower mean acuities. However, when only subjects with acuity of 20/22 Snellen or better were considered, the older age groups (except perhaps the 26-35 years group) still showed reduced foveal sensitivity. Verriest

and Uvijls' results indicated that 'younger' subjects (10-15 years) were less sensitive in the fovea, but more sensitive peripherally than a 'medium' group (16-41 years). This was a general finding over all wavelengths used excepting 480 and 553 nm, for which the young group was more sensitive at all points tested (180° meridian, 45° nasal to 0°). The wide range of their 'medium' group makes it difficult to compare this to Lakowski and Aspinall's results. In general, both studies indicate that for large age differences, age exerts a significant effect on luminance difference thresholds.

Practice has been shown to influence increment thresholds, but the effect is not the same for all subjects (Aulhorn & Harms, 1972). Pre-selection of subjects showing consistent responses to the task of threshold determination would be expected to reduce this practice effect.

There is some question concerning the importance of prior knowledge of stimulus location. Grindly and Townsend (1968) and Mertens (1956) found that foreknowledge of stimulus location did not significantly affect the probability of detection. However, Engel (1971) found that such foreknowledge did increase the 'conspicuity area', the retinal area within which a 75 millisecond peripheral stimulus is detected. If, in fact, foreknowledge of the location influences detection, it is important in perimetry that either random presentation be used or that the subject know prior to testing the sequence of test locations to be used.

Pupil size is a subject variable which influences increment thresholds by limiting the amount of light reaching the retina (Sloan,

1940).. Experimental control of pupil size can be attained through use
of an artificial pupil or drugs to fix pupil size. Neither of these
methods are appropriate for a perimetric examination (Sloan, 1940).
Use of an artificial pupil requires rigid stabilization of the subject
using a full dental-bite apparatus, as any small movement of the eye
may change the relative positions of the artifical and natural pupils.
This would present practical difficulties not necessarily justified
by the gain in precision. The use of drugs to fix pupil size is not
advisable for practical and theoretical reasons. Not only would it
necessitate the presence of a medical assistant at all test sessions,
but the use of drugs is only possible on the assumption that they
affect only the autonomic and not the central nervous system, an
assumption which seems unwarranted considering the involvement of
parts of the CNS in some autonomic reflexes (such as the accommodation
reflex, Barr, 1974).

Spatial Summation and Static Perimetry

The effects of stimulus area (A) and stimulus luminance (L) on
absolute threshold are generally accepted to be inversely related for
small targets, but the exact relationship appears to depend on many
factors. Ricco's law of complete spatial summation ($L \cdot A = $ constant)
seems to hold in the fovea, but only for very small targets (less than
10') (Baumgardt, 1972); Piper's law of partial summation ($L \cdot A^{\frac{1}{2}} = $
constant) has been shown to hold in the periphery for stimuli up to
1° (Baumgardt, 1972). However, factors such as stimulus duration and
chromaticity can influence the relationship between A and L at threshold.

Assuming that no simple law exists relating the two under all condi-
tions, it would be useful to have some measure of this relationship
which could be compared among conditions varying along one dimension
only: for example, chromaticity.

Goldmann (1945a, 1945b) suggested 'k', the 'exponent of summation',
as a measure of the area-luminance relationship at thresholds obtained
via kinetic perimetry. K was defined by the following equation:

$$\Phi = \left(\frac{F_o}{F} \right)^k \qquad (1)$$

where Φ is the transmittance of the neutral-density filter required to
maintain the field size obtained with a stimulus of size F_o , using
a stimulus of size F. This formula gives an objective measure of the
area-luminance relationship based on thresholds obtained via kinetic
perimetry, with k = 1 representing complete spatial summation and
k = 0 representing no summation. Goldmann found that k = 0.84 fit his
data well.

Kinetic perimetry gives different data than does static perimetry,
and by its nature, yields data in which spatial and temporal summation
interact. Even if one adapted Goldmann's formula for use with static
data, the resulting k values could not be directly compared to those
obtained with kinetic methods.

From the proposed inverse relationship between A and L, spatial
summation can be defined by the formula $L \cdot A^k$ = constant, where k is
the exponent of summation which theoretically can vary from 1 (no
summation) to 1 (complete summation) (LeGrand, 1957). From this
formula, the value of k for a change in stimulus size from A_1 to A_2

may be defined by the following formula:

$$k = \frac{\log L_1 - \log L_2}{\log A_2 - \log A_1} \quad \text{(Gougnard, 1961)} \quad (2)$$

where L_1 and L_2 are the absolute thresholds obtained with stimuli of areas A_1 and A_2, respectively.

This formula provides an objective measure of spatial summation when absolute thresholds are involved, and can therefore by justifiably used for perimetric data obtained under fully-scotopic conditions. However, when perimetry involving any adaptation luminance is done, a problem arises in how to define k. Spatial summation has been studied and the laws thereof defined strictly in terms of absolute rather than increment thresholds (Baumgardt, 1972); some measure of spatial summation under photopic or mesopic conditions is required.

What is in fact required is a measure of the difference between the luminance increments necessary for detection for stimuli of different areas. It would seen appropriate then to use ΔL in place of L in the expression $L \cdot A^k$ = constant. If comparison is required between data obtained at different adaptation luminances, $\frac{\Delta L}{L}$ could replace L to take into account the fact that ΔL is proportional to adaptation luminance. Calculation of k via formula (2) would thus yield the same k values using either ΔL or $\frac{\Delta L}{L}$ if L was constant. Hence, formula (2) may be replaced by the following forumla for calculating k under conditions of constant adaptation illumination:

$$k = \frac{\log \Delta L_1 - \log \Delta L_2}{\log A_2 - \log A_1} \quad (3)$$

However, comparison between k values calculated for absolute thresholds
(formula 2) and increment thresholds (formula 3) must be done taking
into account the fact they are distinct entities: one reflects the
spatial summation capacity of retina when absolute thresholds are
involved, while the other reflects spatial summation with respect to
increment thresholds.

Specific Review of Relevant Research. In his original work,
"Grundlagen exakter Perimetrie", Goldmann (1945a) studied the summa-
tion capacities of the retina using kinetic perimetry. He defined the
summation exponent k by formula (1), and found that it had a value of
approximately 0.84 in the normal retina. This value has been widely
quoted in studies of summation involving static perimetric methods.
The fact that this k value was derived using two moving targets, and
pertains to a point in the periphery where equivalent isopters were
were obtained using different area-luminance stimuli, makes it
questionable whether it can be compared to static data.

Fankhauser and Schmidt (1958, 1960) compared the spatial summation
seen in static and kinetic perimetry using the Goldmann perimeter. They
did not calculate values of k, but used the slope of and separation
between sensitivity gradients as a measure of summation. The summa-
tion factor determined using kinetic perimetry with different speeds
of movement (5°/sec and 1°/sec) was not constant, being greater for
the greater target speed. Scatter was also increased for a higher
speed of movement. However, both the static and the two kinetic
methods indicated that summation increased from the central to peri-
pheral fields (indicated by an increase in the vertical separation

between gradients obtained with different sizes), and that summation

decreased as stimulus size increased. It would seem then that static

and kinetic methods lead to similar general conclusions concerning

spatial summation, but that the static method is preferable as it

avoids complication by temporal variables.

Fankhauser and Schmidt (1960) also studied summation under dif-

ferent levels of adaptation, from 0.04 to 40 asb (0.013 - 12.7 cd.m.$^{-2}$).

They found that summation increased as adaptation decreased, the

magnitude of this effect being similar centrally and peripherally.

Fankhauser and Schmidt also noted that there was considerable

variability in all the results, and while no statistically significant

correlation between adaptation luminance and scatter was found, the

data did indicate an increase in scatter with decreased adaptation

luminance.

Sloan (1961), using static perimetry, determined values of k

under mesopic (L = 10 cd.m.$^{-2}$, CIE Illuminant 'A') conditions in the

Goldmann perimeter. She confirmed the results of earlier researchers:

spatial summation was shown to decrease with increasing size and to

increase with eccentricity. In addition, she was able to quantify

these results in terms of the summation exponent k. Rather than cal-

culate k according to formula (3), Sloan plotted the increment thres-

hold as a function of stimulus area, and then took the slope of the

best-fitting line as $-k$ according to the line equation log $\Delta L =$

$-k$ log A + constant (Figure 10). She found that a straight line could

be fit to the points corresponding to Goldmann sizes 0-3 (.0687 to

4.4 mm^2), but not to those for the larger two sizes. Considering then
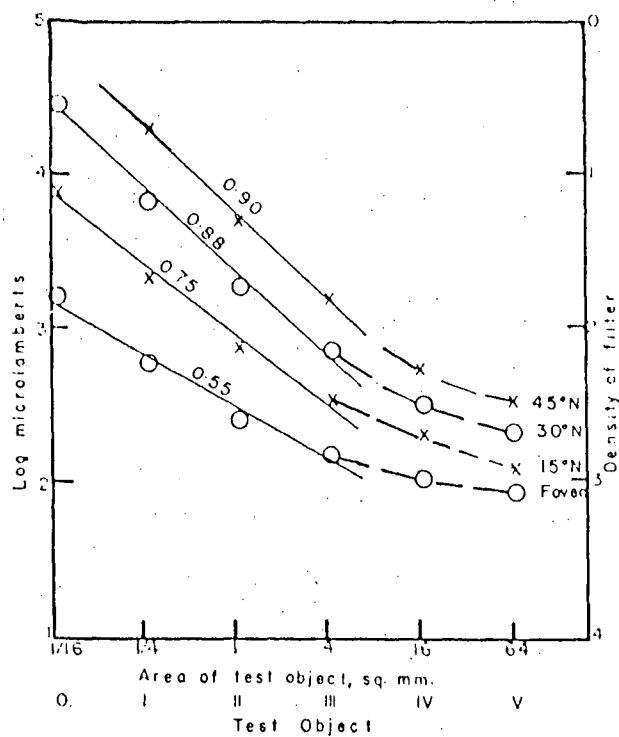
The average summation graph of a group of normal eyes, for the fovea and for various locations in the nasal field. The value of the summation coefficient, k, is shown above each curve.

Figure 10   From Sloan, 1961, p. 33.

only sizes 0 to 3 , Sloan obtained values of k ranging from 0.90 (at 45° nasal) to 0.55 (at 0°) which decreased as eccentricity decreased. From this data one would expect that values of k calculated via formula (3) would be very similar, at a given eccentricity and at an adaptation of 10 cd.m.$^{-2}$, for sizes 0-3, 1-2, and 2-3. The larger sizes would be expected to give generally lower values, as the slopes of lines drawn between sizes 3 and 4 or 4 and 5 in Figure 10 would be lower than the slopes determined for the smaller sizes.

Gougnard (1961), again using the Goldmann perimeter with an adaptation of 10 cd.m.$^{-2}$, CIE Illuminant 'A', obtained values of k between sizes 0 to 1   for thresholds obtained on the nasal meridian for 20 normal subjects. He also determined k for sizes 1-2, 2-3, and 3-4 but only on the lower temporal meridian. He again, confirmed that the value of k (reflecting summation capacity) increased with eccentricity and decreased with increasing stimulus size. His k values were cal-culated for each individual eccentricity measures (using formula 3). For the fovea, he obtained k = 0.49 (sizes 0-1), 0.39 (sizes 1-2), 0.17 (sizes 2-3), and 0.18 (sizes 3-4). These are all lower than Sloan's mean value of k, for sizes 1 to 3, of 0.55. Conversely, at 30° nasal, Gougnard's k values of 0.99 (sizes 0-1) and 1.09 (sizes 1-2) are higher than Sloan's (0.88). Both studies were done using the same instrument, Sloan having used an auxiliary fixation device for measuring foveal thresholds, but it is possible that some unspecified variables such as stimulus duration, age, or refractive error of sub-jects (Gougnard specified his subjects as emmetropes aged 22-25 years; Sloan specified her subjects as 'normal') may have been partially

responsible for the differences. However, the large standard devia-
tions found by Gougnard (Table 1) indicate that considerable individual
variation exists in spatial summation as reflected by k.

The general conclusions which can be drawn from the foregoing
investigations may be summarized as follows. First, spatial summation
is inversely proportional to stimulus size and adaptation luminance,
and directly proportional to eccentricity. Second, considerable
variation is seen in the normal retina's threshold responses upon
which measures of spatial summation are based. Because of the multi-
tude of factors which can influence threshold measurement (subject age,
acuity, colour vision; stimulus spectral composition, duration, etc.),
it is difficult to determine how much variation is actually due to
variability of the light-sense itself. Therefore, variability in
summation capacity as measured by k (e.g., Gougnard, 1961, see Table 1)
may, in fact, reflect variance in only the light sense rather than in
summation capacity. The exact nature of the proportionalities mentioned
in the first point have not been defined, largely due to this wide
variability.

Proposal

It was apparent from the literature that little information has
been presented on retinal sensitivity gradients to chromatic stimuli
under adaptation conditions capable of separating the photopic and
scotopic response systems. Photometric-equivalence of chromatic stimuli
had rarely been used, and the spatial summation of chromatic stimuli
had not been investigated. It was therefore proposed that normal

Table 1

Means and Standard Deviations of Summation Coefficients (k)

Determined with Goldmann Targets 0 and 1 on the

Nasal Horizontal Meridian (Gougnard, 1961)

Eccentricity	$\bar{X}$	σ
0°	0.49	0.20
5°	0.87	0.25
10°	1.02	0.20
15°	0.98	0.22
20°	1.03	0.16
25°	1.00	0.13
30°	0.99	0.13

retinal sensitivity gradients be established for photometrically-equated chromatic stimuli of varying size under both fully-photopic and fully-scotopic conditions. In addition, it was proposed that the spatial summation capacities of the normal retina be explored for such photometrically-equated stimuli using several stimulus sizes under fully-photopic and fully-scotopic conditions.

Hence, achromatic thresholds were to be determined at 13 points on the $0-180^{\circ}$ meridian, from 40° nasal to 40° temporal. Stimuli subtending 6.8, 13.6, 27.2, and 54.3 minutes at the eye (at 30 centimeters) were to be presented, gradients being obtained for each size with an achromatic (T_c = 6000K) and red (λ_D= 623 nm), green (λ_D= 504.5 nm), and blue (λ_D=460 nm) chromatic stimuli. Such gradients were to be obtained under conditions of fully-photopic (L = 250 cd.m.$^{-2}$) and fully-scotopic (L = 0, dark-adaptation) conditions.

METHOD

Apparatus

Perimeter. All data was obtained using a modified Goldmann Pro-
jection Perimeter (Lakowski et al., 1977; Lakowski & Dunn, Note 2) (see
Figure 11). It is a hemispheric perimeter allowing the determination
of luminance thresholds at specific points in the visual field. The
stimulus is projected on the inside of the hemisphere (the adaptation
bowl) along a light path consisting of a series of front-surface
mirrors, focusing lenses, and a prism. A pantograph connecting the
stimulus projector arm and a marker on the data chart provides precise
specification of the position of the stimulus.

Both the adaptation field (for the photopic condition) and the
stimulus were provided by xenon-arc lamps, of correlated colour tem-
perature T_c = 6000K. The spectral distribution of the xenon-arc appro-
ximates that of the CIE Illuminant 'C' (see Figure 12). Thus, the
photopic adaptation luminance was high quite consistantly across the
visible spectrum, so that all response-systems of the eye were under
fully-photopic conditions. The spectral distribution of the stimulus
xenon-arc source, together with its high luminous output (8000 cd.m.$^{-2}$)
provided the required high luminance at all visible wavelengths
including the short (blue) wavelengths. The stimulus source was a
Leitz XE 75, a 75-watt xenon-arc lamp housed in a Leitz Lamphouse 100,
mounted behind the hemisphere on the subject's left. The adaptation-
field source was a Leitz XBO-150, a 150-watt xenon-arc lamp, housed
in a Leitz Lamphouse 250 mounted on the upper edge of the adaptation
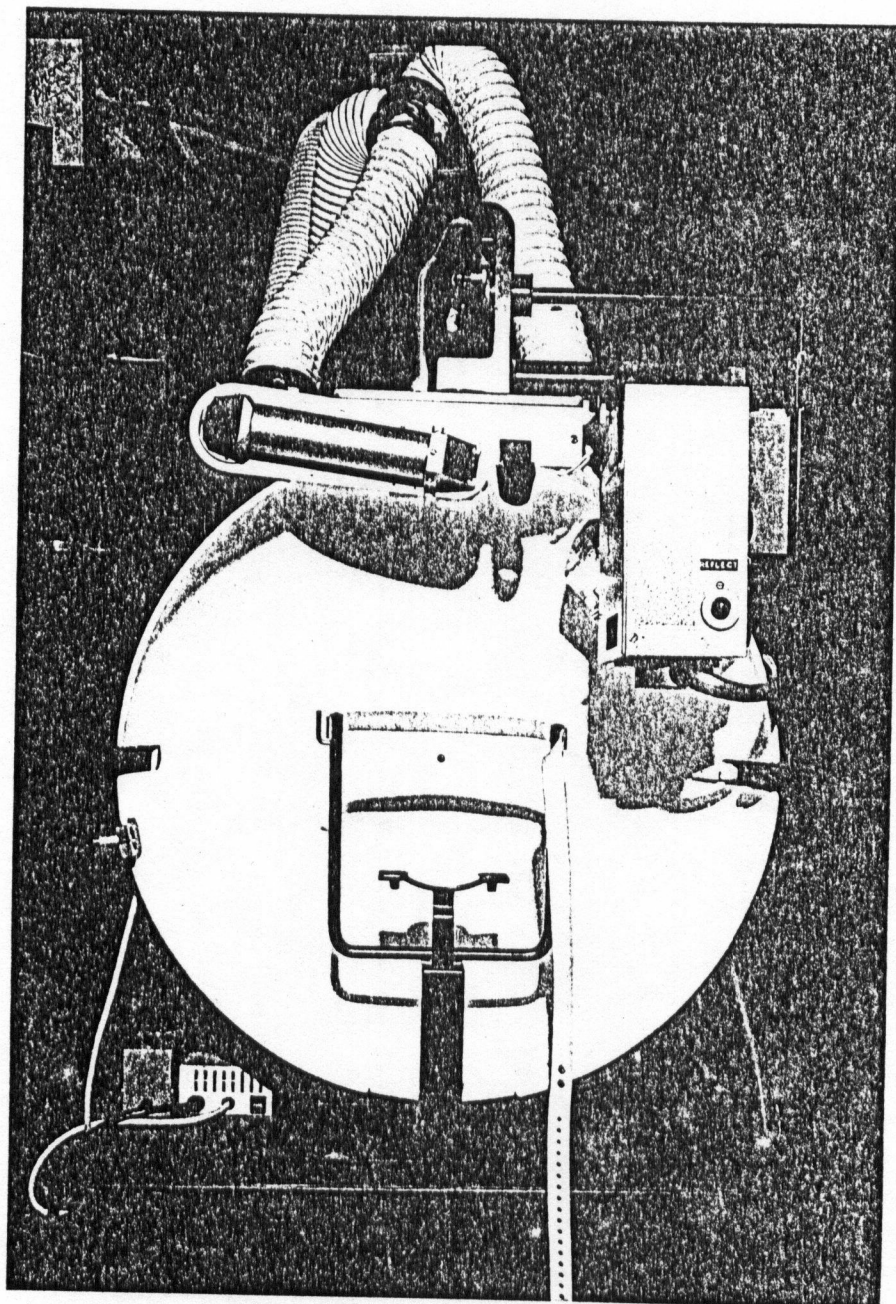
Figure 11   The modified Goldmann Perimeter
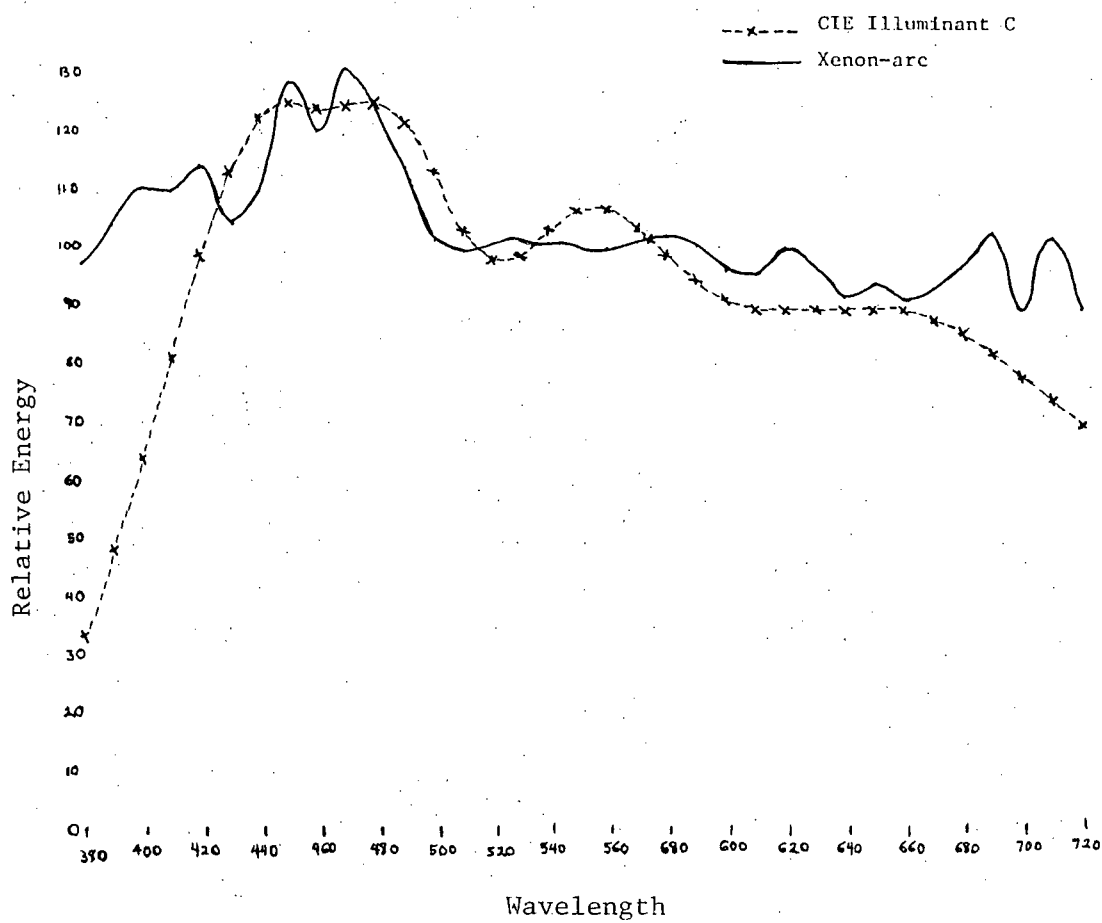
Figure 12   Relative spectral energy distribution of C.I.E.
Illuminant C and Xenon-arc. From Wyszecki and stiles, 1967.

bowl on the subject's right. Both lamps were cooled by an extraction

fan, which directed some of the heat as well as the ozone produced

by the lamps into the building's exhaust duct. The output of the

adaptation source was directed up to the top of the adaptation bowl

from which it was diffused throughout the bowl. A diffusion baffle

mounted across the upper edge of the bowl aided this diffusion and

decreased loss of light out of the bowl. The high luminance, Illu-

minant 'C' character of the adapting field was further ensured by the

surface of the bowl, which was painted with Kodak Eastman White

Reflectance Paint. This provided a surface with 98% reflectance across

the visible spectrum. In this way, an adapting field of 250 cd.m.$^{-2}$,

T_c = 6000K was achieved.

The luminance of the stimulus was varied by placing neutral

density filters in the light path. A series of such filters are

mounted in the instrument, allowing reduction of stimulus luminance by

two log units, in 0.1 log unit steps. Two filter caps, each of which

reduces the stimulus luminance by two log units, can be mounted on the

projector arm. In addition, two sets of neutral density filters[1], each

set reducing stimulus luminance by 2 log units, could be inserted

directly in front of the stimulus source. As a result, the stimulus

luminance was variable, in 0.1 log unit steps, over a range of ten

log units. The stimulus size was varied by means of a series of dia-

phragms built into the instrument. The stimulus sizes used were .275,

1.1, 4.4, and 17.6 mm^2, which subtended visual angles of 6.8, 13.6,

[1]Wild Leitz #126131 NG4, diameter = 32 mm.

27.2, and 54.3 minutes of angle at the subject's eye (at a distance of 30 cm).

Stimulus presentation was controlled by an automatic shutter mechanism which presented the stimulus for 150 milliseconds, with an interstimulus interval of one second. During all testing, an auxiliary mechanism kept a steady 'clicking' sound going at one 'click' per second. This served to mask the sound of the shutter opening, which would replace the auxiliary sound when the experimenter activated the shutter mechanism. In this way, the subject could not use the sound of the shutter as a clue to determine when the stimulus was presented.

The eye to be tested was positioned by having the subject sit with his chin in the chin-rest and his forehead against a restraining band, the non-test eye being covered by a white diffusing occluder. The experimenter positioned the eye by moving the chin-rest while the subject fixated on the central black spot in the adaptation bowl. This spot is the base of a telescope through which the experimenter views the eye and centres it using the cross-wires in the telescope. These cross-wires have millimeter gradations for measurement of pupil dia-meter. When the eye was centered, the distance from the corneal surface to any point on the bowl was 30 cm.

For scotopic measurements, a red probe light was used which was inserted in the mounting cylinder for the perimeter's telescope, the luminance being controlled by a variac. This red probe light was the fixation point for all extra-foveal testing under scotopic conditions.

Foveal threshold measurements were made using a alightly different procedure for the photopic and scotopic conditions. For the latter,

the auxiliary fixation device provided with the instrument was used.
This device projects a pattern of four lights in a diamond shape,
each light subtending approximately seven minutes and the entire pat-
tern subtending two degrees of visual angle. This pattern is projected
at a point centered at five degrees to the subject's right of the
adaptation bowl's centre. The subject was instructed to fixate on the
centre of the pattern, and indicate when he saw a light. The projector
was fitted with a red cinemoid filter[2], and its luminance controlled
with a variac. Two scoptopic foveal thresholds were obtained using
this device, one with the fixation pattern just barely visible to the
subject, and one with the pattern slightly higher in luminance.
Another similar fixation pattern which subtended 3.4 degrees of visual
angle was also used to determine the scotopic foveal threshold, again
at two luminance levels. Thus, four determinations of the foveal
threshold were made during each scotopic test.

The auxiliary fixation device described above could not be used
in the photopic condition, as it was not bright enough to be seen
against a background of 250 cd.m.$^{-2}$. Instead, a small plate on which
were painted four black dots was affixed to the edge of the adaptation
bowl on the subject's right, the pattern being centered at 64 degrees
in the 0-180° meridian from the centre of the bowl. This pattern sub-
tended two degrees of visual angle. The subject was instructed to turn
his eye and fixate on the centre of this pattern, and indicate when
he saw a light. This was found to yield the same threshold as the

[2]Primary Red #6, Spectacular Productions Ltd.

four-light pattern method when the two were compared at an adaptation

luminance of 10 cd. m.$^{-2}$.

The perimeter was surrounded by a framework of black cardboard

and cloth which prevented extraneous light from the xenon-arc lamp

or the data-chart illumination from reaching the adaptation bowl during

scotopic testing.

Photometer. The Goldmann perimeter comes equipped with an A.G.

Metrawatt Luxmeter for measuring intensities. Measurements in the

visual laboratory indicated that this was an imprecise instrument, and

in any case, it is not equipped for precise measurement over the range

required for this investigation. Therefore, as in the earlier work

from this laboratory (Lakowski et al., 1976, 1977), a Spectra Pritchard

Photometer (Model 1970-PR) for which correction factors are available

to correct the spectral sensitivity to V_λ was used for all luminance

measurements of both targets and background.

Subjects

Because this investigation was intended to study normal photopic

and scotopic sensitivity gradients to chromatic stimuli, subject vari-

ables thought to influence the thresholds were controlled where pos-

sible. All subjects were emmetropes with normal colour vision, ranging

from 16 to 29 years of age (see Table 2).

In preliminary investigations pupil size was found to be fairly

consistent for the subjects of interest, but pupil dimater was, in any

case, measured before and after each photopic test session, and moni-

tored during photopic testing. This was done using the telescope

through which the experimenter observed the tes eye. The telescope has

Table 2

Subject Data

Subject	Age	Sex	Dominant Eye	Colour Vision[a]	Refraction[b]
LL	17	F	R	normal	+0.50 to 6/4.5
AM	22	F	L	normal	+0.75 to 6/4.5
JL	23	M	R	normal	+1.25 to 6/4.5
RM	29	M	R	normal	-0.50 to 6/4.5
KH	29	M	L	normal	+0.25 to 6/6

[a] Colour vision assessed with Dvorine and Ishihara PIC plates, Farnsworth-Munsell 100-Hue test, and Pickford-Nicholson anomaloscope.

[b] All subjects assessed as 'emmetropic' at the Department of Ophthalmology, University of British Columbia. 'Emmetropia' is here defined as being emmetropic within 0.99 diopters, spherical equivalent.

cross-wires marked in millimeters for this purpose. In the scotopic

condition, pupil diameter was not measured as there was no light in the

bowl.

To minimize any practice effects, trial sequences were counter-

balanced among subjects. In addition, a standard learning trial

(achromatic stimulus subtending 6.8' visual angle, backround luminance =

250 cd.m.$^{-2}$) was given before the experimental trials began, and was

repeated after the last testing for an indication of the magnitude of

the practice effect. Subjects were higher selected, not only in terms

of acuity, age, and colour vision, but also for consistency of response

and stability of fixation. This was expected to minimize further

practice effects.

In this investigation, only one eye of each subject was tested.

As it has been shown that most individuals have a dominant eye which

is superior to the non-dominant eye motorically and is favoured in

visual situations requiring choice (Porac & Coren, 1976), only dominant

eyes were tested. This was the right eye in three cases and the left

in two cases.

The possible influence of foreknowledge of stimulus location on

threshold was controlled as follows. Because of instrumental limitations,

it is impractical to present the stimuli randomly using the Goldmann

perimeter; a standard presentation order was necessary. With practice,

the subject learns the order, so that foreknowlegde concerning stimulus

location would operate as an uncontrolled variable if no information on

testing sequence was given initially. Thus, subjects were informed

before any testing of the stimulus presentation sequence to be followed

on all trials. This was expected to decrease the practice effect.

Experimental Parameters

Adaptation Field. A full hemispheric field was provided by the perimeter adapting bowl so that field size, texture, and distance from the corner (30 cm) were all held constant. For the photopic condition, uniform field luminance and chromaticity of 250 cd.m.$^{-2}$, 6000K were provided by the 150-watt xenon-arc lamp as previously described. There was no adaptation field in the scotopic condition. Pre-adaptation was carried out for four minutes and twenty-five minutes for photopic and scotopic testing, respectively. These periods were found to be adequate to give the same thresholds as longer pre-adaptation periods. Because of the extensive preadaptation required for scotopic testing, once the subject was dark-adapted, a number of trials were run, so that longer adaptation was given for the majority of trials. These trials, as well as the photopic ones, were counterbalanced among and within subjects.

Stimuli. The stimulus characteristics manipulated were size, retinal location, and chromaticity. The test luminance necessary for detection was the dependent variable, ΔL. Differential effects of other factors on the increment thresholds obtained were eliminated when possible. To this end, stimulus duration was held constant at 150 milliseconds. This is in accordance with Enoch (Note 3), who states that perimetric stimulus duration should lie between 100 milliseconds (below which ΔL x duration of exposure = constant, and above which ΔL = constant) and 250 milliseconds (above which saccadic eye movements may occur). Stimulus duration was, therefore, held at 150 milliseconds.

(a) <u>Retinal location</u>. Due to the time-consuming and fatiguing nature of the experimental task, it was impractical to obtain thresholds along more than one retinal meridian. The horizontal (0-180°) meridian has been used almost exclusively in previous experimental static perimetry, and seems the logical choice. Unfortunately, some diseases characterized by visual field losses, notably glaucoma, result in losses to areas not on this meridian. Studies concerned with such pathological field losses must involve the investigation of other retinal meridians in normal as well as clinical populations. The major purpose of this work was to study normal thresholds in chromatic perimetry, and thus the horizontal meridian was used. Measurements were made at 13 points along this meridian, from 40° in the temporal to 40° in the nasal field. The luminous output of the stimulus projection system prevented the determination of thresholds beyond 40° in the periphery in the photopic condition.

(b) <u>Size</u>. Stimulus size was set at 0.275, 1.1, 4.4, or 17.6 mm, corresponding at all retinal locations to visual angles of 6.8, 13.6, 27.2, and 54.2 minutes at 30 mm (the distance from the cornea to the adaptation bowl surface). These are not the nominal values on the Goldmann instrument, but are the actual values as specified by Goldmann in his early work (Goldmann, 1945a), (Verriest, 1965a).

(c) <u>Chromaticity</u>. The Goldmann perimeter uses selective filters to attain chromatic stimuli. The original filters accompanying the instrument are compared with a set of cinemoid filters in Figure 13 and Table 3. When choosing chromatic filters, one wishes to obtain maximal luminous transmission, maximal excitation purity and thus minimal
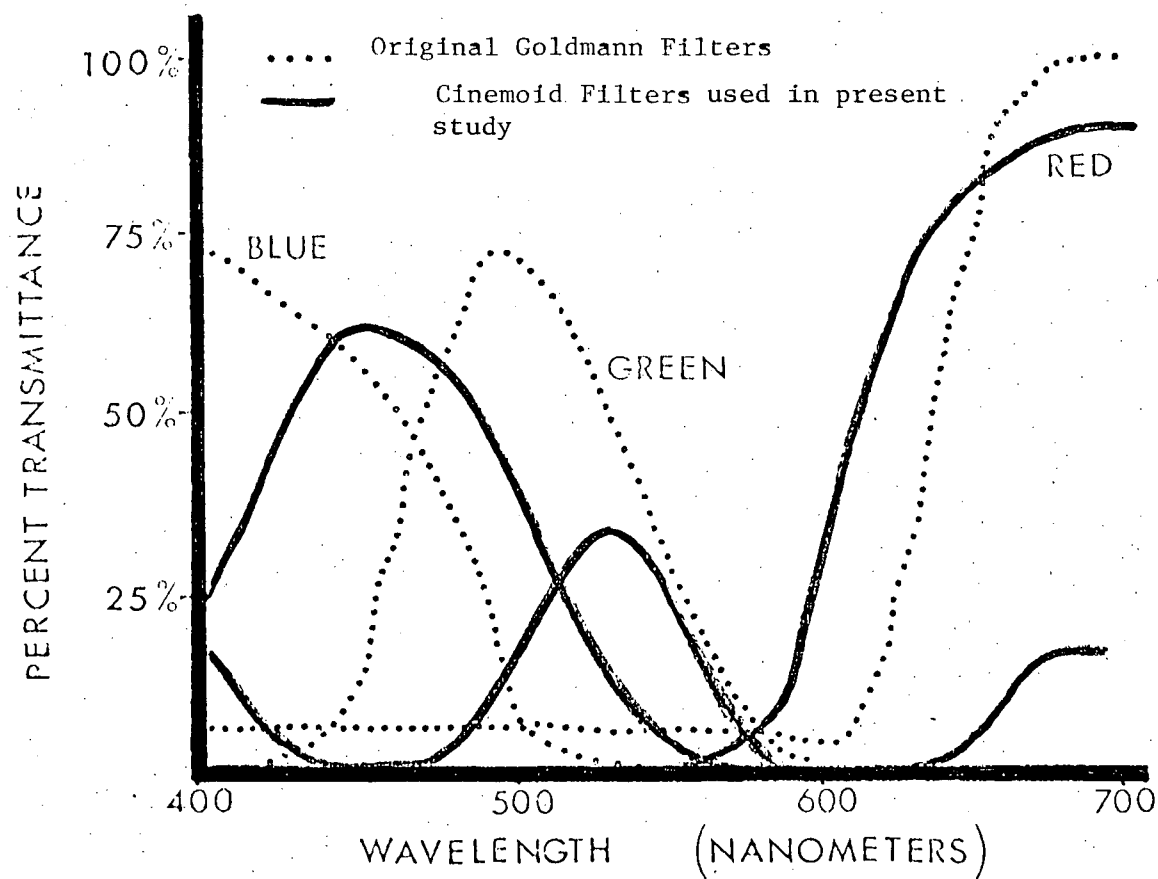
Figure 13   Spectral transmission curves for chromatic filters
(from Lakowski et al., 1977)

Table 3

Comparison of Original with Cinemoid Filters

| Stimulus Filter | Specifications under CIE Illuminant 'C' | | | | Excitation Purity |
	$\underline{x}$	$\underline{y}$	$\underline{Y\%}$	λ_D	
Goldmann blue	.1562	.0233	1.635	460 nm	
Goldmann green	.2331	.6466	24.180	504.5nm	
Goldmann red	.729	.2704	0.913	623	
*Cinemoid #32 medium blue	.1417	.1180	10.21	474	0.86
*Cinemoid #39 primary green	.2145	.6973	14.43	535	0.81
*Conemoid #6 primary red	.6738	.3134	10.21	617	0.97
Unfiltered Stimulus Source: xenon-arc $T_c = 6000°K$	.3220	.3318			

*Filters used in the present investigation.

(Cinemoid filters from Spectacular Productions, Ltd.)

overlap among the filters, and peak transmissions as close as possible
to the peaks of the cone response systems. The first two requirements
are diametrically opposed, so that a compromise must be made such that
sufficient luminance can be attained at the expense of some overlap
among the three filters' spectral transmission curves.

Taking into account these criteria, the cinemoid filters described
in Figure 13 and Table 3 were substituted for the original Goldmann
filters in the earlier modification of the Goldmann perimeter (Lakowski
et al., 1976, 1977). These cinemoid filters gave the higher luminance
necessary to explore the visual field with small stimuli. The reduced
luminous transmission of the cinemoid compared to the Goldmann green
was not a problem, as sufficient luminance in the middle wavelengths
was easily obtained. The advantages of the cinemoid green are its
narrower transmission curve and its peak transmission within the 535-
555 nm. range found for the peak of the 'green' or middle-wavelength
response system (Stiles, 1959; Brown & Wald, 1963; 1964; Rushton,
1963; Marks, Dobelle, & MacNichol, 1964; Baker & Rushton, 1965). The
Goldmann 'green' is actually a blue-green, with λ_D = 504.5 nm.

While the cinemoid red was substituted for the Goldmann red
mainly to achieve higher luminance, neither of these filters peaks
anywhere near the peak of the longest wavelength cone system, at
570 to 590 nm. It is not clear why there is no 'red' cone system,
though the trivariance of normal volour vision indicates that colour
matching requires a long, as well as short and middle, wavelength
stimulus.

In comparing the Goldmann and the cinemoid blue filters, it is

clear that the cinemoid has far greater luminous transmission than does the Goldmann filter. However, the gain in Y% is accompanied by a shift in peak transmission away from the range found for the peak of the 'blue' response system, from 440 to 450 nm (Stiles, 1959; Brown & Wald, 1963, 1964; Rushton, 1963; Marks, Dobell, & MacNichol, 1964; Baker & Rushton, 1965). This shift may be very significant, as the 'relative central scotoma' to short-wavelength stimuli found using the Goldmann blue (Verriest & Israel, 1965a) has not been duplicated with this cinemoid blue (Lakowski & Dunn, 1978). In this respect as well the cinemoid is superior to the Goldmann blue filter for the present purposes. It is proposed here that normal sensitivity gradients be established; these can then be compared with gradients obtained in pathological eyes. Hence, it would not be advantageous to have normal physiological scotomata which could mask or be confused with patho-logical scotomata. The Goldmann blue has the added disadvantage that it shows no discrete peak in the visible spectrum, but plateaus down into the untraviolet wavelengths (Figure 13). By contrast, the cine-moid blue shows a well-defined peak transmission.

In summary, it appeared that the cinemoid filters used by Lakowski et al. (1976, 1977) were preferable to those accompanying the Goldmann instrument for the present purposes, particularly as very high luminance levels were required. For comparative purposes, achromatic stimulus thresholds were also determined, using the xeono-arc output without selective filtering. These thresholds were determined against an adaptation luminance of the same colour-temperature (6000K) as the target, as both were produced by xenon-arc.

Experimental Design

    I.   Subjects: 5 emmetropic normal trichromats, 3 males and 2

females, aged from 16 to 29 years, were selected

for stability of fixation. Only the dominant eye

of each was tested; this resulted in data from

3 right and 2 left eyes (see Table 2).

   II. Constant Condition: A. Stimulus duration: 150 milliseconds.

                            B. Interstimulus interval: 1 second.

  III. Independent Variables:

        A. Adaptation Luminance: 1. zero $cd.m.^{-2}$ (pre-adaptation:

                                                25 minutes)

                              2. 250 $cd.m.^{-2}$ (preadaptation:

                                            4 minutes)

        B. Stimulus Location: 13 points on the horizontal ($0-180^{\circ}$)

meridian were tested in the following

order: 0°, 5°, 10°, 15° nasal field;

5°, 10°, 20°, 25°, 30°, 40° temporal;

20°, 30°, 40° nasal field.

        C. Stimulus Size: 1. 0.275 mm^2, subtending a visual angle of

6.8' at 300 mm

                          2. 1.1 mm^2, subtending a visual angle of

13.6' at 300 mm

                          3. 4.4 mm^2, subtending a visual angle of

27.2' at 300 mm

                          4. 17.6 mm^2, subtending a visual angle of

54.3' at 300 mm.

D. Stimulus Chromaticity[1] : 1. Achromatic (xenon-arc,

T_c = 6000K)

2. Blue λ_D = 474

3. Red λ_D = 535

4. Green λ_D = 617

IV. Dependent Variable: ΔL, the minimal stimulus luminance required to obtain a threshold response. This was variable in 0.1 log unit steps.

Procedure

Each subject was tested for acuity monocularly on the Bausch and Lomb Orthorater and the Snellen Chart. They were refracted at the UBC Department of Ophthalmology to establish subjectively that they were emmetropic. Monocular colour-vision assessment was done using the Dvorine and Ishihara PIC plates, the Farnsworth-Munsell 100-Hue test, and the Pickford-Nicholson anomaloscope. Eye dominance was tested using the Asher test (Asher, 1961) and the Miles ABC Test (Miles, 1929, 1930). A learning trial was given (achromatic stimulus subtending 6.8' visual angle, background luminance = 250 cd.m.$^{-2}$). On the basis of these tests the subjects were selected. Before the learning trial the subject was told the order of retinal locations to be tested on all trials.

The order of test trials was counterbalanced among and within subjects with respect to stimulus size and chromaticity (see Appendix 1). All photopic tests were done first; the experimenter thus could

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[1] For further specification see Figure 13 and Table 3.

monitor fixation during the earlier trials when the subject was less experienced. The lengthy pre-adaptation period necessary for scotopic testing made it advantageous to run several trials once the subject was adapted; this resulted in a different counterbalancing order for the scotopic as opposed to the photopic tests. Testing was done for periods of two to three hours, as it had been found in previous investigations that after this time fatigue began to influence the results. The subject rested between tests: he left the test room between photopic tests, but remained at the instrument between scotopic tests.

After all 24 test trials had been completed, the initial learning trial was repeated.

Trial Procedure.

1. After setting up the test conditions, that is, selecting the appropriate adaptation luminance and stimulus size and chromaticity, the experimenter measured and recorded the luminances of both the stimulus to be presented and the background using the Pritchard Photometer.

2. The subject was seated at the perimeter and positioned as comfortably as possible with the eye to be tested centered on the perimeter telescope, through which the experimenter could see the eye. An opaque white occluder was placed over the other eye. The positioning was done by means of the adjustable chair and the movable chin-rest, on which the subject was positioned with his forehead against a restraining band. In this way, the distance from the cornea to the stimulus was held constant at 30 cm.

3. Room illumination was extinguished and the subject was pre-adapted to the adaptation background for 25 minutes (scotopic condition) or 4 minutes (photopic condition). This was timed with a stopwatch. In the photopic condition, during this time the subject was instructed to move his gaze around the bowl, not fixating on the dark central fixation spot. After-images were thus avoided.

4. When the pre-adaptation was over, in the photopic condition, the pupil diameter was measured with the subject fixating on the fixation spot, which was the base of the telescope. The stopwatch was then reset to time the test session.

5. All threshold measurements were obtained by the following ascending method of limits. The subject was instructed to tap on the instrument table when he saw a light flash. The experimenter then increased the stimulus luminance by 0.1 log unit steps, allowing two exposures at each step, until the subject responded. Stimulus luminance was then decreased to a level varying from .5 to .1 log units below the threshold just obtained, and again increased until the subject responded. This was repeated until the subject's response occurred consistently at the same luminance level two or three times; this generally took only three or four ascending runs with most subjects under most conditions.

6. Using the ascending method of limits described above the foveal threshold was determined first, in both the photopic and the scotopic conditions. This threshold was measured in slightly different ways in the two adaptation conditions.

Under scotopic conditions, the original instrument's four-light

fixation pattern (with a red filter) was projected at 5° to the right

of the bowl's centre. The subject was instructed to fixate on the

centre of the diamond-shape formed by the four red lights, and in-

dicate when he saw a light there. The usual ascending runs were

then made and the threshold determined. This was done with the

luminance of the four red fixation lights set at two levels. This

procedure was repeated with another, similar four-light fixation pat-

tern which subtended 3.4^o of visual angle (compared to the original

pattern, which subtended 2°). Thus four separate foveal threshold

determinations were made for each scotopic trial. The small size

of these fixation lights (about 6' of visual angle) made it impossible

to precisely specify their luminance; they were (at both settings) not

over .15 cd.m.$^{-2}$.

In the photopic condition, the four-light fixation pattern was

not bright enough to be seen against the background of 250 cd.m.$^{-2}$.

Therefore, an alternate method was used to determine foveal thresholds.

The subject was told to direct his gaze away from the fixation spot

until any after-image had faded. He was then told to look in the centre

of the four-dot pattern affixed to the right side of the adaptation

bowl, and tap on the instrument table when he saw a light. The same

ascending method was then followed.

7. The subject was next instructed to fixate on the fixation

point (central dark spot in the photopic and central red probe in the

scotopic condition). He was told to maintain fixation throughout the

remainder of the testing. Fixation was monitored throughout the

photopic test sessions by the experimenter via the telescope, but

this was not possible in the scotopic condition. In the latter case,
fixation was indirectly monitored by questioning the subject occa-
sionally as to whether the red fixation light seemed to be moving.
Because of the reliance on such an indirect measure of fixation in
the scotopic condition, only subjects showing stable fixation were
used.

8. The subject was told to indicate (by tapping on the instru-
ment table) each time he saw a light. At each retinal location tested,
the same ascending method of limits was used as has been described.
The subject was encouraged to blink his eyes whenever he liked; this
seemed to reduce fatigue. In photopic trials, after all locations had
been tested, the pupil diameter was again measured and the subject
left the testing room while the experimenter again measured and recorded
the luminances of the background and stimulus. During scotopic
testing, a number of trials were done once the subject had dark-adapted.
Thus, the subject rested a few minutes before the next trial began,
but stayed at the instrument.

RESULTS

Retinal Sensitivity Gradients

Sensitivity gradients were obtained under fully-scotopic and fully-photopic adaptation conditions using exactly the same stimuli and subjects. However, because the fully-photopic gradients represent increment thresholds while the fully-scotopic are absolute thresholds, they will first be presented separately and then compared.

Fully-Photopic Adaptation. For each stimulus size used, the three chromatic and the achromatic stimuli yielded similar gradients (see Figure 14). The similarity among the gradients is greatest for the smallest stimulus size (6.8'). As stimulus size increased, it appeared that the achromatic stimulus did not show as large an increase in sensitivity as did the chromatic stimuli , resulting in a separation of the gradient for this stimulus from the others. This was shown particularly well for sizes 3 and 4 (27.2' and 54.3'). Excluding the fovea, the mean thresholds obtained with the chromatic stimulus never differed by more than 0.2 log unit, and generally differed by 0.1 log unit or less. The differences did not show any consistent relationship between the colours; that is, no one colour yielded consistently higher thresholds.

A 4-way analysis of variance was carried out on this data, the summary table of which is presented in Table 4. Significance beyond the .01 level was found for the main effects of colour, size, and subject. Newman-Keuls Multiple Range Tests indicated that the effect of colour was contributed solely by the achromatic stimulus. This
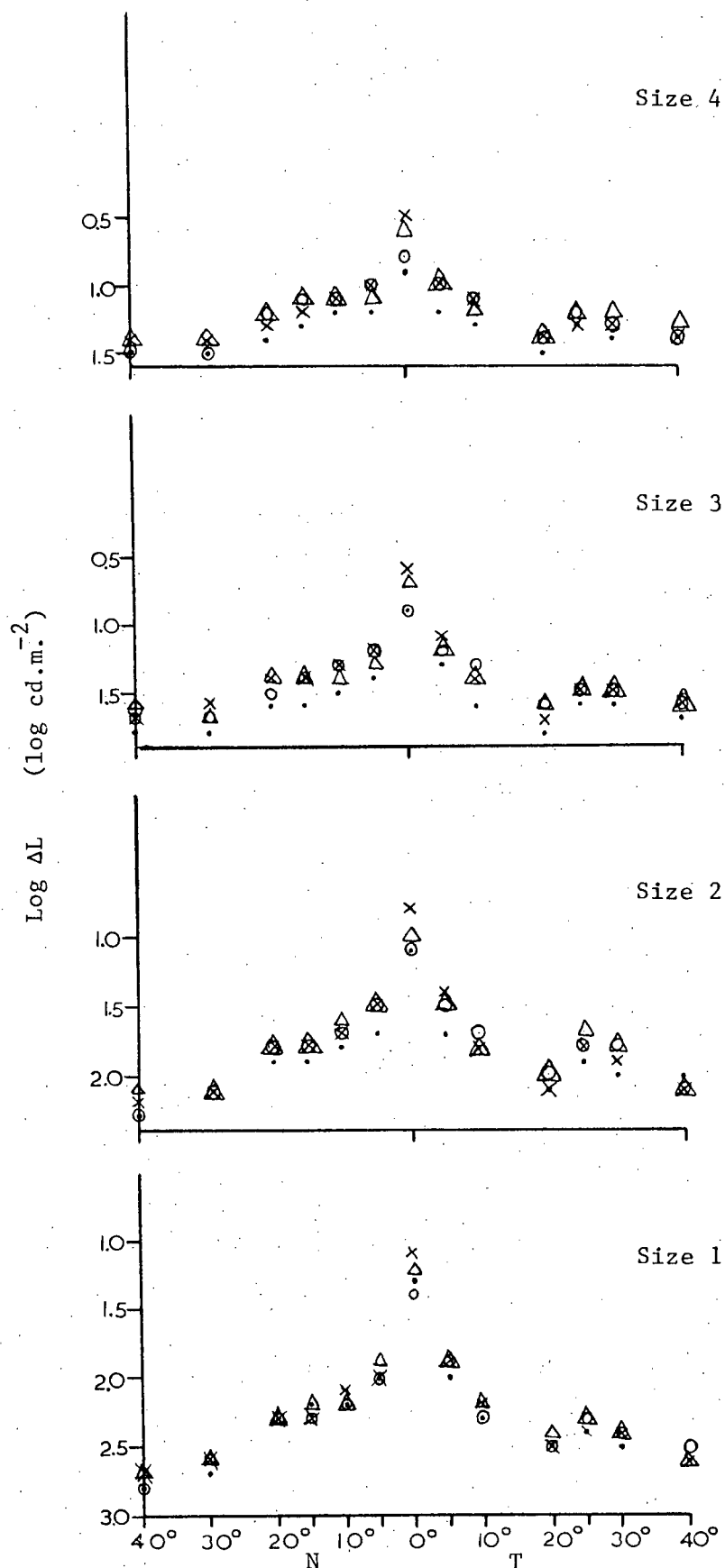
Figure 14 Mean fully-photopic sensitivity gradients for blue(○), green(Δ), red(×), and achromatic(·) stimuli. Adaptation luminance = 250 cd.m.$^{-2}$

Table 4

Analysis of Variance for Photopic Thresholds

Source	df	SS	MS	F	p
Colour	3	2.6353	0.8784	20.2748	0.0000
Size	3	160.0284	53.3428	395.4917	0.0000
Colour x Size	9	0.3747	0.0416	5.9225	0.0000
Subject	4	6.3019	1.5755	15.6055	0.0000
Colour x Subject	12	0.3614	0.3011	4.9284	0.0000
Size x Subject	12	0.6759	0.0563	7.1377	0.0000
Colour x Size x Subject	36	0.54671	0.0152	2.5747	0.0000

confirms the impression given by the gradients in Figure 14. The main

effect of size resulted from significant differences among all four

sizes. The subject variable also was significant, with subject LL

showing significantly higher sensitivity than AM, JL, and RM, all of

whom showed significantly higher sensitivity than KH. This is in-

teresting in view of the fact that subject LL was the youngest (17

years) and KH was one of the oldest (29 years). The main effect of

subject may therefore reflect the age variable.

From Table 4 it can be seen that there were many significant

interaction effects in the data. These were not only first order

but also second order significant interactions. Because of the lack

of independence of the variables as reflected in these interactions,

the true significance of the main effects indicated by the analysis of

variance becomes questionable. In particular, the fact that all

interactions between the subject variable and any others were signi-

ficant may indicate that this variable is accounting for a great deal

of the observed variance. Nonetheless, the analysis does confirm the

interpretation of the data made on the basis of Figure 14, in that

both indicate that the achromatic stimulus yields a lower sensitivity

gradient than do any of the chromatic stimuli.

The foveal thresholds showed the widest variation among the

three chromatic and the achromatic stimuli. A 3-way analysis of

variance was performed on the foveal thresholds (see Table 5) and this

variation with stimulus colour was found to be statistically signifi-

cant ($\alpha < .01$), with the red stimulus yielding significantly higher

sensitivity than the green, which showed higher sensitivity than the

Table 5

Analysis of Variance for Photopic Foveal Thresholds

Source	df	SS	MS	F	p
Colour	3	1.4965	0.4988	68.6074	0.0000
Size	3	3.6215	1.2072	141.6724	0.0000
Colour x Size	9	0.0975	0.0108	1.3277	0.2571

blue and achromatic stimuli (Newman-Keuls Range Test, α = .05). Again, the statistical differences must be interpreted with caution, but the same general pattern is apparent from the plotted foveal sensitivities which indicate the decreasing sensitivity to red, green, and blue, and achromatic stimuli.

The variability of the increment thresholds obtained as a function of retinal location and stimulus size and chromaticity is indicated by the standard deviations shown in Tables 6 and 7. (Complete tables of means and standard deviations for all conditions may be found in Appendix II). From Table 6 it appears that the variability in thresholds obtained is highest in the periphery, decreasing as one moves toward the fovea. This is in agreement with previous investigations (Aulhorn & Harms, 1972). A notable exception to this trend for increasing variation with eccentricity was found at 20° temporal. The large standard deviation found at this point results from its proximity to the blind spot. The relatively small standard deviation at 40° nasal does not fit in with the trend for increasing variability with increasing eccentricity.

There is an indication of some association between stimulus size and variability in the thresholds obtained as shown in Table 7. For each stimulus chromaticity, the standard deviation decreases as stimulus size increases. Ir does not appear that variability changes as a function of stimulus chromaticity.

Fully-Scotopic Adaptation. The close similarity among gradients obtained using equivalent-sized blue, red, green, and achromatic stimuli under fully-photopic adaptation was not duplicated under fully-

Table 6

Average Standard Deviations for Photopic Thresholds

Obtained at Each Retinal Position

Position[*]	Standard Deviation
Nasal	
40°	0.13
30°	0.17
20°	0.14
15°	0.12
10°	0.09
5°	0.09
Fovea	
0°	0.10
Temporal	
5°	0.11
10°	0.13
20°	0.19
25°	0.14
30°	0.14
40°	0.19

[*]Retinal Eccentricity on 0-180° meridian.

Table 7

Average Standard Deviations for all Photopic Thresholds

Obtained with Each Colour-Size Combination

	Stimulus Size			
Stimulus Colour	1	2	3	4
Achromatic	0.16	0.14	0.14	0.12
Blue	0.13	0.14	0.13	0.08
Green	0.16	0.15	0.10	0.12
Red	0.18	0.13	0.13	0.12

scotopic conditions. Figure 15 shows the mean sensitivity gradients obtained under these conditions. For all stimulus sizes, the gradients indicate that the sensitivity at all non-foveal points (with two exceptions at 40° nasal) was in the order (highest to lowest sensitivity) blue, green, achromatic, and red. The sensitivity gradients obtained with the red stimulus were in each case from one to 1.5 log units lower than the gradients obtained with the achromatic stimuli.

A 4-way analysis of variance was carried out on the scotopic threshold data; the summary table appears in Table 8. As with the photopic ANOVA, there were significant first and second order interaction effects, so that the interpretation of significant effects must be made with caution. However, the main effect of size is obvious from Figure 15 as well as from the F-ratio, and a general main effect of colour is expected merely on the basis of the low red gradient. The Newman-Keuls Range Tests indicate, as well as significant differences among all four sizes, a significant difference between the red stimulus and all the others, between the blue and all others, but not between the green and the achromatic. It is interesting that no main effect of subject was found in the scotopic data, though some interactions involving this variable were found to be significant.

Before discussing the foveal thresholds obtained under fully-scotopic conditions, mention must be made of the limited reliability of these measures. As has been stated, verification of fixation is not possible under fully-scoptopic conditions without the aid of some objective method of assessing fixation such as an infra-red fixation monitor. It is not enough to say that thresholds were only obtained
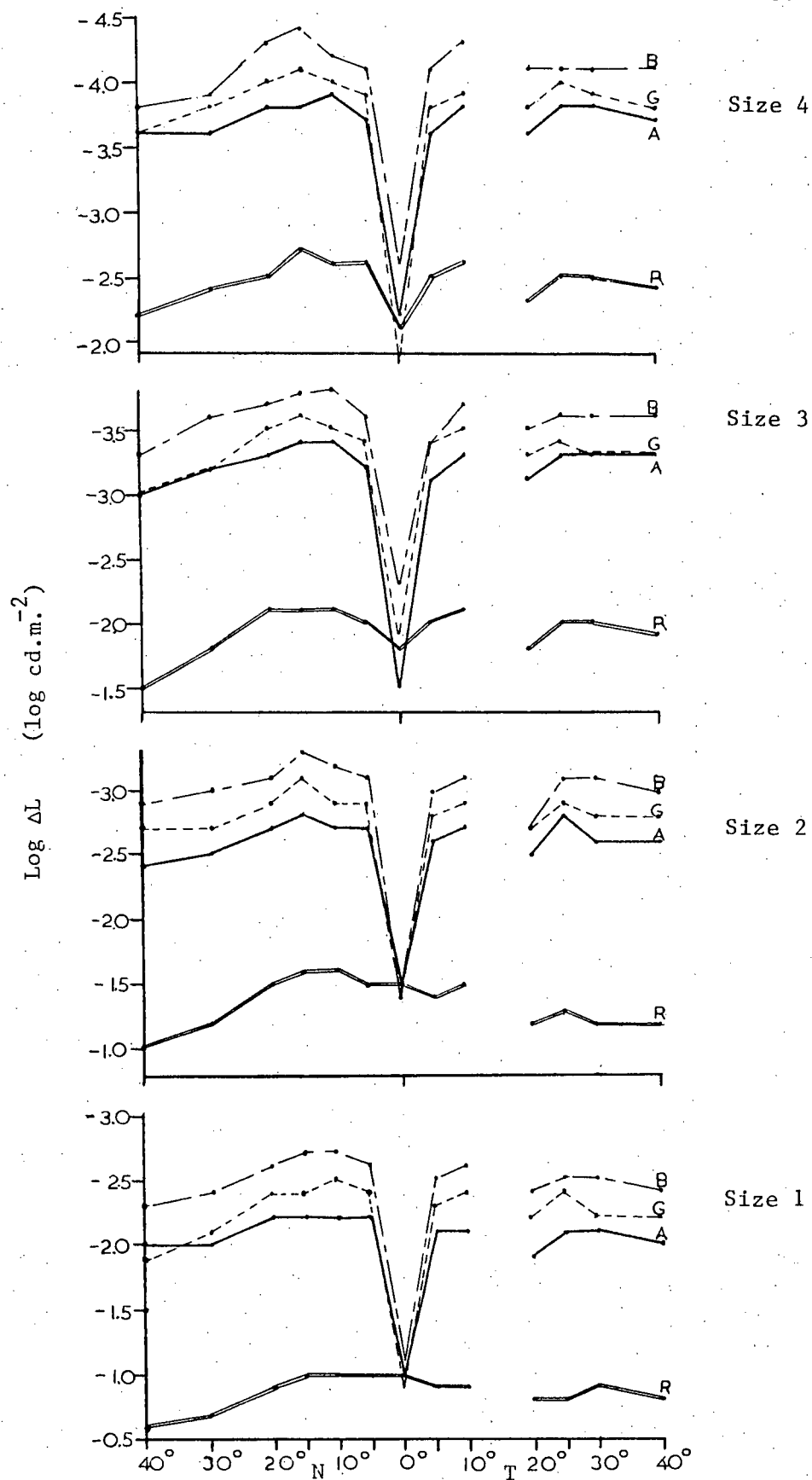
Figure 15 Mean fully-scotopic sensitivity gradients for blue(B), green(G), red(R), and achromatic(A) stimuli.

Table 8

Analysis of Variance for Scotopic Thresholds

Source	df	SS	MS	F	p
Colour	3	372.6065	124.2022	157.7455	0.0000
Size	3	362.9890	120.9963	1721.4514	0.0000
Colour x Size	9	0.2162	0.0240	0.8002	0.6180
Subject	4	0.8702	0.2176	2.1105	0.0931
Colour x Subject	12	1.4946	0.1246	3.2275	0.0004
Size x Subject	12	0.5398	0.0450	1.6320	0.0885
Colour x Size x Subject	36	1.8471	0.0513	2.0641	0.0004

when the subject felt he was fixating. In the present investigation,

it was not possible to obtain a fixation-monitoring device, so that

the foveal thresholds in particular (due to the sharp reduction of

sensitivity at the fovea, see section in the Introduction, "Adaptation")

cannot be considered precise measurements. An attempt was made to

maximize the validity of these measurements as follows. The foveal

threshold in each scotopic trial was assessed four times, as opposed

to once as for the other thresholds, using two fixation patterns at

slightly different luminances as described in 'Method.' An assumption

was then made that the highest threshold obtained (representing the

lowest sensitivity) was the best approximation to the actual foveal

threshold. This assumption was based first on the evidence that

scotopic sensitivity gradients do show a sharp decline in sensitivity

at the fovea; second, it was found that when a wide range of foveal

thresholds was found (sometimes on the order of .5 to 1.0 log unit)

for one trial, the subject reported that some of the lights he saw

were very bright, while others were of 'similar' brightness to the

other threshold values he responded to. The assumption is then that

the 'brighter' lights he saw were seen with the paracentral retina,

which has a much higher sensitivity. Thus, the values taken for

scotopic foveal thresholds were selected according to this system.

The foveal thresholds shown in Figure 15 were determined in the

way described above. (A complete table of all scotopic foveal thres-

sholds obtained is found in Appendix III.) It is apparent that for

sizes one and 2 the different colours and white gave virtually the

same mean foveal thresholds, while sizes 3 and 4 produced a spread in

these thresholds. For size 3 the order of decreasing sensitivity is
blue > green > red > achromatic, while for size 4 it is blue > achromatic
> red > green. Because of the indeterminacy of these values one must
be careful not to attribute too much significance to these differences.
Nonetheless, there does seem to be a consistent difference between the
blue and red thresholds of 0.5 log units for both sizes 3 and 4,
though these thresholds are within 0.1 log unit of each other for
sizes 1 and 2. A 3-way analysis of variance on the scotopic foveal
thresholds indicated that the main effect of colour on the scotopic
foveal thresholds expected on the basis of the differences seen in
Figure 15 for sizes 3 and 4 was not significant (see Table 9). The
main effect of size was significant ($\alpha < .01$), but no significant
interaction between size and colour was found.

In Figure 16 this effect of increased foveal sensitivity with
increased stimulus size is illustrated. There is a clear curvilinear
relationship evident for the red stimulus. A similar relationship
appears for the white and green stimuli if in several cases one highly
irregular threshold is removed and the mean for that colour and size
is recalculated. If this is done, the only stimulus not showing a
smooth curve is the blue. The irregular thresholds are not all ob-
tained from one subject, so that is it not a case of one subject with
completely different foveal sensitivity.

The red stimulus, besides yielding generally lower sensitivity
gradients, shows an interesting effect of size on foveal sensitivity:
as the size is increased, a 'dip' of relatively decreased sensitivity
is seen at the fovea. What is in fact occurring is that with the

Table 9

Analysis of Variance for Scotopic Foveal Thresholds

Source	df	SS	MS	F	p
Colour	3	1.6104	0.5368	2.0319	0.1624
Size	3	15.775	5.2585	35.2473	0.0000
Colour x Size	9	1.5491	0.1721	1.1089	0.3815
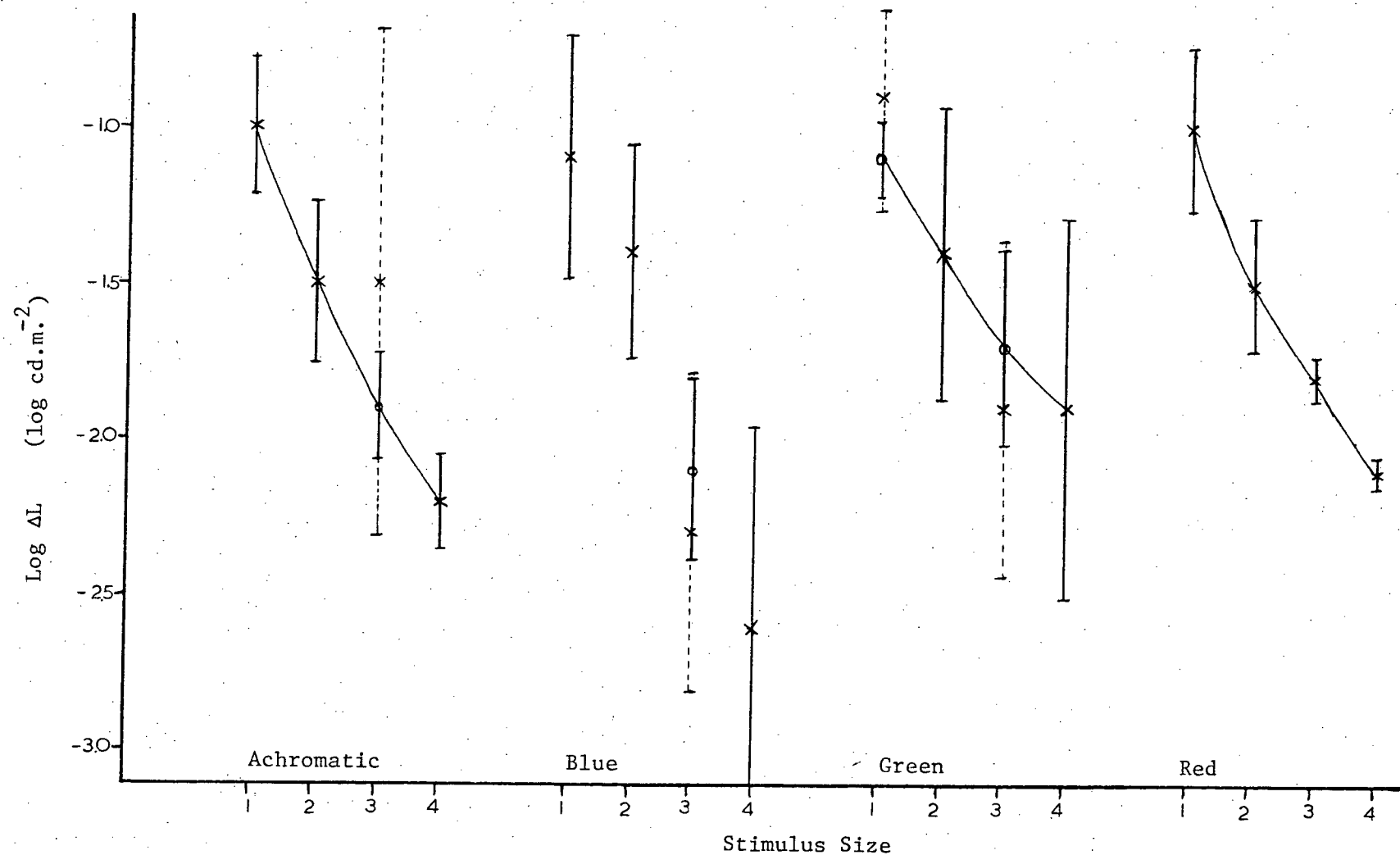
Figure 16   Means (X) and ranges of foveal scotopic thresholds,   sizes 1 to 4.   Broken lines indicate a range obtained without removing an extremely anomalous threshold.   See text for explanation.

larger sizes the paracentral sensitivity increases more rapidly than the foveal, resulting in the so-called 'relative central scotoma.' The general form of the red gradient for each of the four sizes is very similar except in the centre. It is possible that with the more accurate fixation control such a 'dip' would also be found for sizes 1 and 2.

Table 10 gives an indication of the variability in the scotopic thresholds determined, in the form of the average standard deviation for all thresholds obtained at each eccentricity. (A complete table of all means and standard deviations for all conditions may be found in Appendix IV.) The special problems involved in determining scotopic foveal thresholds are reflected in the large average standard deviation for the foveal measurements. Excluding the fovea, a general tendency for standard deviation to increase with increasing eccentricity is seen, with an exceptionally high value at 20° temporal due to its proximity to the blind spot. The relatively high standard deviation obtained at 5° temporal is another exception to the tendency for small variability to be found near the fovea. This could conceivably result from individual variation in the eccentricity at which the relative drop in sensitivity toward the fovea begins.

There was no consistant indication of a difference in variability for different stimulus sizes in Table 11, wherein the average standard deviations for all thresholds obtained with each stimulus size-colour combination are shown. There appeared to be some tendency for larger sizes to be associated with greater variability for the red and green stimuli, but the trend was not very pronounced. Such a trend would be

Table 10

Average Standard Deviations for Scotopic Thresholds

Obtained at Each Retinal Position

Position*	Standard Deviation
Nasal	
40°	0.16
30°	0.14
20°	0.11
15°	0.11
10°	0.12
5°	0.10
Fovea	
0°	0.37
Temporal	
5°	0.15
10°	0.11
20°	0.21
25°	0.13
30°	0.13
40°	0.16

*Retinal Eccentricity, 0–180° Meridian

Table 11

Average Standard Deviations for all Scotopic Thresholds

Obtained with Each Colour-Size Combination

Stimulus Colour	Stimulus Size			
	1	2	3	4
Achromatic	0.13	0.17	0.18	0.13
Blue	0.18	0.20	0.16	0.20
Green	0.15	0.14	0.18	0.17
Red	0.12	0.12	0.14	0.16

the converse of what was found under photopic conditions, where increasing size was accompanied by a decrease in the standard deviation. There are no indications that variability was different among the different colours.

Fully-Photopic and Fully-Scotopic Adaptation. When the thresholds obtained under the two adaptation conditions are compared, the following points can be made. First, when compared with the fully-photopic sensitivity gradients, the fully-scotopic gradients showed an increase in sensitivity over the photopic sensitivity on the order of 4.5 to 5 log units for all but the red stimulus and excluding the fovea (see Figure 17). The red stimulus yielded an increase in sensitivity of only 3 to 3.5 log units with the change from photopic to scotopic. At the fovea, the sensitivity increase was similar for all colours and the achromatic: on the order of 2 to 2.5 log units. In general, then, the sensitivity increase was found to be greatest outside the fovea for all colours, but of a smaller magnitude for the red stimulus. Second, fully-photopic adaptation yielded similar sensitivity gradients for the chromatic stimuli which were significantly higher than those for the achromatic stimuli, while fully-scotopic adaptation yielded gradients which were highest for the blue, followed by the green and achromatic, and lowest for the red stimulus. Third, both adaptation conditions yielded gradients which were significantly higher for each successive size increase. Fourth, while the photopic foveal sensitivity was the highest obtained across the retina, and showed significant higher sensitivity to blue than green, and to green than blue or achromatic, the scotopic foveal sensitivity was the lowest across the retina for

Mean fully-photopic sensitivity gradients for blue(O), green(△), red(×), and achromatic(·) stimuli. Adaptation luminance = 250 cd.m⁻².

Mean fully-scotopic sensitivity gradients for blue(B), green(G), red(R), and achromatic(A) stimuli.
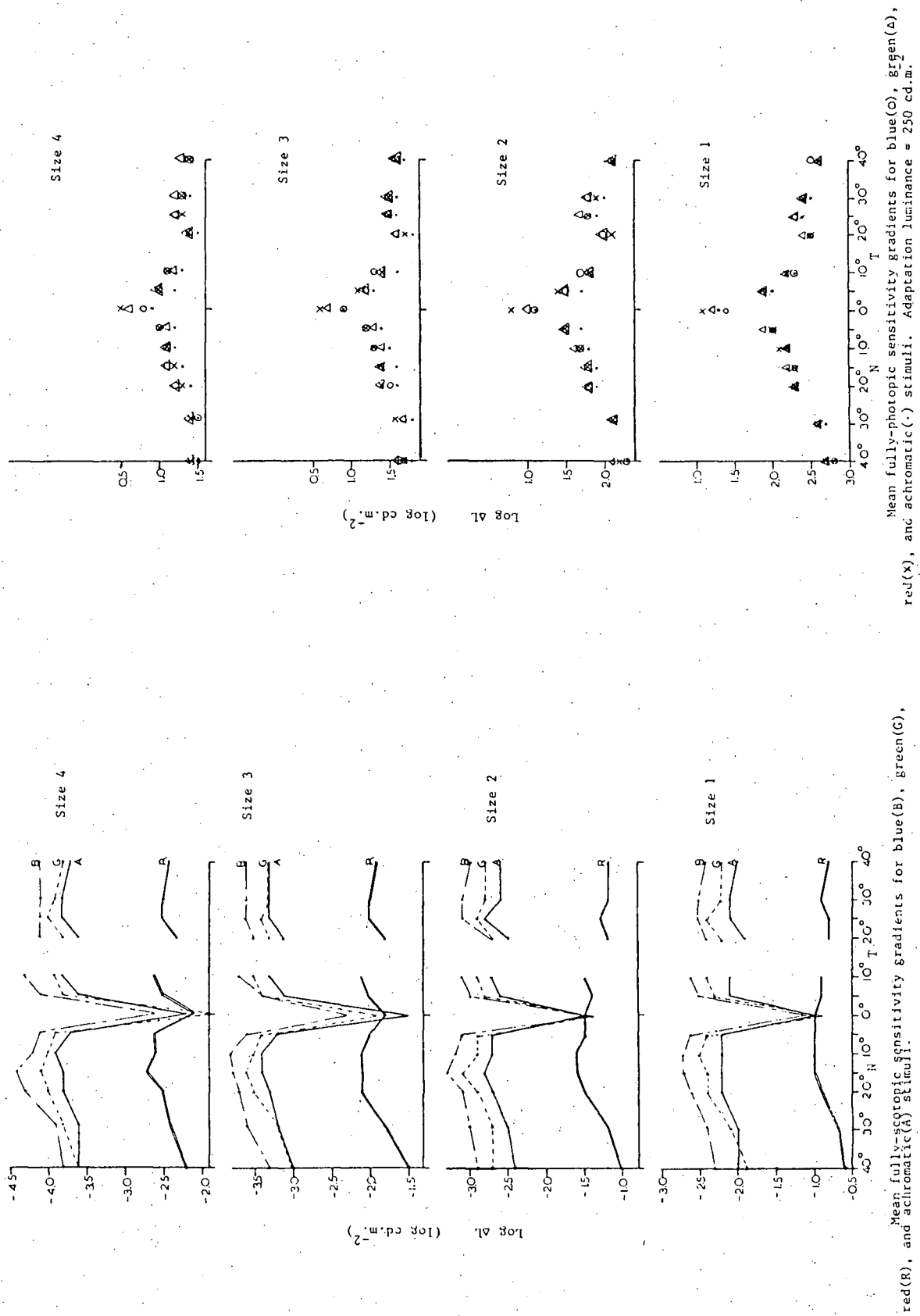
Figure 17

all but sizes 1-3 of the red stimulus, and did not show any significant differences among the colours. The scotopic gradient for the red stimulus did show a foveal 'dip' as did the blue, green, and achromatic, but only for the two larger sizes. Fifth, the photopic data showed a significant effect of subject, with the youngest subject showing significantly more and one of the (two) oldest subjects significantly less sensitivity. The scotopic data showed no significant subject main effect. Finally, photopic threshold variability as reflected by standard deviations appeared to increase with eccentricity and decrease with size, while for scotopic thresholds it seemed to increase with eccentricity but was highest at the fovea, and showed no consistent association with size. The variability in both photopic and scotopic threshold determination did not appear to vary consistently with stimulus chromaticity.

Spatial Summation

The summation capacity of the retina was studied using the same stimuli under fully-photopic and fully-scotopic conditions. The ability of the visual system to summate luminous input spatially may be investigated with the obtained perimetric data in two ways: by studying the change in sensitivity gradient slope with a change in stimulus size, or by calculating the summation exponent k at each retinal location of interest. Both of these approaches were used to gain insight into the spatial summation of the eye under fully-photopic and fully-scotopic adaptation.

Fully-Photopic Adaptation. The effect of an increase in stimulus size on the sensitivity gradient for each chromatic and achromatic

stimulus is shown generally by Figure 18. As well as the overall in-
crease in sensitivity with increased size, there was a tendency for
the gradients to become flatter. To gain a measure of this change,
it would be useful to determine the slope of the gradient. All the
photopic gradients had the same general form, with a sharp peak from
5° nasal and temporal to the fovea, and a more gentle slope from 5°
out to the periphery on both sides. The gradients were therefore
redrawn on the basis of only five retinal locations -- 40^ON, 5^ON, 0°,
5^OT, 40^OT -- thus dividing each gradient into four sections, each of
which had a measurable slope (see Figure 19). The peripheral segments
reflect the original 6-point gradient segments, and thus give an es-
timation of the change in threshold with eccentricity. The slopes
calculated for these gradients are presented in Table 12. For all
four segments of each gradient, it appears that the slope decreases
with increasing stimulus size, indicating that summation is greater
in the periphery than in the central field. The 'flattening' of the
foveal peak in the sensitivity gradient with increasing size, due to
this difference between the foveal and 5° eccentricity summation capa-
city, appears in Figures 18 and 19 to be more pronounced for the blue
and achromatic stimuli than for the green or red. However, the slopes
in Table 12 indicate that this is not the case, in that the red
stimulus 0-5° gradient segments show a slope decrease from size 1 to
size 4 which is as great or greater than that for the blue. It is
certainly true that the size 4 0-5° segments of the blue and achroma-
tic gradients have much smaller slopes than those of the red.

In order to compare the summation capacities quantitatively, the
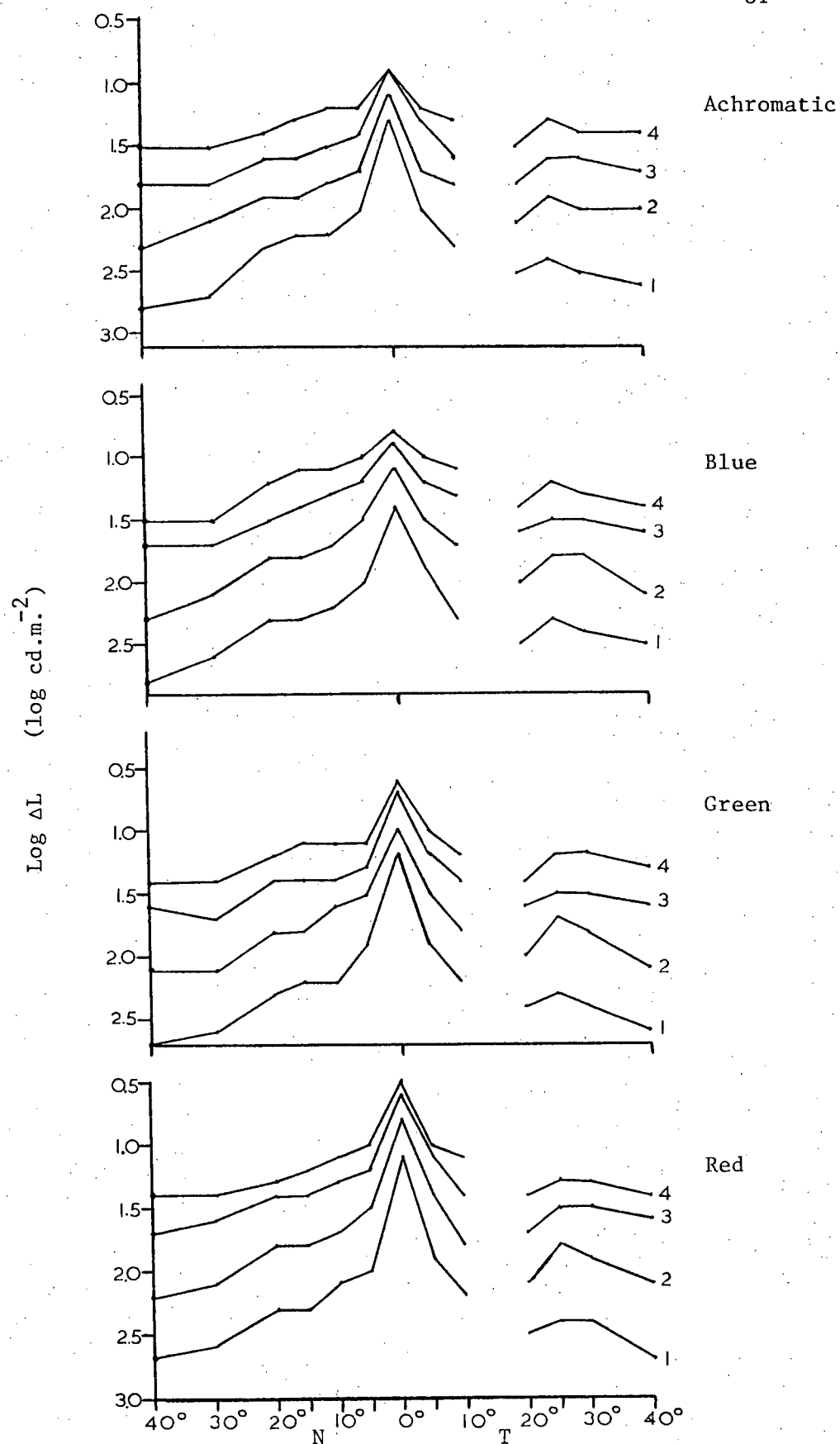
Figure 18 Mean fully-photopic sensitivity gradients, stimulus sizes 1-4.
Adaptation luminance = 250 cd.m.$^{-2}$
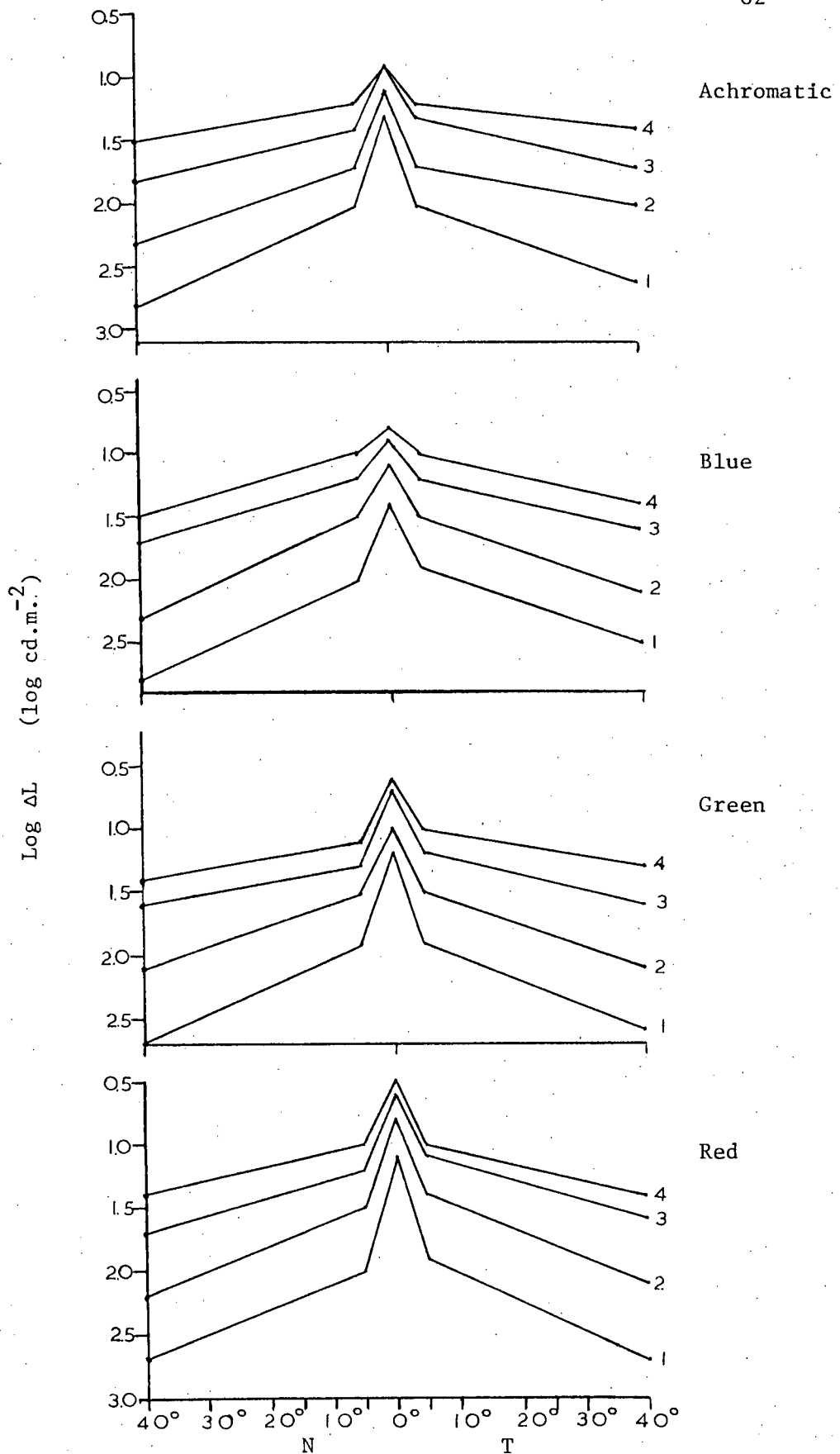
Figure 19 Mean fully-photopic sensitivity gradients, selected eccentric-
ities, stimulus sizes 1-4. Adaptation luminance = 250 cd.m.$^{-2}$

Table 12

Slopes of Photopic Gradient Segments

Gradient Segments	Stimulus Size			
	1	2	3	4
40^ON to 5^ON				
Achromatic	.023	.017	.012	.010
Blue	.023	.021	.015	.013
Green	.022	.016	.010	.019
Red	.021	.020	.016	.013
5^ON to 0°				
Achromatic	.144	.120	.096	.052
Blue	.112	.080	.056	.040
Green	.144	.112	.108	.092
Red	.180	.128	.116	.096
0° to 5^OT				
Achromatic	-.136	-.112	-.084	-.060
Blue	-.096	-.076	-.048	-.032
Green	-.140	-.112	-.100	-.080
Red	-.164	-.120	-.108	-.100
5^OT to 40^OT				
Achromatic	-.019	-.010	-.012	-.006
Blue	-.019	-.016	-.013	-.012
Green	-.019	-.016	-.009	-.009
Red	-.020	-.020	-.004	-.012

summation exponent k was calculated at all retinal locations according to formula (3) (see Introduction and Figure 20). The mean k values obtained for the locations 40° and 5° nasal, 0°, and 40° and 5° temporal are presented in Table 13 and Figure 21. (A complete table of all mean k values may be found in Appendix V.) It seems that in most cases, summation, as reflected by the magnitude of k, increased with eccentricity. Figure 21 also indicates that summation decreased as size increased. This effect appeared to be greatest in the perphery and generally smallest at the fovea. It is of interest that the mean value of k for the green stimulus, sizes 1 and 2 at 40° nasal exceeded the theoretical limit of k = 1.

It is also notable that the mean foveal k value for sizes 3 and 4, achromatic stimulus, was equal to zero, implying no summation.

The extreme values obtained for k (see Figure 20) and the lack of any but the most general regularity in this quantity are characteristic of other determinations of k (Gougnard, 1961). The variability in k values obtained as a function of retinal location, size combination, and colour can be seen in the standard deviations presented in Tables 14 and 15. The standard deviations are quite large right across the retina, including the fovea, and do not differ in a regular way among the stimulus colours or size-comparisons.

Fully-Scotoptic Adaptation. The increase in scotopic sensitivity resulting from an increase in stimulus size is shown in Figure 22 for all chromaticities. The scotopic gradients can not be so neatly divided into four segments as could the photopic gradients. The low foveal sensitivity creates a depression of varying depth in each

Achromatic

Blue

Green

Red

Summation exponent 'K'

40° 30° 20° 10° 0° 10° 20° 30° 40°
N   T
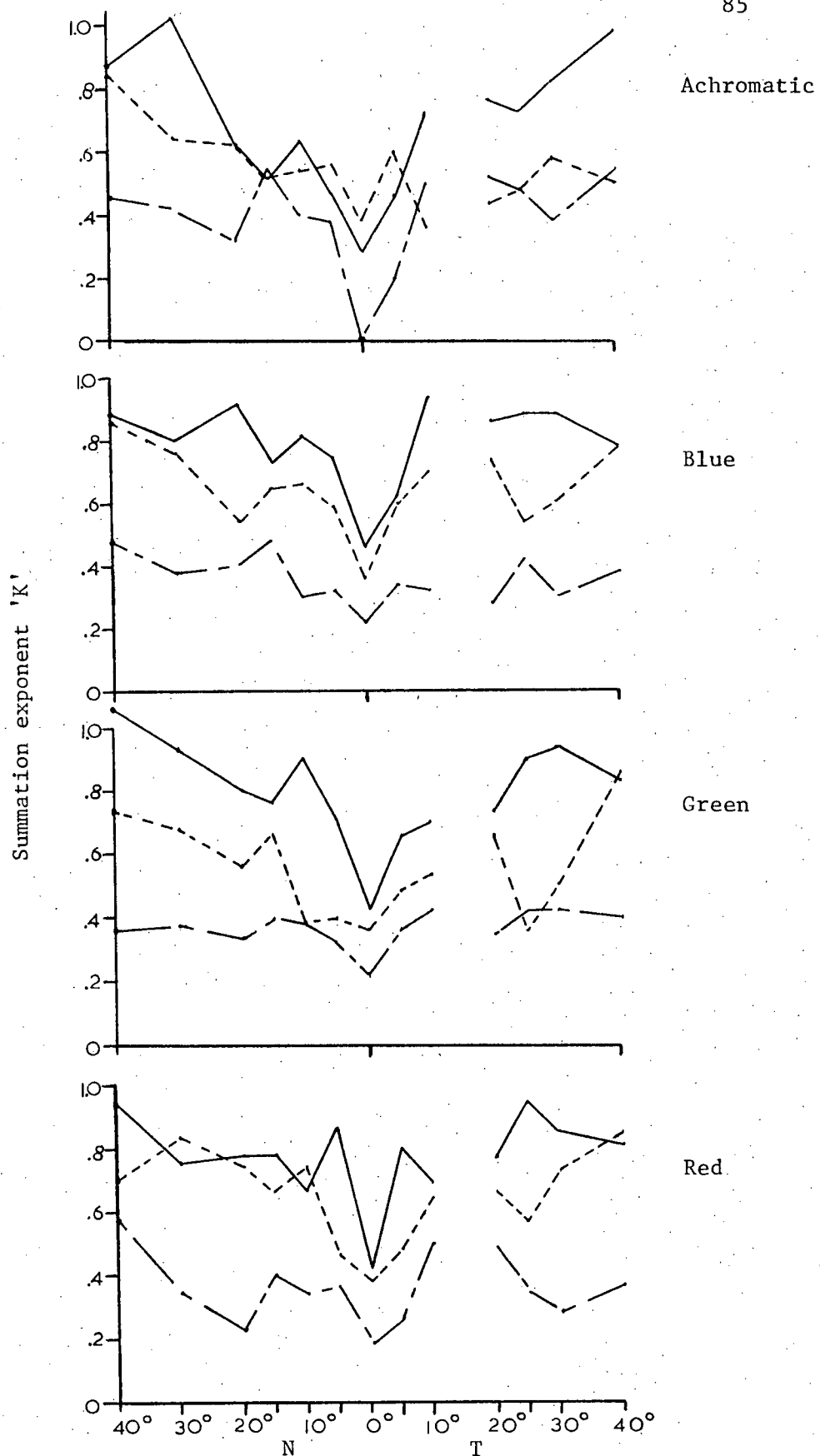
Figure 20   Fully-photopic summation exponents (k) for Goldmann stimulus
sizes 1-2 (——), 2-3 (---), and 3-4 (←—).

Table 13

Mean Photopic k Values at Selected Eccentricities

Stimulus		Retinal Location, 0-180° Meridian				
Sizes Compared	Colour	40°N	5°N	0°	5°T	40°T
1-2	Achromatic	0.86	0.46	0.28	0.46	0.98
	Blue	0.88	0.74	0.46	0.62	0.78
	Green	1.06	0.72	0.42	0.66	0.84
	Red	0.94	0.86	0.42	0.80	0.80
2-3	Achromatic	0.84	0.56	0.38	0.60	0.50
	Blue	0.86	0.58	0.36	0.60	0.78
	Green	0.74	0.40	0.36	0.48	0.86
	Red	0.70	0.46	0.38	0.48	0.84
3-4	Achromatic	0.46	0.38	0.00	0.20	0.54
	Blue	0.48	0.32	0.22	0.34	0.38
	Green	0.36	0.32	0.22	0.36	0.40
	Red	0.58	0.36	0.18	0.26	0.86
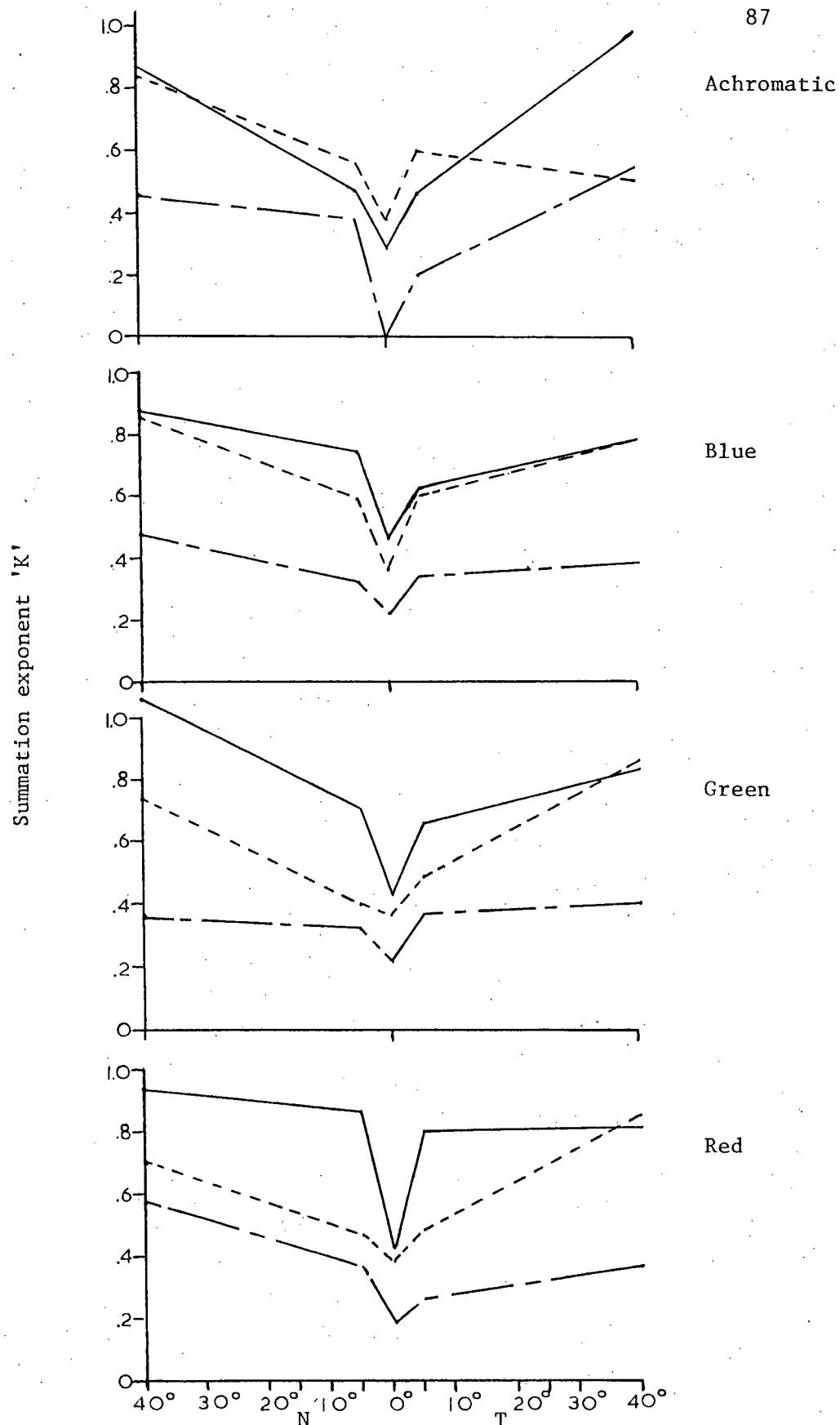
Figure 21   Mean fully-photopic summation exponents (k), at selected eccentricities, for Goldmann stimulus sizes 1-2 (——), 2-3 (----), & 3-4 (— —).

Table 14

Average Standard Deviations for Photopic k Values Obtained

at Each Retinal Position (k_{1-2}, k_{2-3}, k_{3-4})

Position*	Standard Deviation
Nasal	
40°	0.23
30°	0.25
20°	0.25
15°	0.17
10°	0.14
5°	0.17
Fovea	
0°	0.21
Temporal	
5°	0.19
10°	0.15
20°	0.22
25°	0.20
30°	0.17
40°	0.24

*Retinal Eccentricity, 0–180° Meridian

Table 15

Average Standard Deviations for All Photopic k Values Obtained

with Each Colour-Size Combination

	Sizes Compared		
Colour	1-2	2-3	3-4
Achromatic	0.20	0.18	0.19
Blue	0.20	0.16	0.18
Green	0.23	0.21	0.20
Red	0.20	0.15	0.20
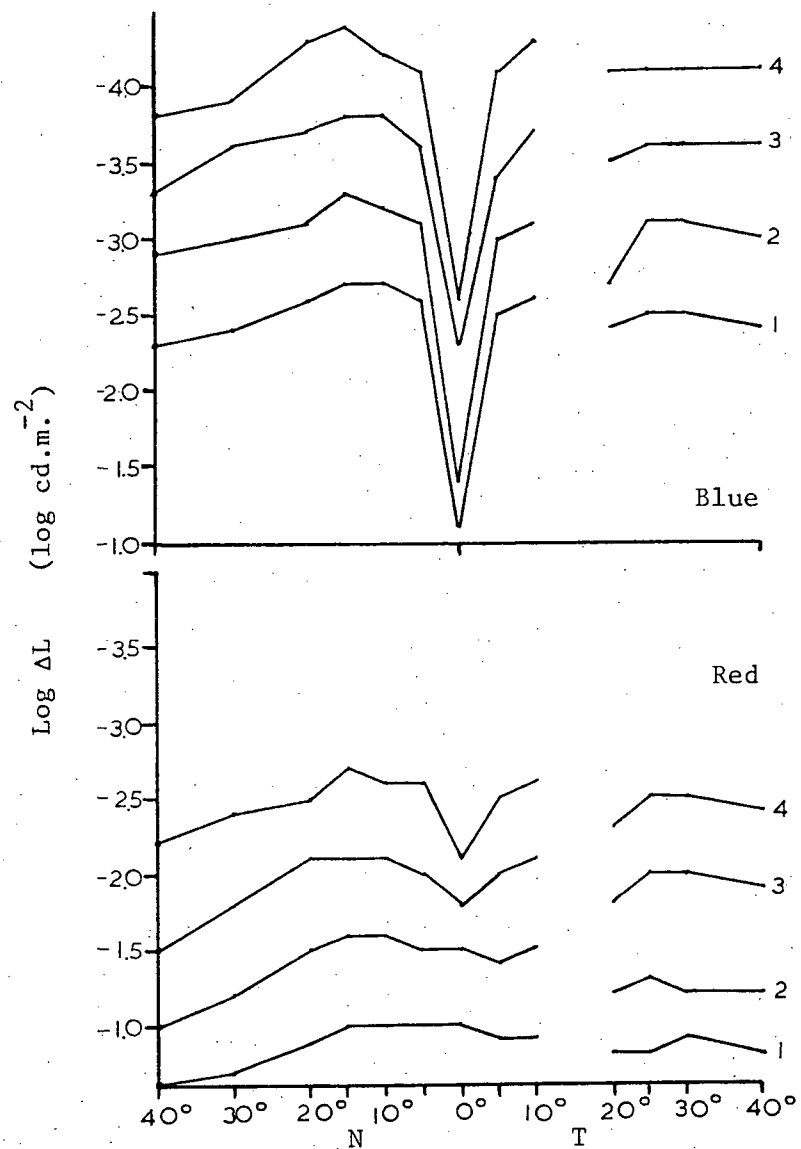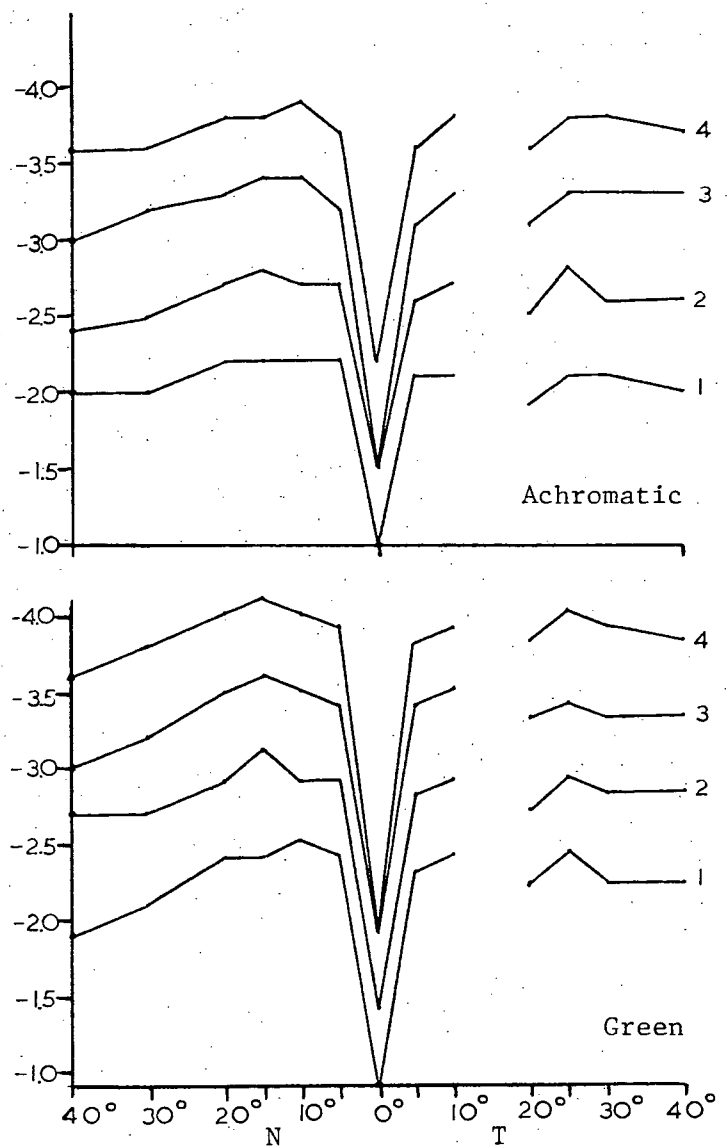
Figure 22   Mean fully-scotopic sensitivity gradients, Goldmann stimulus sizes 1-4.

gradient. The effect of increasing stimulus size on the foveal sensitivity is best seen in Figure 16, where certain highly atypical thresholds have been removed. As a result, each colour shows a regular increase in sensitivity with size except the blue, which shows only a small sensitivity change between sizes 1 and 2 and sizes 3 and 4, but a large change between sizes 2 and 3.

Aside from the fovea, the scotopic gradients can be divided into four segments on the basis of general slope, but the division at one point is different for the achromatic than for the chromatic stimuli. The slope of the gradients for the chromatic stimuli is positive from 0° to 15° nasal, negative (or occasionally 0) from 15° to 5° nasal, positive from 5° to 10° temporal, and negative from to 40° temporal (Figure 23). The achromatic stimulus shows a similar pattern except that the point of inflection in the nasal field is at 10° rather than 15° in two cases, and at 15° in only one (the $10^{\circ}-5^{\circ}$ slope is zero in the fourth case) (see Figure 22). The slopes for the chromatic segments are shown in Table 16. There did not appear to be any consistent trend for the slope of the $40^{\circ}-15^{\circ}$ nasal or $5^{\circ}-40^{\circ}$ temporal segments to be associated with an increase or decrease in stimulus size. However, the $15^{\circ}-5^{\circ}$ and $5^{\circ}-10^{\circ}$ segments showed in most cases (excepting the blue and green $5^{\circ}-10^{\circ}$ temporal segments) an increase in slope with an increase in stimulus size. This would seem to indicate that spatial summation is greater at 15° nasal than 5° nasal, and at 10° temporal than at 5° temporal. The lack of any clear relationship between the slopes of the more peripheral segments and increasing size would seem to indicate that summation is not in
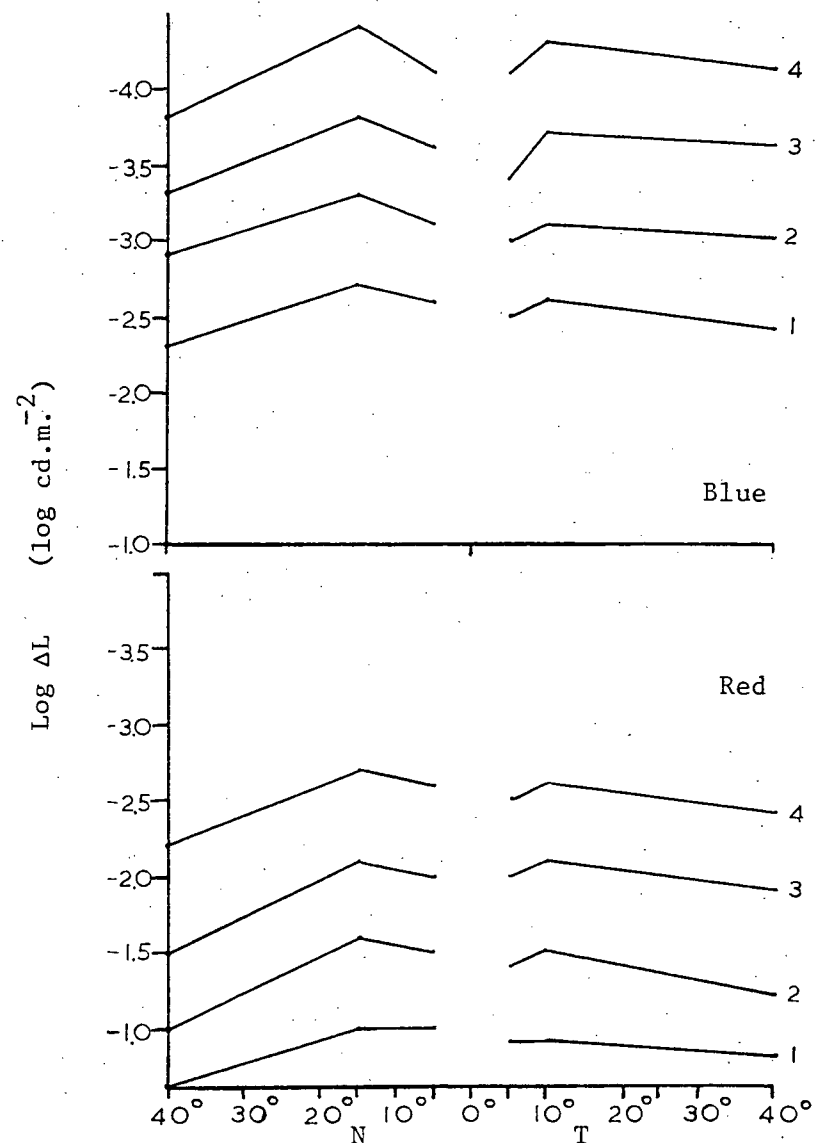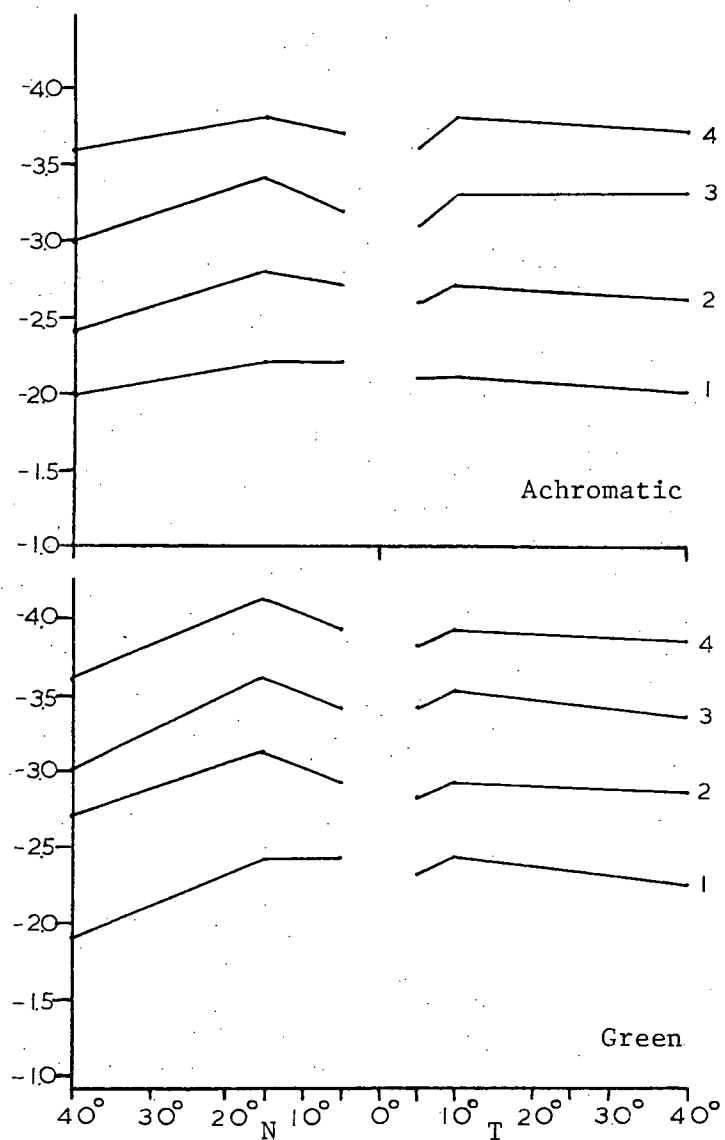
Figure 23 Mean fully-scotopic sensitivity gradients, selected eccentricities, Goldmann stimulus sizes 1-4.

Table 16

Slopes of Scotopic Gradient Segments

Gradient Segments	Stimulus Size			
	1	2	3	4
$40°N$ to $15°N$				
Blue	.016	.013	.019	.025
Green	.020	.016	.022	.018
Red	.017	.022	.024	.018
$15°N$ to $5°N$				
Blue	-.016	-.018	-.018	-.030
Green	.002	-.020	-.020	-.080
Red	.000	-.008	-.012	-.012
$5°N$ to $10°T$				
Blue	.016	.016	.060	.044
Green	.012	.016	.012	.032
Red	.000	.004	.024	.024
$10°T$ to $40°T$				
Blue	-.006	-.001	-.004	-.005
Green	-.007	-.005	-.005	-.006
Red	-.004	-.008	-.007	-.003

general higher in the far periphery than in the near periphery, under

scotopic conditions.

A quantitative assessment of the summation capacities reflected

by the change of gradient slope with increasing stimulus size was ob-

tained from the calculation of the summation exponent k (see Figure 24).

The mean values obtained at 40° and 5° nasal, 0°, 5° and 40° temporal

are presented in Table 17 and in Figure 25. (A complete table of all

mean k values may be found in Appemdix VI.) The k values obtained at

40° and 5° confirm the impression gained from Figure 23 that over all

and within each chromaticity, there is no clear increase in summation from

the near (5°) to the far (40°) periphery. The foveal mean k values

show no regularity at all, ranging from the theoretically impossible

-0.05 to the other extreme at +1.44, also far beyond the theoretical

limit of 1.0. The decrease in summation with increasing size found

for the photopic data is not characteristic of the scotopic data,

except perhaps for the red stimulus, which in the nasal fields shows

an increase in k as size decreases.

The wide variations in k across the retina, among stimulus size-

comparisons and colours (Figure 24) might appear to reflect the absence

of any regularity in summation capacity at all. However, from the

standard deviations shown in Tables 18 and 19 it appears that the

variability in the determination of k is considerable, and as such

may easily be obscuring any regularity existing. This variability

appears to be somewhat greater in the periphery, with very high values

at 20° nasal and temporal, but is greatest of all at the fovea. This

latter effect is to be expected considering the special problems inherent
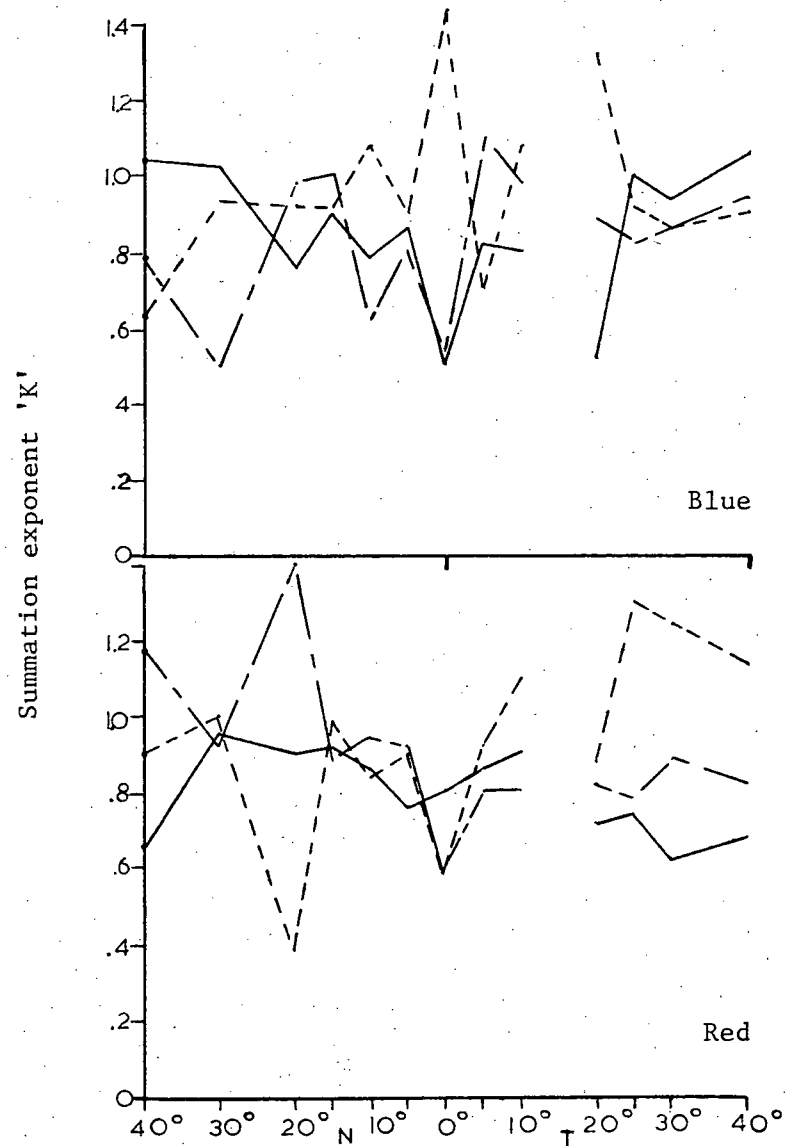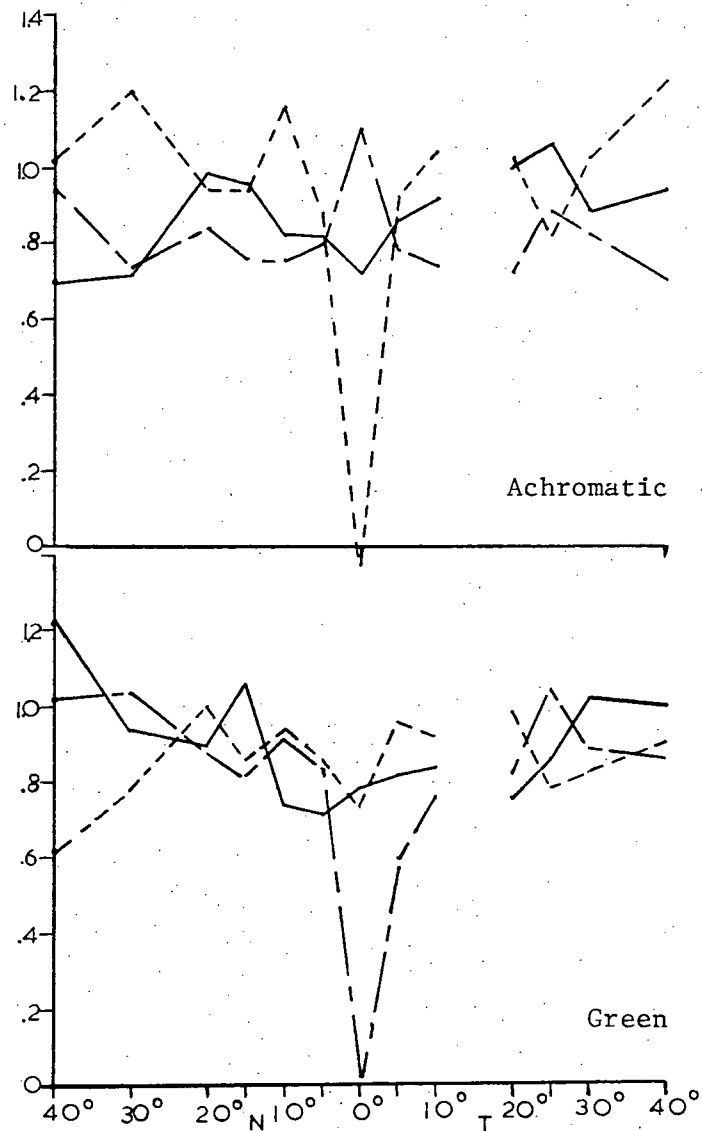
Figure 24   Mean fully-scotopic summation exponents (k) for Goldmann stimulus sizes 1-2 (——), 2-3 (---),
and 3-4 (–—).

Table 17

Mean Scotopic k Values at Selected Eccentricities

Stimulus		Eccentricity, 0-180° Meridian				
Sizes Compared	Colour	40°N	5°N	0°	5°T	40°T
1-2	Achromatic	0.70	0.82	0.72	0.86	0.94
	Blue	1.04	0.86	0.50	0.82	1.06
	Green	1.22	0.72	0.78	0.82	1.00
	Red	0.66	0.76	0.80	0.86	0.68
2-3	Achromatic	1.02	0.88	-.50	0.92	1.22
	Blue	0.64	0.90	1.44	0.70	0.90
	Green	0.62	0.86	0.74	0.96	0.90
	Red	0.90	0.90	0.58	0.92	1.14
3-4	Achromatic	0.94	0.80	1.10	0.78	0.70
	Blue	0.78	0.80	0.54	1.10	0.94
	Green	1.02	0.84	0.02	0.60	0.86
	Red	1.18	0.92	0.58	0.80	0.82
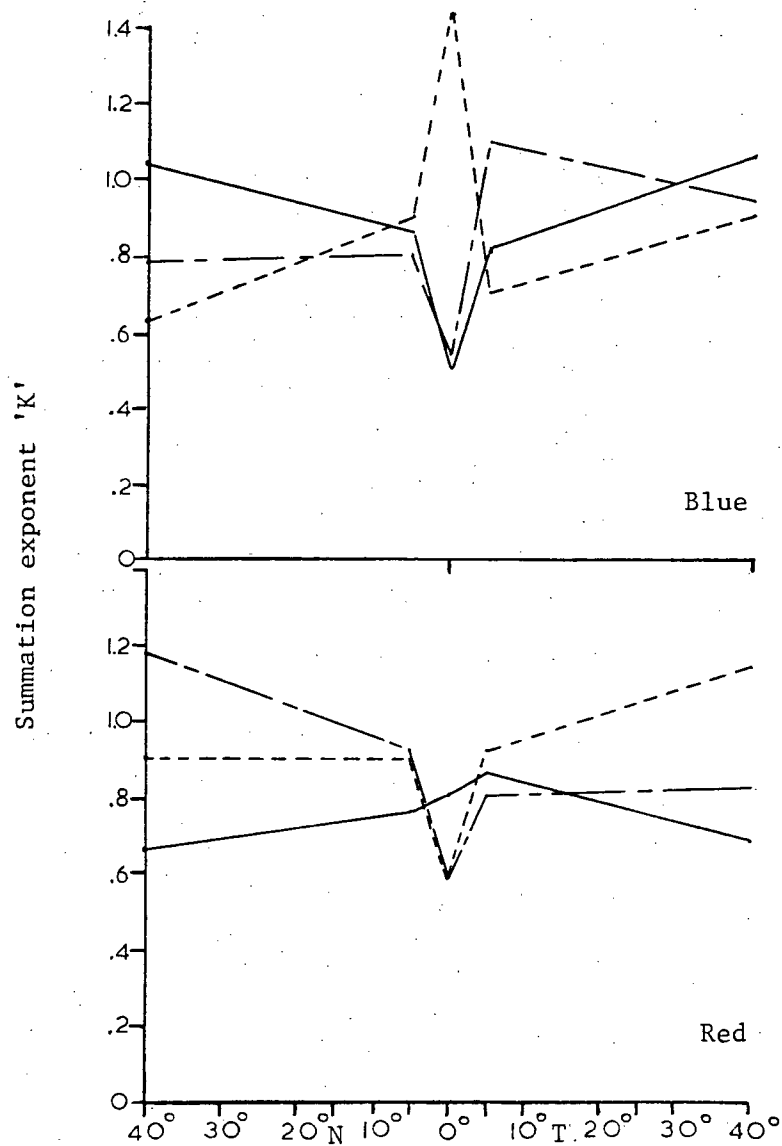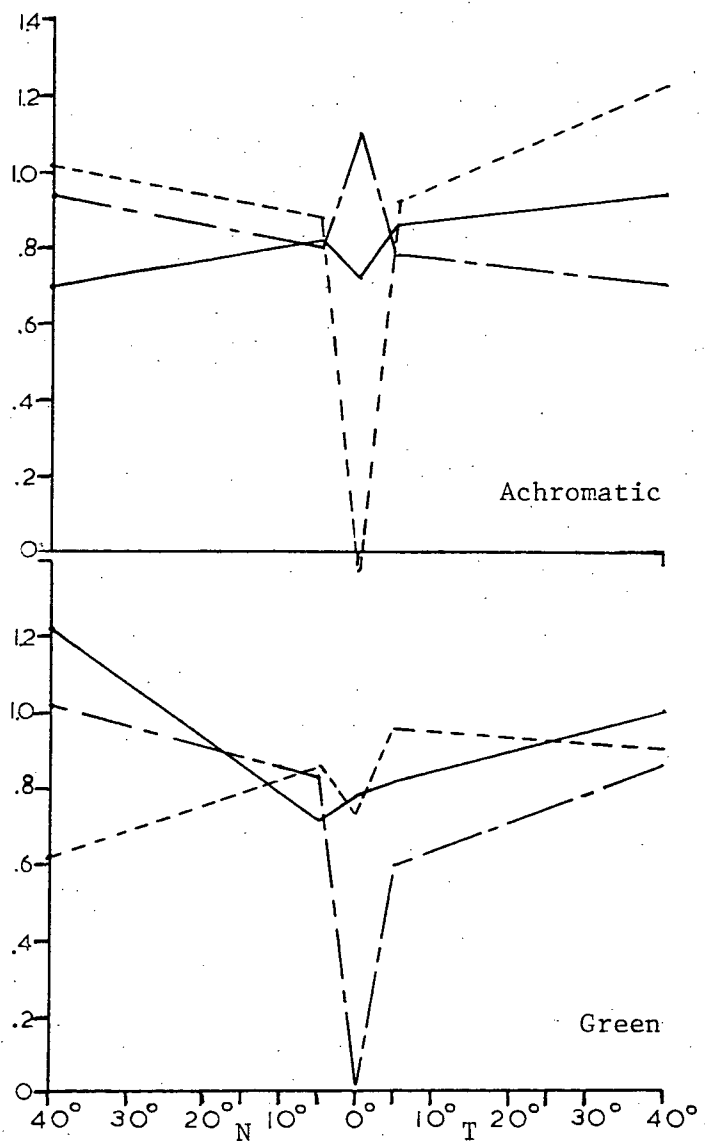
Figure 25   Mean fully-scotopic summation exponents (k), at selected eccentricities, for Goldmann stimulus sizes 1-2 (——), 2-3 (---), and 3-4 (—·—).

Table 18

Average Standard Deviations for Scotopic k Values Obtained

at Each Eccentricity (k_{1-2}, k_{2-3}, k_{3-4})

Nasal							Temporal					
40°	30°	20°	15°	10°	5°	0°	5°	10°	20°	25°	30°	40°
.28	.27	.46	.21	.21	.21	.80	.23	.20	.46	.27	.24	.32

Table 19

Average Standard Deviations for All Scotopic k Values

Obtained with Each Colour-Size Combination

Colour	Sizes Compared		
	1-2	2-3	3-4
Achromatic	0.24	0.37	0.35
Blue	0.34	0.38	0.36
Green	0.23	0.21	0.38
Red	0.26	0.40	0.32

in scotopic foveal threshold determination (see Results section on Fully-Scotopic Gradients). No clear association between the variability of k values and either stimulus size or colour (Table 19) was indicated.

Fully-Photopic and Fully-Scotopic Adaptation. A comparison of the summation capacity of the retina under fully-photopic and fully-scotopic conditions, as reflected by changes in gradient slope and values of the summation exponent k, indicated the following points. First, under photopic conditions summation seemed to increase with eccentricity, while no such trend was found for the scotopic data. Mean photopic k values ranged from 0.36 to 1.06 at 40° eccentricity, from 0.20 to 0.86 at 5° eccentricity, and from 0 to 0.46 at the fovea. Mean scotopic k values ranged from 0.62 to 1.22 at 40° and from 0.60 to 1.10 at 5° eccentricity. The range of mean scotopic foveal k values, from -0.05 to 1.44, may easily reflect methdological problems rather than variations in summation. Summation, therefore, appeared to be greater under scotopic than photopic conditions, both in the periphery and close to the fovea, though the difference was greater in the near than in the far periphery.

The second point is that summation seemed to decrease with an increase in stimulus size under photopic but not under scotopic conditions. This effect under photopic adaptation appeared to be greatest at the fovea.

Finally, there was a great deal of variability in the k values determined; average standard deviations ranged from 0.14 to 0.25 under photopic and from 0.21 to 0.38 under scotopic conditions. It would

seem then that the variability is greater in the scotopic condition. No association between stimulus chromaticity, size, or eccentricity, and the variability observed in k, seemed to characterize the photopic data. Such variability did seem to increase with eccentricity under scotopic conditons, but showed its highest value at the fovea.

DISCUSSION

Retinal Sensitivity Gradients

Fully-Photopic

The sensitivity gradients obtained under fully-photopic

conditions indicate that, outside the fovea, the retina's photopic

response system (assumed to be rod-free) on the horizontal meridian

was equally sensitive to chromatic stimuli which had been equated

photometrically in terms of V_λ. At the fovea this did not seem to be

the case; the foveal sensitivity under these conditions seemed to be

highest for the red, intermediate for the green, and lowest for the blue.

This presents a rather paradoxical picture. V_λ was established on the

basis of foveal measurements; hence it might be expected that the

process of equating the chromatic stimuli in terms of V_λ would yield the

same foveal threshold for all three chromatic stimuli. That this was

not found to be the case implies that either some assumptions made in

interpreting thedata as photometrically-equated stimuli are invalid, or

that some other variable is operating.

The assumptions made in the interpretation of the present data are

as follows.

1. The response-curve and calibration of the photometer is assumed

highly accurate, and the error introduced through interpolation of

spectral transmission values used to derive the cinemoid filter

correction factors is assumed negligible (see Appendix VII for a

complete description of the derivation of the correction factors).

With these assumptions, the stimuli can be considered photometrically-

equated in terms of V_λ.

2. V_λ is assumed applicable under high luminance conditions (L=250 cd.m.$^{-2}$), with small (6.18-54.3 minutes of visual angle) stimuli, using ascending method of limits perimetry. V_λ was derived under conditions of low luminance — for example, one of the studies contributing to the standard V_λ, that of Coblentz and Emerson (1918), used adaptation luminances as low as 1.5 cd.m.$^{-2}$. The stimuli used were 2 to 3°, and flicker and step-by-step heterochromatic photometric methods were used (Wyszecki and Stiles, 1967, LeGrand, 1968).

Fovea The data obtained under photopic conditions in the present study show some interesting patterns. First, the foveal sensitivity is highest to the red, followed by the green and then the blue stimulus. The achromatic yielded the same foveal sensitivity as the blue stimulus. The result is a sort of "reverse Purkinje effect": the opposite to that found under scotopic conditions. A similar effect has been found in preliminary studies done with these stimuli under mesopic (L=10 cd.m.$^{-2}$) conditions, so that it is not purely a result of fully -photopic adaptation. This implies that, granting the aforementioned assumptions, direct application of V_λ to foveal sensitivity as measured by increment-threshold static perimetry cannot be made.

Periphery In contrast to the differential effect of stimulus chromaticity on fully-photopic foveal sensitivity, outside the fovea all three chromatic stimuli yielded similar sensitivities. At each extra-foveal location tested, the red, green, and blue stimuli yielded thresholds within 0.1 to 0.2 log units of each other; no one colour yielded consistantly higher or lower thresholds. This contrasts with

the foveal thresholds, wherein the thresholds (in decreasing order)
were in all cases blue, green, and red, with differences as large as
0.6 log units between the thresholds for the red and blue stimuli.
The fact that photometrically-equivalent chromatic stimuli gave similar
extra-foveal but different foveal thresholds may be interpreted in terms
of the perceptual task required of the subject.

The subject was in all cases required to respond when he saw the
stimulus -- he did not need to identify its colour. Although no
systematic attempt was made to determine when the subjects could identify
the stimulus colour, some subjects reported that the stimulus appeared
coloured only when viewed foveally. If only foveal stimuli were
perceived as coloured, then foveal and extra-foveal threshold determinations
represented different tasks to the subject: the former a task of wave-
length discrimination, the latter a task of luminance-difference
detection. The experimental data support this hypothesis: extra-foveal
sensitivity would be expected to be similar for photometrically-equated
chromatic stimuli if the thresholds were based on luminance-difference
detection alone. The differential foveal chromatic thresholds are
expected if at the fovea the subject is required to make wavelength-
discriminations, as the ability to make such discriminations varies with
wavelength (Wright and Pitt, 1934). On the basis of wavelength
discrimination data, the order of foveal sensitivity expected would be
red > blue > green (ibid), while that found was red > green > blue. The
reversed order of the green and blue may be due to the small field sizes
used, as Willmer and Wright (1945) found with a 20' field discrimination
decreased considerably in the spectral region of the blue stimulus used

here. Most wavelength discrimination data has been obtained with larger

fields on the order of 1°-2° (Wyszecki and Stiles, 1967).

The extra-foveal achromatic sensitivities were similar to those for

the chromatic stimuli for the two smaller stimulus sizes, as was expected

under the interpretation of extra-foveal thresholds as derived from

luminance-difference detection. The lower sensitivity to the achromatic

as opposed to the chromatic for the largertwo stimulus sizes indicates

some interaction between spatial summation and the perceptual task being

performed. It is possible that with largerstimuli the task involves

hue-discrimination even outside the fovea . Determination of the precise

role played by hue-discrimination as opposed to luminance-difference

detection in the perimetric data presented here could be done by studying

the photochromatic interval under equivalent conditions.

Fully-scotopic

Interpretation of the fully-scotopic sensitivity gradients rests

on similar assumptions concerning photometric equalization and V_{λ} as did

the interpretation of the photopic gradients. In addition, the scotopic

thresholds are presumed (excluding the foveal thresholds) to represent

cone-free thresholds, while V_{λ} was presumed to apply strictly to the

cone system. Because of the indeterminacy of the scotopic foveal

thresholds the amount of reliable information to be gained from them is

limited, though no major differences among them as a function of

chromaticity were apparent , at least for the two smaller sizes (Figure 15).

Periphery The fact that all three chromatic stimuli yielded essentially

the same extra-foveal photopic thresholds may be considered when an

interpretation of the scotopic extra-foveal thresholds is sought.

Dark-adaptation, and with it the presumed switch to a cone-free

response system, yielded sensitivity gradients which differed significant-

ly among the chromatic stimuli. An increase in sensitivity was found

for all three colours, but this increase was generally greatest for the

blue, slightly less for the green, and considerably less (one to one

and one-half log units less) for the red (Figure 17). If the fovea is

disregarded, the gradients for all three chromatic (as well as the

achromatic) stimuli were of very similar form, being relatively flat

across the retina but showing a slight rise in the mid-periphery

(5°-15°). It is only in absolute sensitivity that they differ

(extra-foveally). The differences in sensitivity among the colours

reflect the (Purkinje) shift from V_λ to V'_λ with the blue yielding higher

sensitivity than the green, though each yielded similar sensitivity

gradients under photopic conditions. The very low sensitivity to the

red stimulus again seems to reflect the Purkinje phenomenon. In general

form the photopic and scotopic extra-foveal gradients are very similar,

excepting the relative increase in sensitivity in the 5-15° eccentricity

region which characterizes only the scotopic data. The implication

is that the change from fully-photopic to fully-scotopic adaptation

yields an increase inextra-foveal sensitivity, which is uniform across

the retina with the exception of a greater increase in the mid-peripheral,

5-15° eccentric regions.

Fovea In turning to the interpretation of the foveal scotopic

thresholds, complications arise due to the uncertain validity of scotopic

foveal measurements due to the lack of precise fixation control. To

estimate the relative depth of the foveal 'dip' in the various scotopic

gradients, use can be made of the slopes of the 15-5° nasal and 5-10°

temporal gradient segments (Table 16). A highly sloped gradient adjacent to the dip would indicate a deep foveal depression, as these segments represent the beginnings of the foveal 'scotoma'. On this basis the blue and green stimuli both yielded larger difference between mid-peripheral and foveal sensitivities - that is, they gave higher slopes - than did the red stimulus. This sensitivity difference between the fovea and the adjacent retinal areas generally increased with stimulus size, for all stimuli including the red.

The data thus indicate that under scotopic conditions the fovea is less sensitive than the adjacent retina to blue and green stimuli, and to red stimuli only for larger sizes. This lends support for an interpretation of the scotopic thresholds as rod thresholds outside the fovea and cone-thresholds within it.

The difference between 5° and 0° eccentricity scotopic thresholds for blue and green stimuli reflect the sensitivity difference between dark-adapted rods (at 5°) and cones (at 0°). The minimal difference between 0° and 5° thresholds for the red stimulus reflect the minimal increase in sensitivity of dark-adapted rods over dark-adapted cones to long wavelength stimuli.

It is not immediately clear why the red stimulus yielded a relative decrease in sensitivity at the fovea for only the larger stimuli, but this result agrees with the results of Nolte (1962) and Wentworth (1930). Nolte, with two red stimuli (599 nm and 658 nm) subtending 30' of visual angle did not find the foveal decrease, while Wentworth with a red stimulus (672.5 nm) subtending $1^{\circ}16'$ of visual angle did show the relative decrease at the fovea. In the present investigation the stimuli subtending 6.8' and 13.6' did not yield the foveal decrease, while those

subtending 27.2' and 64.3' did. On the basis of Nolte's data no foveal "relative scotoma" would have been expected with the 27.2' red stimulus. However, the trend for increasing size of the red stimulus to be associated with appearance of the foveal "scotoma" was a highly consistant finding in the present study. Moreover, this trend appears to characterize all the chromatic and achromatic scotopic data, as reflected by the increasing slope of 5°-0° gradient segments which gererally accompanies increasing stimulus size.

Two processes could explain the observed trend for increasing stimulus size (particularly for the red stimulus) to be associated with increasing difference between foveal and 5°-eccentricity sensitivity. Either the increased size is associated with a decrease in the foveal sensitivity, or with an increase in the para-central sensitivity. Figure 22 indicates that the latter explanation is the more likely, which would seem more logical in any case. This indicates then that the scotopic sensitivity increased proportionally more in the para-central than in the foveal retina with an increase in stimulus size. This is tantamount to saying that spatial summation was greater in the mid-periphery than it was in the fovea, an interpretation consistant with previous investigators (Sloan, 1961; Gougnard, 1961).

The distribution of retinal elements may be considered relevent to an interpretation ofthe photopic and scotopic gradients; figure 26 shows the retinal distribution of rods and cones. While there is no direct correlation between cone distribution and the photopic gradients, in general the peaked photopic gradient reflects very generally the cone density which is highest foveally and tapers off peripherally.
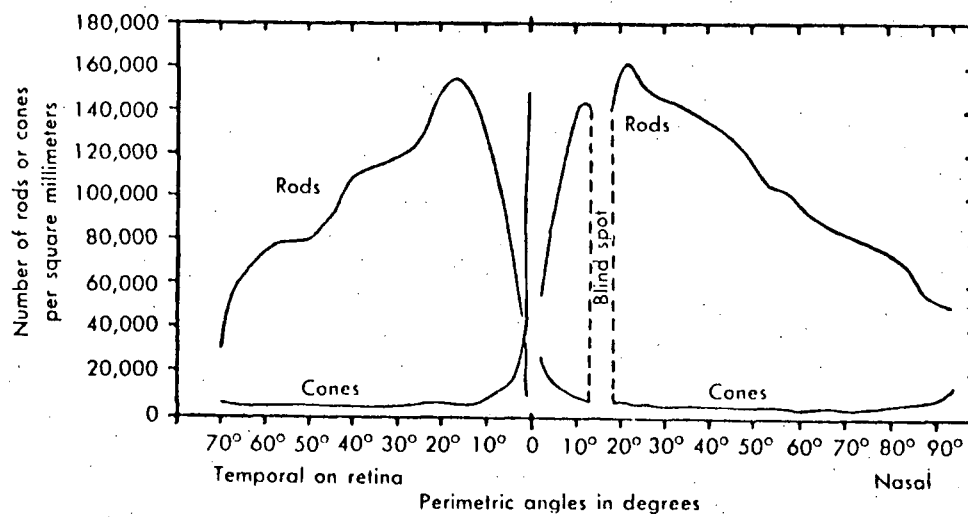
Figure 26 Distribution of rods and cones in human retina, based on Østerberg, 1935. From Moses, 1975, p. 382.

The extra-foveal scotopic gradients reflect rod distribution to the extent that both the highest rod density and the highest scotopic sensitivity fall in the mid-periphery. The lack of any precise correlation between receptor density and sensitivity is not surprising, as many other factors such as absorption by the ocular media affect sensitivity.

Throughout this discussion , many interpretations have been made based on the assumption that certain threshold measurements represent responses from either the rods or the cones. Hence, all foveal thresholds have been presumed to reflect cone sensitivity, while peripheral thresholds were presumed to represent cone sensitivities under photopic and rod sensitivities under scotopic adaptation. These assumtions are not held with equal certainty, however. While it seems quite certain that the photopic foveal measurements represent only cone sensitivities, it is less certain that the peripheral photopic measurements represent only cone sensitivities. Interpretation of the peripheral photopic data as purely cone sensitivities rests on the evidence of Aguilar and Stiles (1954) that the rods are saturated at an adaptation of 250 cd.m.$^{-2}$. under scotopic conditions it seems likely that the peripheral measurements represent only rod sensitivities, but it is with considerably less certainty that one states that scotopic foveal measurements represent only cone sensitivities due to the lack of precise fixation control. Because of the uncertainty of the relationships among the various sensitivities and the distribution of retinal elements, conclusions based on these relationships tend to take the form of tentative generalities rather than precise statements.

Before leaving the topic of sensitivity gradients, one further

cautionary note is necessary. An attempt has been made to interpret the

results obtained in terms of V_λ and of the retinal distribution of

photoreceptors. Although the C.I.E. 1924 V_λ curve is universally

accepted as the standard luminous efficiency curve, it is an average of

many individual curves. Individual luminous efficiency curves can differ

substantially from this average function (LeGrand, 1968). For example,

Coblentz and Emerson (1918) using flicker photometry found in 125

normal subjects a range of 549 to 570 nm for the peak of the luminous

efficiency curve. These represent departures up to 15 nm from the peak

of the C.I.E. 1924 V_λ. On the other hand, virtually all information on

the distribution of the rods and cones is based on only one human eye

(Østerberg, 1935). In the light of these facts, variation in any visual

function based on and interpreted in terms of these standards may be

expected to be considerable. Ideally for the present study, one would like

to determine each subject's individual luminous efficiency curve and

then photometrically equate the stimuli using his own V_λ. Were this done,

the results might be expected to be more easily interpretable, and would

in any case eliminate the error due to the departure of each subject's

visual system from the average standard system.

Spatial Summation

From the slopes of the sensitivity gradients obtained in this study

as well as the derived values of the summation exponent K, some

indication of the spatial summation capacities of the normal retina can

be seen. Spatial summation would appear to vary as a function of retinal

location, adaptation, and stimulus size, but the exact nature of the

interrelationships among these variables which may influence summation is far from clear. The measures of spatial summation used did seem to indicate a distinct difference in this capacity between the fully-photopic and the fully-scotopic retina.

Fully-Photopic

Under fully-photopic conditions, summation appeared to increase with distance from the fovea in a fairly regular fashion (Figure 20) for all chromatic and achromatic stimuli. This is in agreement with previous investigators who used achromatic stimuli under mesopic (10 cd.m.$^{-2}$) conditions (Farkhauser and Schmidt, 1958; Sloan, 1961; Gougnard, 1961). The results of these previous studies might be interpreted to indicate the increasing contribution of rods to the thresholds obtained under mesopic conditions as one moves peripherally from the fovea. However, if fully-photopic thresholds are assumed to be rod-free this cannot explain the present results. In this case it would appear that peripheral cones showed a greater capacity for spatial summation than did the central cones. This is consistent with the greater convergence of receptors, and the greater numbers of cones connecting with each horizontal cell, which characterize the peripheral as opposed to the cenral retina (Rodieck, 1973).

For all chromatic and achromatic stimuli under fully-photopic conditions it was also found that spatial summation varied inversely with stimulus size (Figure 20). This is also in agreement with previous investigations with achromatic stimuli under mesopic conditions (ibid). Thus spatial summation under photopic conditions is an important determinant of visual function for small stimuli of achromatic and

chromatic character.

Comparison of the present results with previous studies indicates then that spatial summation in the fully-photopic retina is similar to that in the mesopic retina, increasing with eccentricity and decreasing with stimulus size. In magnitude, summation as reflected by K seems to be greater in the mesopic than the fully-photopic condition (Table 20); this presumably reflects the contribution of rods to the mesopic thresholds.

Fully-Scotopic

Spatial summation under fully-scotopic conditions presents a different picture. First, there is a general increase in summation with the change from fully-photopic to fully-scotopic adaptation. This overall increase in summation from photopic to scotopic adaptation presumably reflects the change from cone to rod functioning. However, the relationships between summation and stimulus eccentricity and size found under photopic conditions were not duplicated under scotopic conditions. There did not appear to be any consistant relationship between spatial summation in the scotopic retina and either eccentricity (excluding the fovea) or stimulus size, over the ranges of eccentricity and size used. The lack of any consistant change in summation from the near to the far periphery under scotopic conditions implies that spatial summation involving the rod system does not precisely reflect rod distribution, despite the regularity of this distribution (Figure 26). Instead, scotopic extra-foveal summation appears to be independent of rod distribution and hence of eccentricity, and this independence seems to apply to all the chromatic and achromatic stimuli.

Table 20

K Values Obtained in Various Investigations With an Achromatic Stimulus

Eccentricity	Goldmann Sizes Compared	K Value Obtained			
		Sloan (1961)	Gougnard (1961)	Present Study I	II
$0°$	0-1		.49		
	1-2	.55	.39	.28	.72
	2-3		.17	.38	-.05
	3-4		.18	0	1.10
$15°N$	0-1		1.02		
	1-2	.75		.52	.96
	2-3			.52	.94
	3-4			.54	.76
$30°N$	0-1		.99		
	1-2	.88		1.02	.72
	2-3			.64	1.20
	3-4			.42	.74
$40°N$	0-1				
	1-2			.86	.70
	2-3			.84	1.20
	3-4			.46	.94
$45°N$	0-1				
	1-2	.90			
	2-3				
	3-4				

Adaptation: Sloan: C.I.E. Illuminant A, 10 $cd.m.^{-2}$
Gougnard: C.I.E. Illuminant A, 10 $cd.m.^{-2}$
Present Study I : C.I.E. Illuminant C, 250 $cd.m.^{-2}$
                        II : L = zero

The inverse relationship between spatial summation and stimulus size found in the photopic data has no clear parallel in the scotopic results; scotopic summation appears to vary in no consistant way with stimulus size for any of the chromatic or achromatic stimuli or sizes used.

The scotopic summation results imply that summation in the rod system does not vary in any predictable way with stimulus size, colour, or (non-foveal) retinal location. This contrasts with the situation under fully-photopic adaptation, wherein summation seems to vary directly as a function of eccentricity and inversely as a function of stimulus size. This difference may be related to the difference response systems presumed to be involved, the cones under photopic and the rods under scotopic conditions. However, such a conclusion may not be warranted in view of the wide variability in the summation exponents derived, especially as this variability was found to be greater under scotopic than photopic conditions.

The variability found in the summation exponent K is considerable under both photopic and scotopic conditions, though greater in the latter. This might seem to imply that the summation capacity of the retina is itself highly variable, even under an invariant set of conditions. However, the possibility exists that the variability in K reflects at least partially the variance in the threshold values from whick K is derived rather than variance in summation per se.

SUMMARY AND CONCLUDING REMARKS

The present investigation was designed to study the sensitivity

and spatial summation properties of the normal retina under well-defined,

precisely controlled conditions. The use of three chromatic stimuli (as

well as an achromatic) gave information on the differential sensitivity

of the retina to stimuli of varied spectral composition, while the use

of four stimulus sizes yielded data on the ability of the retina to

summate luminous input spatially. Thus sixteen stimulus size-

chromaticity combinations were presented at points on the horizontal

meridan to five emmetropic normal trichromatic observers under both

fully-photopic and fully-scotopic adaptation conditions . The use of

these two extreme adaptation luminances (250 and 0 cd.m.$^{-2}$) allowed the

separation of the photopic and scotopic response systems.

The results of these investigations may be summarized as follows:

1. Under fully-photopic conditions, the chromaticity of the stimulus

had no effect on extra-foveal sensitivity: all three chromatic stimuli

yielded equivalent mean gradients which were slightly higher than the

gradients yielded by the achromatic stimuli. Conversely, fully-photopic

adaptation yielded foveal thresholds which varied as a function of

stimulus chromaticity, the foveal sensitivities being (in decreasing order)

red, green, and blue. These results were discussed with reference to

the applicability of the standard C.I.E. 1924 luminosity function (V_λ) to

these conditions, the perceptual task required of the observer, and the

distribution of retinal receptors.

2. Fully-scotopic adaptation yielded extra-foveal sensitivity gradients

which were similar in form for all chromatic and achromatic stimuli,

being generally flat across the retina but showing a rise at 10°-15°

nasal and falling off toward the central field. The relative heights of

these gradients reflected the Purkinye shift from V_λ to V_λ', being in

decreasing order blue, green, and red. Dark-adaptation thus produced

the greatest increase in sensitivity to the blue and the least to the red

stimulus. The scotopic foveal thresholds were not clearly interpretable

due to the lack of precise control of fixation under scotopic conditions.

However, a major difference was found between the red stimulus, which

yielded slightly lower foveal sensitivity relative to the para-foveal

region only for the larger two stimulus sizes, and the other stimuli,

all of which yielded foveal sensitivities markedly reduced relative to

the para-foveal areas. These results were discussed with reference to

the earlier work of Wentworth (1930) and Nolte (1962). A notable

discrepancy was seen between the red stimulus sizes expected on the basis

of this earlier work to yield the "relative central scotoma", and those

which did yield such an effect. Distribution of retinal elements and

the indeterminacy of the scotopic foveal thresholds were also discussed.

3. Spatial summation under either adaptation conditions was not found

to vary in any systematic way with stimulus chromaticity. For all

chromatic and achromatic stimuli summation increased with eccentricity

and decreased with increasing stimulus size under fully-photopic condit-

ions, in agreement with previous investigations using achromatic

stimuli under mesopic (10 cd.m.$^{-2}$) conditions. No clear relationship

between summation and stimulus size or eccentricity was found under

scotopic conditions. The change from photopic to scotopic adaptation

conditions was associated with a general increase in spatial summation. These results were discussed with reference to the visual response systems assumed to be involved.

4. Variability in the determined thresholds and in the derived summation exponent k was found to be considerable under both adaptation conditions, but was not found to vary as a function of stimulus chromaticity. Variability in thresholds, as reflected by the standard deviation for mean thresholds, was found to increase with eccentricity under both fully-photopic and fully-scotopic adaptation, but to decrease with increasing stimulus size only under the former condition. In general variability was greatest at the fovea under scotopic conditions (presumably due at least in part to methodological problems). Variability in the summation exponent, as reflected by standard deviations of mean k values, was found to be greater under fully-scotopic conditions. The variability in the obtained data was discussed with reference to method-ological problems. Whether the variability in k reflected true variance in summation or merely variance in the threshold determinations on which k is based could not be determined.

These results have been interpreted as representing the character-istic response of the normal retina under the specific conditions des-cribed, and as such could be considered norms against which clinical data might be compared. Such applicability must take into account the dependence of this type of psychophysical data on the many stimulus, observer, and surround variables which together determine the response. In view of this fact, specification of these factors increases the scope of applicability of any such data. The results obtained from the present

investigation might be extended by the following experimental revisions:

1. Use of each subject's own empirically-derived V_λ, to equate the
chromatic stimuli photometrically, would aid in interpretation of
thresholds obtained with such stimuli under various conditions of
adaptation and stimulus size.

2. Assessment of whether the subject is perceiving the stimulus as
coloured or achromatic, and thus whether more than luminance-difference
detection is involved, might be determined under similar conditions
to those used here.

3. Precise control of fixation under scotopic conditions is manditory
for the determination of scotopic thresholds, particularly at the fovea.
This could be done using an infra-red camera system.

Reference Notes

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Note 2. Lakowksi, R. & Dunn, P.M. In preparation.

Note 3. Enoch, J.M. Draft two of the International Perimetric

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APPENDIX I

Counterbalancing

Subject	Testing Session	Trials Run Per Testing Session[a]						Adaptation
LL	1	W1	B1	R1	G1	B2		Photopic
	2	R2	G2	W2	R3	G3		
	3	W3	B3	G4	W4			
	4	B4	R4					
	5	W2	W3	W4	W1	B4		Scotopic
	6	G1	G2	G3	G4	B1		
	7	R3	R4	R1	R2	B2	B3	
AM	1	W1	B1	R1				Photopic
	2	G1	B2	R2	G2	W2		
	3	R3	G3	W3	B3			
	4	G4	W4	B4	R4			
	5	G1	G3	G4	G2			Scotopic
	6	W1	W2	W3	W4			
	7	R2	R3	R4	R1	B2		
	8	B3	B4	B1				
JL	1	G4	W4	B4	R4	W1	B1	Photopic
	2	R1	G1	B2	R2	G2	W2	
	3	R3	G3	W3	B3			
	4	G4	W4	B4	R4			Scotopic
	5	R1	R2	R3	B2	B3	B1	
	6	G3	G1	G2	W1	W2	W3	
RM	1	R3	G3	W3	B3			Photopic
	2	G4	W4	B4	R4			
	3	W1	B1	R1	G1			
	4	B2	R2	G2	W2			
	5	R1	R2	R3	R4			Scotopic
	6	B3	B4	B1	B2			
	7	G2	G3	G4	G1			
	8	W4	W1	W2	W3			

APPENDIX I continued

Subject	Testing Session	Trials Run Per Testing Session[a]					Adaptation
KH	1	B2	R2	G2	W2		Photopic
	2	R3	G3	W3	B3		
	3	G4	W4	B4	R4		
	4	W1	B1	R1	G1		
	5	W3	W4	W1	W2		Scotopic
	6	G2	G3	G4	G1		
	7	B1	B2	B3			
	8	R4	R1	R2	R3	B4	

[a] W = White (T_c = 6000K); B = blue; R = Red; G = Green.   e.g., B1 = Blue stimulus, size 1.

APPENDIX II

MEANS AND STANDARD DEVIATIONS FOR FULLY-PHOTOPIC THRESHOLDS

MEANS $(\log \mathrm{cd.m.}^{-2})$

ECCENTRICITY

		NASAL							TEMPORAL				
	40	30	20	15	10	5	0	5	10	20	25	30	40
W 1	2.8	2.7	2.3	2.2	2.2	2.0	1.3	2.0	2.3	2.5	2.4	2.5	2.6
W 2	2.3	2.1	1.9	1.9	1.8	1.7	1.1	1.7	1.8	2.1	1.9	2.0	2.0
W 3	1.9	1.8	1.6	1.6	1.5	1.4	.9	1.3	1.6	1.8	1.6	1.6	1.7
W 4	1.5	1.5	1.4	1.3	1.3	1.2	.9	1.2	1.3	1.5	1.3	1.4	1.4
B 1	2.8	2.6	2.3	2.3	2.2	2.0	1.4	1.9	2.3	2.5	2.3	2.4	2.5
B 2	2.3	2.1	1.8	1.8	1.7	1.5	1.1	1.5	1.7	2.0	1.8	1.8	2.1
B 3	1.7	1.7	1.5	1.4	1.3	1.2	.9	1.2	1.3	1.6	1.5	1.5	1.6
B 4	1.5	1.5	1.2	1.1	1.1	1.0	.8	1.0	1.1	1.4	1.2	1.3	1.4
R 1	2.7	2.6	2.3	2.3	2.1	2.0	1.1	1.9	2.2	2.5	2.4	2.4	2.6
R 2	2.2	2.1	1.8	1.8	1.7	1.5	.8	1.4	1.8	2.1	1.8	1.9	2.1
R 3	1.7	1.6	1.4	1.4	1.3	1.2	.6	1.1	1.4	1.7	1.5	1.5	1.6
R 4	1.4	1.4	1.2	1.2	1.1	1.0	.5	1.0	1.1	1.4	1.3	1.3	1.4
G 1	2.7	2.6	2.3	2.2	2.2	1.9	1.2	1.9	2.2	2.4	2.3	2.4	2.6
G 2	2.1	2.1	1.8	1.8	1.6	1.5	1.0	1.5	1.8	2.0	1.7	1.8	2.1
G 3	1.6	1.7	1.4	1.4	1.4	1.3	.7	1.2	1.4	1.6	1.5	1.5	1.6
G 4	1.4	1.4	1.2	1.1	1.1	1.1	.6	1.0	1.2	1.4	1.2	1.2	1.3

STANDARD DEVIATIONS

	40	30	20	15	10	5	0	5	10	20	25	30	40
W 1	.19	.15	.21	.16	.07	.15	.17	.13	.15	.22	.15	.15	.24
W 2	.24	.17	.11	.07	.10	.13	.05	.12	.15	.21	.15	.11	.18
W 3	.04	.15	.15	.13	.11	.07	.13	.15	.17	.23	.15	.15	.13
W 4	.09	.14	.11	.11	.06	.13	.08	.08	.12	.12	.13	.18	.13
B 1	.11	.16	.21	.13	.09	.09	.11	.07	.10	.24	.08	.13	.13
B 2	.31	.22	.13	.10	.08	.05	.09	.13	.09	.17	.13	.13	.19
B 3	.15	.18	.09	.13	.07	.07	.13	.13	.09	.13	.09	.16	.27
B 4	.11	.05	.08	.09	.07	.10	.10	.05	.05	.07	.07	.12	.11
R 1	.15	.19	.24	.24	.12	.13	.08	.12	.15	.27	.19	.15	.22
R 2	.05	.11	.17	.08	.04	.11	.11	.16	.16	.19	.18	.12	.24
R 3	.09	.16	.14	.12	.08	.06	.07	.11	.11	.20	.15	.11	.23
R 4	.17	.16	.11	.11	.09	.05	.15	.04	.08	.16	.11	.20	.16
G 1	.19	.29	.15	.13	.15	.11	.04	.08	.11	.16	.17	.23	.27
G 2	.11	.25	.19	.13	.11	.08	.05	.13	.17	.30	.18	.07	.19
G 3	.04	.11	.11	.08	.04	.04	.09	.05	.13	.16	.07	.10	.18
G 4	.07	.16	.11	.05	.05	.04	.18	.13	.13	.19	.09	.11	.15

W = Achromatic   B = Blue   G = Green   R = Red

Scotopic Foveal Thresholds

Stimulus			Log ΔL (cd.m.$^{-2}$)					Highest Threshold	
			Fixation A[b]		Fixation B[c]		Highest Threshold		
Colour	Size[a]	Subject	1	2	3	4	Obtained	$\bar{X}$	σ
Achromatic	6.8	LL	-1.1	-1.0	-1.6	-1.6	-1.0	-1.0	.22
		AM	-1.2	-1.1	-1.0	-1.0	-1.0		
		JL	-1.4	-1.3	-1.5	-1.4	-1.3		
		RM	-1.5	-1.1	-1.1	-1.5	-1.1		
		KH	-1.8	-1.7	-1.7	-1.7	-1.7		
	13.6	LL	-1.5	-1.3	-1.9	-1.8	-1.3	-1.5	.26
		AM	-1.9	-1.5	-2.2	-2.2	-1.5		
		JL	-1.9	-1.9	-1.9	-1.9	-1.9		
		RM	-1.6	-1.5	-1.3	-1.4	-1.3		
		KH	-1.6	-1.3	-2.1	-2.2	-1.3		
	27.2	LL	-2.1	-1.7	-2.1	-1.7	-1.7	-1.5	.81
		AM	-1.9	-1.9	-2.7	-2.5	-1.9	(-1.9)	(.17)
		JL	-0.3	-0.1	-0.5	-0.6	-0.1*		
		RM	-2.1	-1.8	-2.6	-2.5	-1.8		
		KH	-2.0	-2.1	-2.4	-2.3	-2.1		

Stimulus			Log ΔL (cd.m.$^{-2}$)				Highest Threshold Obtained	Highest Threshold	
			Fixation A[b]		Fixation B[c]				
Colour	Size[a]	Subject	1	2	1	2		$\bar{X}$	σ
Achromatic	54.3	LL	-2.4	-2.0	-2.5	-2.6	-2.0	-2.2	.15
		AM	-2.4	-2.5	-3.2	-3.1	-2.4		
		JL	-2.4	-2.2	-2.3	-2.3	-2.2		
		RM	-2.2	-2.1	-2.2	-2.1	-2.1		
		KH	-3.0	-2.2	-2.9	-2.8	-2.2		
Blue	6.8	LL	-1.1	-1.0	-2.2	-2.0	-1.0	-1.1	.39
		AM	-0.7	-0.7	-1.3	-1.1	-0.7		
		JL	-2.2	-1.6	-2.1	-2.2	-1.6		
		RM	-1.2	-0.9	-2.0	-1.3	-0.9		
		KH	-1.9	-1.5	-2.2	-1.8	-1.5		
	13.6	LL	-1.3	-1.5	-2.2	-2.2	-1.3	-1.4	.34
		AM	-2.3	-1.9	-2.8	-2.6	-1.9		
		JL	-2.0	-1.7	-2.2	-2.0	-1.7		
		RM	-1.4	-1.2	-1.5	-1.2	-1.2		
		KH	-1.1	-1.3	-2.8	-2.8	-1.1		
	27.2	LL	-1.8	-1.9	-2.6	-2.7	-1.9	-2.3	.51
		AM	-2.7	-2.3	-2.8	-3.3	-2.3	(-2.1)	(.29)
		JL	-3.1	-2.4	-2.9	-2.9	-2.4		
		RM	-1.8	-3.6	-1.9	-1.9	-1.8		
		KH	-3.2	-3.1	-3.8	-3.8	-3.1*		

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Stimulus			Log ΔL (cd.m.$^{-2}$)				Highest Threshold Obtained	Highest Threshold	
			Fixation A[b]		Fixation B[c]				
Colour	Size[a]	Subject	1	2	1	2		$\overline{X}$	σ
Blue	54.3	LL	−3.0	−2.8	−3.2	−3.2	−2.8	−2.6	.64
		AM	−2.4	−2.1	−2.4	−2.3	−2.1		
		JL	−3.3	−3.2	−3.8	−3.5	−3.2		
		RM	−2.4	−1.8	−2.4	−2.3	−1.8		
		KH	−3.3	−3.2	−3.4	−3.6	−3.2		
Red	6.8	LL	−1.1	−1.1	−1.1	−1.1	−1.1	−1.0	.26
		AM	−1.0	−1.0	−1.0	−0.9	−0.9		
		JL	−1.0	−1.0	−1.0	−1.0	−1.0		
		RM	−1.3	−1.3	−1.2	−1.2	−1.3		
		KH	−0.8	−0.6	−0.8	−0.9	−0.6		
	13.6	LL	−1.7	−1.7	−1.7	−1.7	−1.7	−1.5	.21
		AM	−1.2	−1.4	−1.3	−1;2	−1.2		
		JL	−1.6	−1.7	−1.6	−1.6	−1.6		
		RM	−1.6	−1.6	−1.5	−1.5	−1.5		
		KH	−1.3	−1.3	−1.3	−1.3	−1.3		
	27.2	LL	−1.9	−1.8	−2.0	−2.0	−1.8	−1.8	.07
		AM	−1.9	−2.1	−1.8	−1.8	−1.8		
		JL	−2.0	−1.9	−1.8	−1.8	−1.8		
		RM	−1.9	−1.9	−1.9	−1.9	−1.9		
		KH	−1.7	−1.8	−1.8	−1.8	−1.7		

Stimulus			Log ΔL (cd.m.$^{-2}$)				Highest Threshold Obtained	Highest Threshold	
			Fixation A[b]		Fixation B[c]				
Colour	Size[a]	Subject	1	2	1	2		$\bar{X}$	σ
Red	54.3	LL	-2.2	-2.2	-2.3	-2.2	-2.2	-2.1	.05
		AM	-2.2	-2.4	-2.1	-2.2	-2.1		
		JL	-2.2	-2.2	-2.2	-2.2	-2.2		
		RM	-2.1	-2.1	-2.2	-2.1	-2.1		
		KH	-2.2	-2.2	-2.3	-2.1	-2.1		
Green	6.8	LL	-1.0	-1.2	-1.2	-1.1	-1.0	-0.9	.37
		AM	-.07	-0.5	-0.6	-0.3	-0.3*	(-1.1)	(.12)
		JL	-1.3	-1.2	-1.5	-1.4	-1.2		
		RM	-1.0	-1.0	-1.1	-1.0	-1.0		
		KH	-1.7	-1.2	-1.9	-1.4	-1.2		
	13.6	LL	-1.5	-1.5	-2.2	-1.9	-1.5	-1.4	.47
		AM	-0.9	-0.9	-1.0	-0.8	-0.8		
		JL	-2.2	-2.1	-2.5	-2.4	-2.1		
		RM	-1.3	-1.3	-1.4	-1.4	-1.3		
		KH	-1.7	-1.5	-1.6	-1.4	-1.4		
	27.2	LL	-2.5	-1.8	-2.8	-2.7	-1.8	-1.9	.54
		AM	-1.2	-1.6	-1.9	-1.7	-1.2	(-1.7)	(.31)
		JL	-2.7	-2.7	-2.9	-2.9	-2.7*		
		RM	-1.8	-1.7	-2.4	-1.9	-1.7		
		KH	-2.6	-1.9	-2.5	-2.0	-1.9		

Stimulus			Log ΔL (cd.m.$^{-2}$)				Highest Threshold Obtained	Highest Threshold	
			Fixation A[b]		Fixation B[c]				
Colour	Size[a]	Subject	1	2	1	2		$\bar{X}$	σ
Green	54.3	LL	-2.2	-2.2	-2.7	-2.6	-2.2	-1.9	.61
		AM	-2.1	-1.6	-2.4	-2.5	-1.6		
		JL	-2.9	-2.8	-1.0	-1.0	-1.0		
		RM	-2.3	-1.9	-2.4	-2.2	-1.9		
		KH	-2.7	-2.6	-2.9	-2.8	-2.6		

[a] Size is in minutes of visual angle

[b] Fixation Devices, L < .15 cd.m.$^{-2}$, 2° visual angle

[c] Fixation Devices, L < .15 cd.m.$^{-2}$, 3.4^o visual angle

*Denotes a highly irregular threshold which was excluded to yield the Mean and Standard Deviation in brackets.

APPENDIX IV

MEANS AND STANDARD DEVIATIONS FOR FULLY-SCOTOPIC THRESHOLDS

MEANS $(\log \text{cd.m.}^{-2})$

ECCENTRICITY

	NASAL							TEMPORAL					
	40	30	20	15	10	5	0	5	10	20	25	30	40
W 1	-2.6	-2.7	-2.2	-2.2	-2.2	-2.2	-1.0	-2.1	-2.1	-1.9	-2.1	-2.1	-2.0
W 2	-2.4	-2.5	-2.7	-2.8	-2.7	-2.7	-1.5	-2.6	-2.7	-2.5	-2.8	-2.6	-2.6
W 3	-3.3	-3.2	-3.3	-3.4	-3.4	-3.2	-1.5	-3.1	-3.3	-3.1	-3.3	-3.3	-3.3
W 4	-3.6	-3.6	-3.8	-3.8	-3.0	-3.7	-2.2	-3.6	-3.8	-3.6	-3.8	-3.8	-3.7
R 1	-2.3	-2.4	-2.6	-2.7	-2.7	-2.6	-1.1	-2.5	-2.6	-2.4	-2.5	-2.5	-2.4
R 2	-2.9	-3.0	-3.1	3.3	-3.2	-3.1	-1.4	-3.0	-3.1	-2.7	-3.1	-3.1	-3.0
R 3	-3.3	-3.6	-3.7	-3.8	-3.8	-3.6	-2.3	-3.4	-3.7	-3.5	-3.6	-3.6	-3.6
R 4	-3.8	-3.5	-4.3	-4.4	-4.2	-4.1	-2.6	-4.1	-4.3	-4.1	-4.1	-4.1	-4.1
B 1	-.6	-.7	-.9	-1.0	-1.0	-1.0	-1.0	-.9	-.9	-.8	-.8	-.9	-.8
B 2	-1.0	-1.2	-1.5	-1.6	-1.6	-1.5	-1.5	-1.4	-1.5	-1.2	-1.3	-1.2	-1.2
B 3	-1.8	-1.8	-2.1	-2.1	-2.1	-2.0	-1.8	-2.0	-2.1	-1.8	-2.0	-2.0	-1.8
B 4	-2.2	-2.4	-2.5	-2.7	-2.6	-2.6	-2.1	-2.5	-2.6	-2.3	-2.5	-2.5	-2.4
G 1	-1.9	-2.1	-2.4	-2.4	-2.5	-2.4	-0.9	-2.3	-2.4	-2.2	-2.4	-2.2	-2.2
G 2	-2.7	-2.7	-2.9	-3.1	-2.9	-2.9	-1.4	-2.8	-2.9	-2.7	-2.9	-2.8	-2.8
G 3	-3.0	-3.2	-3.5	-3.6	-3.5	-3.4	-1.9	-3.4	-3.5	-3.3	-3.4	-3.3	-3.3
G 4	-3.6	-3.8	-4.0	-4.1	-4.0	-3.9	-1.9	-3.8	-3.9	-3.8	-4.0	-3.9	-3.8

STANDARD DEVIATIONS

	40	30	20	15	10	5	0	5	10	20	25	30	40
W 1	.13	.16	.15	.15	.11	.13	.22	.15	.11	.15	.08	.10	.10
W 2	.12	.23	.15	.19	.11	.04	.26	.19	.14	.16	.09	.11	.31
W 3	.20	.18	.14	.11	.11	.04	.17	.25	.13	.11	.14	.11	.37
W 4	.15	.22	.10	.05	.16	.07	.15	.12	.15	.19	.12	.09	.11
B 1	.18	.12	.23	.13	.16	.09	.39	.23	.14	.13	.14	.19	.16
B 2	.15	.12	.12	.15	.16	.04	.34	.16	.13	.65	.14	.23	.15
B 3	.13	.04	.11	.12	.08	.13	.51	.20	.11	.19	.09	.14	.18
B 4	.22	.18	.05	.12	.14	.19	.64	.18	.07	.17	.24	.22	.15
R 1	.21	.11	.13	.18	.11	.18	.26	.18	.08	.16	.09	.11	.13
R 2	.14	.13	.18	.17	.19	.15	.21	.19	.05	.05	.04	.05	.07
R 3	.19	.11	.11	.11	.15	.04	.07	.15	.11	.31	.15	.15	.15
R 4	.18	.19	.13	.11	.13	.11	.05	.13	.10	.43	.10	.13	.13
G 1	.25	.17	.21	.08	.15	.05	.37	.17	.12	.09	.08	.04	.11
G 2	.09	.10	.13	.11	.04	.09	.47	.18	.11	.12	.15	.11	.15
G 3	.05	.11	.15	.11	.11	.13	.54	.19	.13	.22	.19	.15	.20
G 4	.09	.08	.19	.04	.09	.19	.61	.16	.09	.27	.16	.16	.11

W = Achromatic   B = Blue   G = Green   R = Red

APPENDIX V

MEANS AND STANDARD DEVIATIONS FOR FULLY-PHOTOPIC SUMMATION EXPONENTS

MEANS

ECCENTRICITY

	MACULAR							TEMPORAL						
	40	30	20	15	10	5	0	5	10	20	25	30	40
W 1-2	.96	1.02	.62	.52	.64	.46	.28	.46	.72	.76	.72	.92	.98
W 2-3	.84	.64	.62	.52	.54	.56	.38	.56	.36	.44	.48	.58	.50
W 3-4	.46	.42	.32	.54	.40	.29	—	.38	.50	.52	.48	.38	.54
B 1-2	.88	.86	.92	.74	.82	.62	.46	.74	.94	.86	.98	.88	.78
B 2-3	.86	.76	.54	.64	.66	.58	.36	.58	.70	.74	.54	.60	.78
B 3-4	.48	.38	.40	.48	.30	.32	.22	.32	.32	.28	.42	.36	.38
R 1-2	.94	.76	.78	.78	.66	.80	.42	.86	.68	.76	.94	.84	.80
R 2-3	.70	.84	.74	.66	.74	.48	.28	.45	.64	.66	.56	.72	.84
R 3-4	.34	.34	.22	.42	.24	.26	.13	.36	.50	.48	.34	.28	.36
G 1-2	1.06	.94	.86	.76	.90	.66	.42	.72	.70	.74	.90	.94	.84
G 2-3	.74	.48	.56	.66	.38	.48	.36	.40	.54	.66	.36	.50	.84
G 3-4	.26	.38	.32	.46	.38	.32	.22	.32	.42	.34	.42	.42	.46

STANDARD DEVIATIONS

	MACULAR							TEMPORAL						
	40	30	20	15	10	5	0	5	10	20	25	30	40
W 1-2	.31	.18	.22	.26	.23	.27	.26	.27	.13	.05	.26	.11	.25
W 2-3	.21	.13	.11	.18	.22	.19	.22	.19	.13	.24	.20	.11	.20
W 3-4	.19	.24	.11	.17	.14	.28	.29	.28	.20	.20	.23	.18	.17
B 1-2	.41	.37	.18	.13	.11	.05	.23	.05	.15	.31	.11	.16	.13
B 2-3	.31	.18	.09	.13	.09	.11	.13	.11	.09	.25	.17	.22	.18
B 3-4	.23	.28	.14	.18	.09	.11	.18	.11	.11	.22	.11	.26	.31
R 1-2	.24	.18	.22	.36	.23	.25	.11	.25	.11	.18	.19	.09	.21
R 2-3	.12	.21	.05	.09	.05	.17	.22	.17	.13	.09	.24	.04	.27
G 1-2	.24	.21	.13	.22	.09	.13	.28	.13	.14	.20	.21	.29	.25
G 2-3	.10	.35	.21	.05	.26	.18	.11	.18	.12	.36	.30	.22	.42
G 2-3	.12	.46	.16	.15	.18	.20	.19	.20	.22	.29	.22	.14	.23
G 3-4	.15	.30	.06	.20	.11	.11	.46	.11	.30	.27	.11	.11	.26

APPENDIX VI

MEANS AND STANDARD DEVIATIONS FOR FULLY-SCOTOPIC SUMMATION EXPONENTS

MEANS

ECCENTRICITY

	NASAL							TEMPORAL					
	45	30	20	15	10	5	0	5	10	20	25	30	40
W 1-2	.70	.72	.98	.96	.82	.82	.72	.86	.92	1.00	1.06	.88	.94
W 2-3	1.02	1.20	.64	.94	1.16	.88	-.05	.92	1.04	1.02	.82	1.02	1.22
W 3-4	.04	.74	.84	.76	.76	.80	1.10	.78	.74	.72	.88	.84	.70
B 1-2	1.04	1.02	.76	.90	.78	.85	.50	.82	.80	.52	1.00	.94	1.06
B 2-3	.64	.94	.92	.92	1.08	.90	1.44	.70	1.08	1.22	.92	.86	.90
B 3-4	.78	.50	.98	1.06	.62	.80	.54	1.10	.98	.83	.82	.86	.94
R 1-2	.66	.96	.96	.92	.86	.76	.89	.86	.93	.72	.74	.62	.68
R 2-3	.90	1.00	.98	.98	.84	.90	.58	.92	1.10	.88	1.30	1.24	1.14
R 3-4	1.10	.92	1.40	.98	.94	.92	.58	.89	.93	.82	.78	.88	.82
G 1-2	1.22	.94	.88	1.06	.74	.72	.78	.82	.84	.76	.86	1.02	1.00
G 2-3	.62	.78	1.00	.86	.94	.86	.74	.96	.92	.98	.78	.82	.90
G 3-4	1.02	1.02	.96	.82	.92	.84	.82	.60	.75	.82	1.04	.88	.86

STANDARD DEVIATIONS

	NASAL							TEMPORAL					
	45	30	20	15	10	5	0	5	10	20	25	30	40
W 1-2	.00	.31	.23	.22	.33	.31	.31	.19	.23	.26	.19	.11	.46
W 2-3	.23	.26	.10	.16	.15	.11	.98	.22	.09	.23	.25	.23	.68
W 3-4	.24	.26	.15	.18	.26	.12	1.36	.13	.40	.30	.30	.27	.57
B 1-2	.31	.20	.25	.14	.04	.13	.97	.28	.12	1.04	.34	.30	.19
B 2-3	.27	.30	.11	.31	.19	.30	1.05	.30	.11	1.13	.22	.26	.34
B 3-4	.49	.34	.25	.26	.29	.44	.81	.29	.23	.43	.39	.47	.19
R 1-2	.23	.36	.26	.31	.26	.25	.38	.25	.20	.18	.18	.22	.28
R 2-3	.20	.31	1.63	.33	.39	.20	.33	.24	.35	.52	.22	.18	.25
R 3-4	.34	.22	1.62	.11	.25	.22	.19	.12	.12	.51	.18	.24	.11
G 1-2	.40	.10	.22	.19	.18	.64	.45	.30	.09	.18	.31	.18	.21
G 2-3	.22	.22	.31	.13	.13	.13	.18	.17	.24	.23	.31	.30	.20
G 3-4	.28	.17	.24	.11	.11	.35	1.61	.41	.18	.47	.39	.24	.31

Appendix VII

Calculation of Correction Factors for
Photometric Equating of Chromatic Filters

The sensitivity of the Pritchard photometer used in the present investigation deviates from V_λ, and the difference between the instrument's spectral response curve (V_λ^p) and V_λ must be taken into account by correction factors which are applied to the instrumental readings. The formula used to calculate these correction factors was the following:

$$CF = \frac{\sum_{i=1}^{N} T_i \frac{Y_i}{Y_i^p}}{\sum_{i=1}^{N} T_i}$$

where CF= the correction factor which when multiplied by the instrumental

reading yields the corrected Y value.

T_i= transmission of the filter at the wavelength i.

Y_i= the value of V_λ at the wavelength i.

Y_i^p= the value of V_λ^p at the wavelength i.

The values of T_i were obtained using the Zeiss RFC-3 Automatic Colorimeter, an automatic colorimeter. Interpolation of some values was required as the RFC-3 makes measurements at 13nm intervals, while the values of T_i at 10nm intervals were required.

The values of Y_i were obtained from Stiles and Wyszecki (1967). Judd's 1951 correction of V_λ in the blue wavelengths was used.

The values of Y_i^p were obtained from the instrumental spectral response data supplied with the Pritchard photometer.