Human S-cone vision: Relationship between perceptive field and ganglion cell dendritic field

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We measured the S-cone contrast threshold for stimuli of different size modulated along the white –90 deg direction in the isoluminant plane of DKL color space. The stimuli were presented at eccentricities of 5–30 deg in the horizontal temporal retinal meridian. Ricco’s area of complete spatial summation was estimated using a bilinear fit of the log threshold/log area function. Ricco’s area increased towards the retinal periphery to include an increasing number of S-cones while remaining 1.6–1.8 times larger than the dendritic field area of the small bistratified and parasol retinal ganglion cells. Assuming constant coverage factor by the dendritic field, Ricco’s area incorporated a constant number (three to four) of small bistratified cells. It was also found that the threshold contrast for stimuli that matched Ricco’s area was constant across the studied eccentricity range, similar to previous findings for achromatic vision. Our data support the point of view that this invariance is the result of a constant number of cells involved in stimulus detection.

Keywords: S-cones, spatial summation, Ricco’s area, local scale

Introduction

Visual performance under isolated stimulation of the short-wavelength cones (S-cones) is considered a “good vehicle” for the study of the relationship between visual perception on the one hand and physiology and morphology of the visual pathways on the other (Metha & Lennie, 2001). Making the link between perception and structure is facilitated by the uniqueness of S-cone distribution (e.g., Curcio et al., 1991) and recent advances in knowledge of their pathways (reviewed by Calkins, 2001; Schein, Sterling, Ngo, Huang, & Herr, 2004). Furthermore, the isolation of S-cone vision is relatively easy owing to the difference of S-cone spectral selectivity from that of M- and L-cones. In this study, we are interested in the relationship between the spatial summation properties of human S-cone vision and the underlying retinal structure. Ricco’s law of spatial summation states that for sufficiently small stimulus sizes, the threshold intensity is inversely related to stimulus area, that is, the threshold luminous flux is constant (Ricco, 1877, cited in Brindley, 1970). The largest stimulus area up to which the law is obeyed is known as the area of complete physiological summation, the critical area, Ricco’s area, or the perceptive field (e.g., Ransom-Hogg & Spillmann, 1980).

Spatial summation reduces visual acuity yet its existence is unsurprising in the presence of quantal and neural noise. Detection of weak signals is considered a process of discrimination of signal from noise. From this perspective, Ricco’s area is the background area over which the visual system integrates noise to compare it with the signal. If the stimulus is small in comparison with that area, the background noise does not depend on the stimulus and the threshold is inversely proportional to stimulus size (Ricco’s law). For stimuli larger than Ricco’s area, the relevant noise is proportional to stimulus area and the threshold is inversely proportional to the area to the power of 0.5, that is, it obeys Piper’s law (Barlow, 1957, 1958; Brindley, 1970; Glezer, 1965).

Both neural and optical factors account for complete spatial summation (Brindley, 1970; Davila & Geisler, 1991). The neural factor is commonly associated with the retinal ganglion cell-receptive field center as measured in single-unit recordings (e.g., Glezer, 1965; Hallet, 1962; Lie, 1980; Wilson, 1970). The size of the receptive field center is determined by the ganglion cell dendritic field...
multiplied by a constant factor owing to contribution of bipolar cell dendritic fields that reach beyond it (Peichl & Wässle, 1983). It is reasonable therefore to expect Ricco’s area to depend on the dendritic field size of the ganglion cells involved in stimulus detection, if not determined by the optical factors. The relatively large Ricco’s area observed for S-cone vision would lead us to conclude that its size is determined by neural rather than optical factors despite the presence of chromatic blur and the dioptric difference between test and background spectral composition (Volbrecht, Shrago, Schefrin, & Werner, 2000).

Two recent studies of human S-cone vision compared Ricco’s area with retinal structure. In the first study, Volbrecht et al. (2000) measured Ricco’s area in the 0–20 deg range across the superior retinal meridian. Ricco’s area was compared with the density of photoreceptors and ganglion cells as well as with the dendritic field size of several types of ganglion cells. Either the long-wavelength cones (L-cones) or the S-cones were preferentially stimulated in their experiments. Under conditions favoring stimulus detection through the L-cones, Ricco’s area closely followed the dendritic field size of parasol ganglion cells. Not so clear was the case for S-cone vision. As far as one could judge from their Figure 9, Ricco’s area increased at a higher rate than the dendritic field size of the small bistratified cells (SBCs) known until recently as the only S-cone ON cells (Dacey & Lee, 1994). In the second study, Vassilev, Mihaylova, Racheva, Zlatkova, and Anderson (2003) confirmed this finding for the temporal horizontal retinal meridian. Volbrecht et al. (2000) found it “difficult to conclude whether Ricco’s area for the S-cone mechanism is directly related to dendritic field size”. Vassilev et al. suggested that the source of a greater increase of the area of complete summation with eccentricity was an extension of lateral contribution by the retinal bipolar cells.

Here we again test the hypothesis that for human S-cone vision, Ricco’s area correlates with, and thus might depend on, the dendritic field size of the small bistratified cells across the retina. The present study differs from those of Volbrecht et al. (2000) and Vassilev et al. (2003) in the method of selective S-cone stimulation. It is here achieved using isoluminant stimuli modulated in color along the tritan axis instead of Stiles’ two-color threshold method employed previously. The intense yellow background used in the method of Stiles to silence the middle and long-wavelength cones causes postreceptoral channel polarization (Mollon & Polden, 1979) and could change the spatial properties of the S-cone pathways. It was necessary, therefore, to repeat the previous measurements on a neutral white background. The data collected allowed us in addition to revisit a previous finding of constancy of the detection threshold of stimuli that match Ricco’s area for achromatic vision (Glezer, 1965; Wilson, 1970) and to test this in the case of S-cone vision.

### Methods

#### Stimuli

Stimuli were generated on a gamma-corrected Sony Trinitron monitor (Rover Scan 117FD) by a video graphic card VSG 2/3 (Cambridge Research Systems, Rochester, UK) run by the Psycho program from the same manufacturer. Viewing distance was 57 cm in most cases. The background field size was 23 × 31 deg at this distance. The background was white (x = 0.310, y = 0.316) and its luminance was 25 cd/m². Frame rate was 80 Hz and each pixel subtended 1.8 min of arc at the eye. We measured the threshold color modulation in the white – 90 deg direction in DKL color space (Derrington, Krauskopf, & Lennie, 1984). These stimuli are further denoted as S90 and their appearance was pale purple. The available gamut ranged from the white to x = 0.262, y = 0.201 along the conventional tritan axis, producing S-contrast close to 100%. Theoretically, stimulus modulation along this axis would increase only the quantal catch by the S-cones, leaving the quantal catch by the M- and L-cones unchanged. It has been recognized that various factors, such as changes of the preretinal media absorption with age and eccentricity might affect the position of the tritan axis (Cottaris, 2003; Smith & Pokorny, 1995). The variation of the tritan axis can create contrast in L- and M-cones and change the S-cone contrast. Since our stimuli occupied retinal loci practically free of the yellow macular pigment (5–30 deg from the fovea), we measured threshold color modulations from the same white background along an additional axis, assuming that there is no absorption by the macular pigment. This new axis was calculated using a modified set of cone fundamentals obtained by removing the standard macular pigment transmission spectrum from the Smith–Pokorny cone fundamentals. The end point of this axis, producing S-cone contrast close to 100%, had chromaticity coordinates of x = 0.271, y = 0.21. Within the monitor gamut, the difference between the two chromatic axes at the maximum available distance from the white point was very small. This is in agreement with the conclusion of Smith and Pokorny (1995), that even the extreme combination of factors that affect the position of the tritan line causes no more than a 1 deg line rotation in the cone excitation space. Control experiments showed no significant difference between the threshold/area curves obtained along the two chromatic axes. We decided therefore to present the stimuli along the conventional tritan axis. As an additional independent test, we repeated the experiments using the two-color threshold method of Stiles with one of our observers (see Results).

Rod intrusion is of some concern with the stimuli used in our experiments. To evaluate whether retinal illumination was high enough to avoid rod intrusion, the pupil size
was monitored by a video camera during the experiment and was between 3.9 and 5 mm for the different observers. The effective pupil size was reduced by 14% at the largest eccentricity tested. Retinal illumination with the narrower pupil (observers A. V. and M. B. Z.) was 760 scotopic trolands and with the widest pupil (observer I. H.) 1250 scotopic trolands. According to Aguilar and Stiles (1954; see also Wyszecki & Stiles, 1982, p. 546), the sensitivity of the rod mechanism diminishes progressively above 100 scotopic trolands. Furthermore, previous estimates of the excitation of the rods and cones by stimuli generated on a monitor with phosphors similar to those of our monitor (Shapiro, Pokorny, & Smith, 1996) show that no rod intrusion should occur around threshold with our test stimuli. (Shapiro et al.’s calculations are for a 30 cd/m² background and a 2-mm pupil. However, the wider pupils of our observers more than compensate for our lower background luminance resulting in an even higher retinal illuminance). However, some reports suggest that even at high photopic light intensity, rod signals may still affect S-cone vision (e.g., Trezona, 1970; Naarendorp, Rice, & Sieving, 1996). A control experiment under conditions of rod bleach was performed to test for rod intrusion.

The test stimuli were circular sharp-edged patches of variable size, isoluminant with the background. Isoluminance was determined for each subject and each retinal position by the method of minimum flicker at 15 Hz. This method was unreliable in the visual field periphery (30 deg) owing to adaptation to flicker (Troxler effect) as noted previously (e.g., Schieting & Spillmann, 1987). In such cases, we additionally measured visual resolution acuity with gratings, the color of which varied between white and S90. The white luminance was fixed and the luminance of the test color was varied. We plotted resolution against luminance of the test color. There was usually a plateau of minimum resolution in the curve so obtained. The luminance in the middle of the plateau was assumed to be equiluminant with the white background (Vidinova-Zlatkova, Anderson, & Vassilev, 2004) and used in the subsequent experiments.

The test stimuli were presented along the temporal horizontal retinal meridian of the right eye at eccentricities of 5, 10, 15, 20, and 30 deg. Viewing distance was reduced to 40 cm when the stimuli were presented at 30 deg eccentricity. Since the monitor screen was flat, the angular distance between the stimulus and the fixation mark affected the distance between the eye and the test stimulus as well as the horizontal diameter of the stimulus retinal image. Corrected retinal size of the test stimuli was used in the analysis of the data. While negligible at the eccentricity of 15 deg and less, the difference between nominal and real retinal stimulus area was 14.8% at 20 deg eccentricity and 31.8% at 30 deg.

Viewing was with the natural pupil. Stimulus duration was 100 ms. It was not possible to use a shorter presentation time. Pilot experiments have shown that stimuli of a size falling within Ricco’s area are subthreshold at shorter durations. We did not use longer durations to reduce artifacts due to eye movements known to occur during attempted gaze fixation. Gaze direction and accommodation were assisted by a fixation mark (a cross of 0.5 deg diameter, or a 0.4 deg spot of the S90 color).

**Calibrations**

All spectral and luminance measurements were performed using a spectroradiometer/photometer (Spectrascan PR650, PhotoResearch). To calculate the chromaticity coordinates of the S90 color, the radiance spectra of the three monitor guns were measured in 4-nm steps and r, g, and b modulation depths required to produce an L-, M-, S-cone contrast vector in the isoluminant plane (0, 0, 1) were calculated (Cottaris, 2003) using Smith–Pokorny cone fundamentals (Smith & Pokorny, 1975). These modulation depths were then converted into x, y chromaticity coordinates. Both background and test stimulus x, y coordinates were measured using a PR650 Spectrascan at the eye position and a Minolta xyl colorimeter at the test stimulus location on the screen and adjusted if required before each experimental session.

**Psychophysical procedure**

The experiments were performed in a dark room. Observers adapted for 10 min in darkness and then to the background for 2 min. Contrast detection threshold was measured by a two-interval forced choice method combined with a staircase procedure (three correct – one incorrect variant). Step size was 1 dB. A staircase continued until six reversals around a steady level were obtained. Each daily session lasted 45–60 min and included measurements at a fixed eccentricity and 8–10 stimulus sizes. The data were expressed as S-cone contrast by calculating the cone excitations created by the threshold stimuli (Golz & MacLeod, 2003). The cone contrasts were defined as an incremental cone excitation divided by the cone excitation of the background. The results were calculated as the geometric means from three to four daily sessions.

**Observers**

Three of the authors, I. I. (male, 25 years), M. B. Z. (female, 55 years), and A. V. (male, 68 years), as well as a naive subject (I. H., male, 24 years) served as observers. This variation in age is somewhat less than that of the donor eyes used in the morphological studies, 16–82 years (Dacey, 1993) with which we compare. No comments about the effect of age are available in that study. I. I. and
I. H. were emmetropes and wore no habitual optical correction. M. B. Z. and A. V. were astigmatic and presbyopic and wore corrective lenses during the experiments. Refractive error for each peripheral location was initially determined by an experienced optometrist using retinoscopy. Prior to each session, corrective lenses were placed in front of the observer’s eye in line with the test location and subjectively modified to achieve maximum contrast for a high spatial frequency sinusoidal grating of the appropriate chromaticity. In this way we minimized the influence of chromatic focus differences. All observers had normal color vision as tested by Rabkin’s pseudoisochromatic plates (8th ed., Moscow, 1985), Album Tritan de Ph. Lanthony (Lineau Ophthalmologie, Paris, 1985), and the City University Colour Vision Test. None of the observers reported having ocular abnormalities. The experiments were conducted in accordance with the Declaration of Helsinki and approved by the Ethic Committee of both institutions where the study was performed.

**Control experiment: Rod bleach**

Rod intrusion selectively desaturates color stimuli depending on their size (Gordon & Abramov, 1977; Stabell & Stabell, 1999) and could potentially affect the spatial summation results in the present study. We measured the detection thresholds after rod bleach for S90 stimuli of selected sizes, some smaller and some larger than the expected critical size of complete spatial summation, during the cone plateau period of the dark adaptation curve, that is, under conditions where rods are not involved in stimulus detection. Two of the observers (M. B. Z. and I. H.) took part. Bleaching was performed with a 1-min exposure to white (3300K) light 15.5 × 15.5 deg in size and of 5 log scotopic trolands centered on 20 or 30 deg eccentricity. To know the time course of cone-dominated sensitivity, detection threshold was first measured on a dark background. A Yes/No psychophysical procedure was used in combination with a staircase that reversed after each change in response type. The test stimulus had the same spectral composition as the stimulus in the main experiment (S90) and was presented at intervals of 5 s. The procedure started 1 min after bleach and continued for the next 12 min. The cone plateau was observed from the 4th minute up to the 8th minute of dark adaptation for both subjects. Next we measured detection threshold for the S90 stimulus on the white background used in the main experiments. These measurements were performed on separate days. Three minutes of dark adaptation and 2 min of adaptation to the white background followed the bleach. Because of the short duration of the cone plateau, a Yes–No method and staircase, which terminated after the first reversal, was used to measure the thresholds at several time intervals following extinction of the bleaching light. The thresholds were measured during the following 3 min, that is, during the cone plateau. Test stimulus eccentricity was 20 deg (observers M. B. Z. and I. H.) or 30 deg (observer I. H.). All other conditions were the same as in the main experiment. Each data point was a result of at least three separate measurements.

**Results**

Threshold/area curves for two observers are presented in Figure 1. The ordinate is log threshold S-cone contrast in percent. The abscissa is log stimulus area in square minutes. The experimental points are the means with ±1 SEM.
SEM. The two lines through each set of the data points are the least-square fit as determined by the two-phase linear regression model (Seber & Wild, 1989) with the slope of the first line fixed at \( j \). The intercept of the first line, the slope of the second line, and the point of intersection of the two lines were allowed to vary. Statistica software was used for the computations.

The second line slope was estimated to be close to \( j = 0.5 \) across all observers (mean \( j = 0.54, SD = 0.028 \)), that is, the points along the second line closely followed Piper’s law of incomplete summation. In some cases the thresholds for the largest test stimuli deviated upward from the second straight line by more than twice their standard error. Such data were excluded from the fitting procedure but are presented in Figure 1, for example, the largest stimulus at 5 deg eccentricity, observer I. H. Many authors, starting with Barlow (1957), show that Piper’s law holds over a restricted area only and the slope of the curve beyond Ricco’s area decreases with increasing stimulus size. Nevertheless, as the examples in Figure 1 show, the bilinear approximation fits the experimental data quite well (mean \( R^2 = 0.932, SD = 0.029 \)). The arrows in the figures point out the size of Ricco’s area for each retinal eccentricity. The arrows from left to right correspond to Ricco’s area at increasing eccentricity.

Control measurements following rod bleach (see Methods, last paragraph) yielded threshold values close to those of the main experiment. More specifically, the thresholds after bleach were systematically higher by 0.05–0.1 log units with observer M. B. Z. and systematically lower by 0.1–0.15 log units with observer I. H. possibly due to daily threshold variations usually observed in such experiments.

Thus, the increase of Ricco’s area in the periphery could not be explained by rod intrusion.

Data obtained with all observers are summarized in Tables 1A and B. Log Ricco’s area and its standard error estimated as part of the fitting procedure are presented in Table 1A. Log area instead of area is shown to facilitate comparison with Figure 1 where log units were required for the bilinear model analysis. The monitor gamut restricted the range of stimulus contrast and, together with the pixel size, limited the number of experimental points on the branch of complete summation of the threshold/area curve. As a result, Ricco’s area could not be measured in one case and its standard error could not be determined in three cases (Table 1A). The standard error varied between approximately 0.05 and 0.2 log units in the remaining 16 cases. To increase data reliability, the means across the observers were calculated when necessary. At the same time, Tables 1A and B and Figures 2 and 4 represent individual data to show the systematic variability owing to individual differences.

For easier visualization of the data, the diameters of Ricco’s area are presented in a separate table (Table 1B).

At 5 deg from the fovea, the diameter of the area of complete physiological summation was between 20 and 25.5 min of arc and at 30 deg eccentricity was between 63

<table>
<thead>
<tr>
<th>Ecc/Obs</th>
<th>I. H.</th>
<th>I. I.</th>
<th>M. B. Z.</th>
<th>A. V.</th>
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<tr>
<td>A 5 deg</td>
<td>2.68 ± 0.057</td>
<td>*</td>
<td>2.71 ± 0.08</td>
<td>2.50 ± 0.088</td>
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<td>10 deg</td>
<td>2.89 ± 0.12</td>
<td>3.04 ± 0.061</td>
<td>2.90 ± 0.051</td>
<td>3.27 ± 0.057</td>
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<tr>
<td>15 deg</td>
<td>3.04 ± 0.055</td>
<td>3.33*</td>
<td>3.34 ± 0.189</td>
<td>3.34 ± 0.078</td>
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<tr>
<td>20 deg</td>
<td>3.15*</td>
<td>3.45 ± 0.051</td>
<td>3.45 ± 0.048</td>
<td>3.51 ± 0.065</td>
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<tr>
<td>30 deg</td>
<td>3.67 ± 0.072</td>
<td>3.63*</td>
<td>3.49 ± 0.104</td>
<td>3.80 ± 0.047</td>
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<tr>
<td>B 5 deg</td>
<td>24.6</td>
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<td>25.5</td>
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<td>10 deg</td>
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<td>77.7</td>
<td>74.1</td>
<td>63.1</td>
<td>90.1</td>
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Table 1. (A) Log Ricco’s area (min²) and its standard error as a function of retinal eccentricity. Data of all four observers. Asterisks indicate that either Ricco’s area or its standard error could not be determined (see the text). (B) Diameter of Ricco’s area (min of arc) as a function of retinal eccentricity.

Figure 2. Ricco’s area (data of all four observers) and dendritic field area of the small bistratified cells as functions of retinal eccentricity. The SEMs of Ricco’s area are presented in Table 1A. Dendritic field area is from Dacey (1993).
and 90 min of arc. It is seen from Tables 1A and B that the area of complete summation increased monotonically in the 5–30 deg range by about one log unit (i.e., by a factor of 10). Insofar as S-cone density decreases by about a factor of two in this range (Curcio et al., 1991), the 10-fold increase in Ricco’s area means about a fivefold increase in the number of S-cones within the area of complete physiological summation. Averaged across the observers, the mean number of S-cones per Ricco’s area increased monotonically from about 10 at an eccentricity of 5 deg to about 50 at an eccentricity of 30 deg. This finding confirms previous data (Vassilev et al., 2003; Volbrecht et al., 2000) that Ricco’s area includes a larger number of S-cones at larger eccentricity. An increased convergence of S-cone signals in the retinal periphery has also been incorporated in a recent model of S-cone vision to fit it with visual acuity (Metha & Lennie, 2001).

Figure 2 compares Ricco’s area and the dendritic field area of the small bistratified cells in the human retina. Ricco’s area is shown separately for each observer. The morphological data are from Dacey (1993). The size of the larger, inner-tier dendritic field was used for the comparison. It can be seen that the enlargement of Ricco’s area with eccentricity correlates with the enlargement of the dendritic field. Most individual areas exceeded the size of the dendritic field. We calculated the Ricco’s area versus dendritic field area quotient for each observer. The mean quotient ±1 SEM is shown as a function of retinal eccentricity in the next figure (Figure 3). The mean varied within a narrow range of 1.6–1.8 and showed no systematic dependence on eccentricity (slope +0.0027, SE = 0.027, p = .59).

It is seen from Figure 2 and Tables 1A and B that Ricco’s area tended to be larger for our oldest observer (A. V.) in comparison with the younger ones. Age-related changes were not the scope of the present study. Such an investigation requires inclusion of a large number of observers of different ages. It is, however, worthy to note that the area of complete summation increases with age under scotopic conditions (Schefrin, Bieber, McLean, & Werner, 1998) and this might also be the case with S-cone vision.

The constant ratio between Ricco’s area and dendritic field was paralleled by another constancy, illustrated in Figure 4. The symbols in the figure represent individual S-cone contrast thresholds for stimuli that match Ricco’s area. The values are actually the ordinates at the intersection of the bilinear fit in the S-cone contrast/stimulus area functions similar to those presented in Figure 1. While Ricco’s area increased about 10 times at 30 deg compared with 5 deg, the detection threshold was practically constant with eccentricity. The slope of the regression line fit to the data points did not differ significantly from zero (slope −0.0014, SE = 0.027, p = .618).

We calculated the number of small bistratified cells within a single Ricco’s area across the retina. Our calculation was based on Dacey’s (1993) estimation of cellular density and Drasdo and Fowler’s (1974) nonlinear transformation between angular and linear retinal dimensions. Dacey’s estimates were based on the dendritic field size and the assumption of a constant coverage factor across the retina. About three to four cells turned out to be included in a single area of complete spatial summation, this number being independent of the retinal eccentricity within the 5–30 deg range.

The results obtained in the present study and in our previous study with blue-light increments on an intense yellow background (Vassilev et al., 2003) are compared in Figure 5. The diameters rather than areas of Ricco’s zone are shown for easier visualization. Each experimental point shows the mean across four observers and the
vertical bars denote ±1 SEM. Where not seen, the error bars were smaller than the symbols. It is apparent that despite applying different methods of S-cone selective stimulation, both experiments yielded similar estimates of Ricco’s area. At no location was the difference between the means significant at the .05 level of confidence including 10 deg, where the difference was the largest. We repeated the blue-on-yellow experiment at all locations except for 30 deg with observer I. I. and compared the data with his isoluminant results. The estimated Ricco’s area did not differ significantly at any location.

Discussion

Ricco’s area and retinal structure

To our knowledge, the present work is the first to report a constant relationship between the psychophysically determined area of complete spatial summation (Ricco’s area) under selective S-cone stimulation and the dendritic field of the small bistratified retinal ganglion cells in the human retina. Both Ricco’s area and the cell dendritic field increased about 10 times across the 5–30 deg temporal horizontal retinal meridian while their ratio varied within the narrow range of about 1.6–1.8 showing no effect of retinal eccentricity. The constant ratio supports the hypothesis that the area of complete summation depends on the cell dendritic field.

Insofar as previous studies (Volbrecht et al., 2000; Vassilev et al., 2003) were also concerned with the relationship between Ricco’s area and ganglion cell dendritic field, the question arises as to how their results compare with the present ones. The results obtained with blue-on-yellow S-cone increments by Vassilev et al. (2003) and the present data are compared in Figure 5. The experimental points depicted different trends, accelerating dependence of Ricco’s area on retinal eccentricity in our previous study and a decelerating one in the present study. Dendritic field diameter of the small bistratified ganglion cells is also a decelerating function of retinal eccentricity (Dacey, 1993); thus, the present results parallel the dendritic field function already shown in Figure 2 while the previous ones do not. We assume that the reasons for a different trend in our previous study included unidentified random factors (e.g., low estimate at 10 deg) as well as the narrower eccentricity range employed.

With regard to the work of Volbrecht et al. (2000), the ratio of Ricco’s area and dendritic field size of the small bistratified cells increased with eccentricity in the 4–20 deg range (we calculated the ratio using values inferred from their Figure 9). Ricco’s area diameter, averaged across the observers at 20 deg eccentricity, the most distant point in their experiments, is almost twice the diameter found in our previous (Vassilev et al., 2003) and present study. Volbrecht et al. presented the stimuli along the superior vertical retinal meridian and we presented them along the horizontal temporal meridian. Stimulus location might be the source of quantitative difference between the results, as substantial meridional variations in both S-cone-mediated sensitivity and acuity have been reported (Beirne, Zlatkova, & Anderson, 2005; Sample, Irak, Martinez, & Yamagishi, 1997). S-cone density decreases with retinal eccentricity at a higher rate along the superior meridian that along the temporal meridian (Curcio et al., 1991). Unfortunately, no published morphological data exist to compare the small bistratified cells along the meridians and all comparisons with Ricco’s area are based on the average dendritic field values reported by Dacey (1993).

Our assumption is that, under the present experimental conditions, Ricco’s area for S-cone vision is about the size of the receptive field of a single small bistratified cell. Recordings from a retinal ganglion cells in cat show that the size of the central zone of their receptive field is larger than the dendritic field owing most probably to inputs from the dendritic fields of bipolar cells that spread beyond the boundaries of the ganglion cell dendritic field (Peichl & Wässle, 1983). Ricco’s area was also larger than the dendritic field of the small bistratified cells. In fact the ratio between them was of the same magnitude as between the receptive field and dendritic field in the experiments of Peichl and Wässle (1983). It could be argued that the similarity is purely coincidental; the ratio between the receptive field and dendritic field of the small bistratified cells might not be the same as in the cat a cells. More direct support is
provided by recent physiological (Chichilnisky & Baylor, 1999) and morphological (Schein et al., 2004) data. These show that blue-ON/yellow-OFF cells of macaque retina receive common but unequal inputs from one or more S-cones thus generating overlapping receptive fields. A single ganglion cell receives from up to 11 S-cones according to Chichilnisky and Baylor (1999) in the 20–50 deg eccentricity range. Our finding of about three to four ganglion cells and 10–50 S-cones included in a single Ricco’s area are in correspondence with these data.

The dendritic field size of the parasol cells is of the same order as that of the small bistratified cells across the human retina (Dacey, 1993); thus, the correlation with Ricco’s area applies to them too. Derrington et al. (1984) found that many magnocellular neurons in the lateral geniculate body of the macaque receive some input from S-cones and Chatterjee and Callaway (2002) report that they are driven forward by the retinal parasol cells. The contribution of the magnocellular neurons to stimulus detection at threshold is, however, unlikely owing to their low sensitivity to S-cone contrast (Chatterjee & Callaway, 2002; Derrington et al., 1984). Furthermore, there are several ganglion cell types that receive S-cone input, the large bistratified cells (Dacey, Peterson, Robinson, & Gamlin, 2003), S-cone OFF cells (Dacey, Peterson, & Robinson, 2002), narrow-field, and wide-field blue-yellow cells (Schein et al., 2004). The question about the role of these diverse cells to the detection of S-cone selective stimuli is open at present.

Assuming that stimulus detection depends entirely on the small bistratified cells, the constant relationship between Ricco’s area and their dendritic field does not mean that the dendritic field is the only factor to determine spatial summation. Both background luminance and stimulus presentation time were fixed in the present experiments. Studies of achromatic vision have shown that they affect spatial summation. Ricco’s area decreases when the retinal background illumination is increased (e.g., Barlow, 1958; Glezer, 1965) or when stimulus duration is increased (Barlow, 1958). It has been recently reported that the perceptive field for hue and saturation decrease if the test stimulus luminance is increased (Pitts, Troup, Vollbrecht, & Nerger, 2005). However, these data were obtained following dark adaptation and some of the results were accounted for by influence of rods on perceptive field size. We are not aware of data regarding the effect of the level of retinal light adaptation, particularly with respect to the level of S-cone background excitation, on the spatial summation of S-cone selective stimuli, except the work of Brindley (1954) who measured Ricco’s area with violet stimuli on green background and found no influence of background intensity on spatial summation. Testing this factor with our experimental setup is not possible at present owing to the limited blue-light intensity range as well as rod intrusion at low background levels. Age-related sensitivity loss of the S-cone pathway affects mainly the low-intensity part of the threshold versus background intensity function; model analysis has shown that the sensitivity loss involves different mechanisms (Schefrin, Werner, Plach, & Utlaut, 1992). Extending this approach to test stimuli of different size would had shown if spatial summation of S-cone vision is intensity dependent and therefore determined by a more complex mechanism than the correlation between Ricco’s area and the dendritic field of a single class of cells suggests.

Critical duration for S-cone increments decreases at the periphery (Murzacz, Vassilev, & Zlatkova, 2003) and therefore stimulus presentation time could affect the eccentricity dependent changes of Ricco’s area. To evaluate this potential factor, control experiments were performed with two observers (I. H. and A. V.) at 20 deg eccentricity. Stimulus presentation time was 400 ms. A stimulus duration of 400 ms shifted the log threshold/log area curve further downward along the y-axis compared to the 100-ms curve with little or no shift along the x-axis. There was a tendency for a smaller Ricco’s area at the longer presentation time but the effect was too small (less than 0.05 log units) to be statistically significant.

If Ricco’s area accommodates several cells, the receptive fields of which overlap, it is reasonable to expect the higher centers to utilize the information from all of them to reach a decision criterion. Assuming that the source of noise is in the retina and that the signals from separate ganglion cells are uncorrelated, the result would be probability summation (Piper’s law) rather than complete summation without affecting Ricco’s area.

**Ricco’s area and detection threshold**

As seen in Figure 4, S-cone threshold contrast is constant if the test stimulus is equal in size to Ricco’s area regardless of stimulus location on the retina. The threshold averaged across the observers varied within the narrow range of 1.58–1.62 log units (38–42% S-cone contrast) over the 5–30 deg eccentricity range. At the same time, Ricco’s area changed by a factor of 10. Constancy of threshold for stimuli that match the critical area of spatial summation has been reported previously for achromatic vision (Glezer, 1965; Lie, 1980; Wilson, 1967, 1970). Vassilev, Anderson, and Zlatkova (2003) confirmed their findings for S-cone vision isolated by the method of Stiles. They suggested the term “Glezer’s constancy” in honor of the author who first reported it. The present results (Figure 4) extend the previous finding by showing that the constancy of $\Delta I/I$, that is, the constancy of the Weber fraction for stimuli that match Ricco’s area, is also maintained for color contrast using isoluminant stimulation.
In a pioneering work, Fischer (1973) has shown that the number of ganglion cell-receptive fields in the cat retina covering a local receptive field area is constant irrespective of retinal location. He predicted Ricco’s area to accommodate a constant number of cells across the retina, the constancy explaining threshold invariance for stimuli that match Ricco’s area. Several other authors suggested this to be true (e.g., Lie, 1980; Rovamo & Virsu, 1979; Rovamo, Virsu, & Näsänen, 1978; Volbrecht et al., 2000; Watson, 1987). We assume the present study to be the first to support this theory using isoluminant S-cone chromatic vision. The theory is also of clinical significance as the comparison of differential light sensitivity using conventional white-on-white perimetry and data for ganglion cell density suggests (Garway-Heath, Caprioli, Fitzke, & Hitchings, 2000; Swanson, Felius, & Pan, 2004).

Acknowledgments

This work was supported by a Collaborative Research Initiative Grant (066143) from the Wellcome Trust (UK), and, in part, by a grant from the Information Program of the Open Society Institute, New York. We thank the two anonymous referees and JOV editorial staff for their helpful comments on the manuscript.

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