THE RELATIVE CONTRIBUTIONS OF PRE-NEURAL AND NEURAL FACTORS TO AREAL SUMMATION IN THE FOVEA

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(RECEIVED 23 NOVEMBER 1987; IN REVISED FORM 29 AUGUST 1990)

Abstract—In order to determine the relative contributions of pre-neural and neural factors to areal summation in the fovea, measurements of Ricco's area were made. These were compared to the results of an ideal-observer analysis which incorporated only pre-neural factors, up to the level of the photoreceptor. The comparison indicated that Ricco's area in the fovea is largely (if not completely) accounted for by pre-neural factors. Thus, our results, in agreement with the recent analysis of contrast sensitivity by Banks, Geisler and Bennett (1987; Vision Research, 27, 1915-1924), are consistent with the hypothesis that a neural pathway exists which consists of units whose center mechanisms sum over only a single cone or a single row of cones. Our results also imply that the quantum efficiency for detection is constant for test areas up to 256 min², once the effects of the optics and receptor aperture are factored out.

INTRODUCTION

The resolution capacity of the human visual system is limited by spatial summation, the confounding of information from any one point in the stimulus with information from other near-by points. Spatial summation has been studied using both the classical areal-summation paradigm (Lamar, Hecht, Shlaer & Hendley, 1947; Graham, Brown & Mote, 1939) and the contrast-sensitivity paradigm (Van Nes & Bouman, 1967; Kelly, 1977). In the areal-summation paradigm, complete spatial summation occurs when the product of intensity at threshold and stimulus area is constant (Ricco's law). The largest area for which Ricco's law holds is called Ricco's area. In the contrast sensitivity paradigm, the degree of spatial summation is represented indirectly in the reduced sensitivity to high frequencies (high-frequency fall-off) in the contrast-sensitivity function (CSF).

Recently, Banks, Geisler and Bennett (1987) analyzed the high-frequency limbs of foveal contrast sensitivity functions using an ideal-observer analysis (Geisler, 1984, 1989, Geisler & Davila, 1985) that takes into account quantal fluctuations, the optics of the eye, the receptor aperture, and the receptor lattice. This analysis was used in order to determine the relative contributions of pre-neural and neural mechanisms in foveal spatial summation. In the present paper, this same ideal-observer analysis is applied to areal-summation data. In agreement with Banks et al. (1987), we find that the neural mechanisms play a minor (if not negligible) role in foveal areal summation.

BACKGROUND

Spatial summation may originate at different levels of the visual system. At the optical level, both diffraction by the pupil and optical aberrations act to blur the stimulus (cf. Van Meeteren, 1974). At the receptor level, information is summed over the finite cross-sectional area of the receptor aperture (Miller, 1979; Snyder & Miller, 1977; Miller & Bernard, 1983). Finally, it is usually assumed that neural mechanisms sum information spatially.

For the purpose of analyzing the relative contributions of these three factors, it is useful to regard the visual system as a single-channel linear system. Within this framework, summation effects can be described in terms of point-spread functions. Specifically, the point-
spread function of the entire visual system can be regarded as the convolution of point-spread functions for the optical, receptor aperture, and neural components of the visual process. The spatial-frequency counterpart to the point-spread function for the entire visual system is a transfer function (the VTF), which can be regarded as the product of an optical transfer function (OTF), an aperture transfer function (ATF), and a neural transfer function (NTF):

\[ VTF = OTF \times ATF \times NTF. \]

The contrast-sensitivity function (CSF) is often used as the psychophysical estimate of the VTF. Several techniques have been used in attempts to characterize the optical point-spread function or, equivalently, the OTF. For example, Campbell and Gubish (1966) measured line-spread functions and derived OTFs by Fourier transformation; Van Meeteren (1974) used data from measurements of the optical aberrations plus diffraction to compute OTFs; and Campbell and Green (1965) measured the OTF by comparing contrast-sensitivity functions for gratings imaged directly on the retina by laser interferometry with those obtained by traditional imaging. Although for various reasons (cf. Van Meeteren, 1974) the OTFs determined by these different methods show some discrepancies among themselves, all show a considerable decrement in the transmission of high spatial frequencies, and hence indicate a substantial optical component to spatial summation. Furthermore, a recent review of this literature by one of us (Geisler 1989) concluded that the Campbell and Gubish (1966) line-spread functions are likely to be a fairly accurate estimate of optical quality in the fovea.

The interferometric CSF can be considered the transfer function of that part of the visual system subsequent to the optical system, modified by the effects of stray light (Campbell & Green, 1965; Williams, 1985). In other words, it can be regarded as the product of the ATF and the NTF. Interferometric CSFs reveal substantial high-frequency decrements in sensitivity, implying that post-optical factors are contributing to spatial summation. Miller and Bernard (1983) and Williams (1985) show that the ATF is responsible for only part of the high frequency fall-off in interferometric CSFs. In addition to the effects of the receptor aperture, Williams also considered the role of stray light and the spatial arrangement of the receptor lattice. His calculations indicated that all these factors taken together failed to completely account for the high-frequency fall-off. Williams concluded that the remaining effect was neural in origin; the neural mechanism he considered most likely was the summation of information over the output of adjacent cones.

Banks et al. (1987), however, suggested that the residual high-frequency fall-off might be due to the effects of neural summation across a fixed number of grating cycles, at a higher neural level, rather than summation across adjacent cones. This suggestion follows the findings of a number of investigators (e.g. Howell & Hess, 1978; Koenderink, Bouman, Bueno de Mesquita & Slappendel, 1978) that spatial-frequency-selective mechanisms have roughly circularly-symmetric integration areas of a critical size reciprocally related to center frequency. Note that contrast sensitivity is affected in different ways by the two postulated summation mechanisms. In summation over adjacent cones contrast is lost by spatial integration. Thus, the larger the size of a summation area the more contrast is lost at high spatial frequencies. On the other hand, in summation involving spatial-frequency-selective mechanisms, sensitivity is lost by the neglect of information falling outside the integration region. Thus, the smaller the summation area (e.g. the fewer the number of cycles in the mechanism’s receptive field) the more contrast information is lost at the mechanism’s optimal spatial frequency.

To test their hypothesis, Banks et al. obtained traditional (noninterferometric) CSFs using targets with a fixed number of cycles, and then separated the effects of the eye’s optics and the receptor aperture from neural effects with an ideal-observer analysis (Geisler, 1984, 1989; Geisler & Davila, 1985) that allows one to compute the effects of pre-neural mechanisms and of quantal noise on performance in visual-discrimination tasks. Banks et al. found that the shape of the CSFs was essentially the same for both the real observers and for the ideal observer, although the ideal observer was more sensitive overall. Thus, they concluded that the NTF under these circumstances had no appreciable high-frequency fall-off. Banks et al. also showed that it was possible to reconcile their results with those of Williams (1985). The fact that the NTF of Banks et al. had no appreciable high-frequency fall-off suggests that the neural mechanism which is responsible for the high-frequency fall-off may be the limitation of inte-
The other major method that has been used to study spatial summation has been the areal summation paradigm. Measures of Ricco’s area have traditionally been used to estimate the area over which neural pooling of stimulus information takes place. This summation area has been interpreted as equivalent to the receptive-field center size, either specifically for retinal ganglion cells (Glezer, 1965) or for an unspecified neural unit (Richards, 1967; Lie, 1981). Table 1 lists the estimates of Ricco’s area derived from the work of these authors and from the earlier study by Lamar et al. (1947). For the fovea adapted to moderate intensities, the range of the estimates is from 2.2 to 15.2 min², corresponding to receptive-field center diameters of about 3–8 cones.

If these estimates are valid indicators of receptive-field-center size, then they support the assertion that the smallest receptive-field centers sum over an area considerably larger than a single cone. However, these estimates are problematical, because the studies from which they came did not fully take into account the optical effects which have been considered in many of the contrast-sensitivity studies.

In the present study we evaluated the effects of optical factors, the receptor aperture and the receptor lattice structure on areal summation by comparing human performance with an ideal observer operating at the level of the quantum catch in the photoreceptors. Furthermore, we attempted to optimize the efficiency of the human observers by using a fairly small artificial pupil (3 mm), a stimulus duration matched to the duration of temporal integration (100 msec), and a two-alternative forced-choice procedure.

**METHODS**

The subjects were four men of ages 21, 22, 33 and 38 yr. All were emmetropic, scoring 20/20 or better on a Snellen eye chart, and had normal color vision, as measured by the Dvorine color plates. All had participated in at least one other visual psychophysical experiment. Subject WG, one of the authors, has had extensive practice in psychophysical tasks.

The stimuli for the main experiment consisted of green, square increment patches added to a green, 2.1 deg, square background. The fixation target consisted of four black lines arranged in an implied cross-hair pattern. The fixation lines were 5 min by 1 min and were located 18 min from the center of the target display.

The stimuli were created by a PDP 11/73 computer and displayed on a Tektronix 690SR color monitor, using an Adage graphics processor. Only the "green" gun of the color monitor was used; its x,y chromaticity point is (0.310, 0.595), according to the manufacturer’s specifications. The luminance of the background was 10 cd/m² (8 cd/m² for subject JB). A 3-mm artificial pupil was used, thus creating a background retinal illuminance of 70 td (56.5 td for JB). A 3-mm artificial pupil was used, thus creating a background retinal illuminance of 70 td (56.5 td for JB). A 3-mm artificial pupil was used, thus creating a background retinal illuminance of 70 td (56.5 td for JB).

In a subsequent experiment areal summation measurements were also made on a dark background for two of the subjects. In this condition the fixation bars were 10 cd/m² green lines of the same size and location as before.

The display was viewed monocularly at a distance of approx. 716 cm. A bite bar was used for head stabilization. Subjects aligned themselves in the artificial pupil using the chromatic-aberration technique. Prior to testing, the subjects adapted to the background level for

<table>
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<tr>
<th>Table 1. Ricco’s areas for real and ideal observers</th>
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<tr>
<td>Previous studies</td>
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<td>Glezer (1965)</td>
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<td>Lie (1981)</td>
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<td>Richards (1967)*</td>
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<td>Lamar et al. (1947)</td>
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* Richards’ summation values are from his own calculations. Because his method for calculating Ricco’s area is different from the method described in the text, we did not calculate Ricco’s area corresponding to the conditions in his study. Summation areas for the other studies were calculated from the published data using the method described in the text.
2 min when the background was 10 cd/m², and for 10 min when the background was dark.

Stimuli were presented in a two-interval, forced-choice, double-interleaved staircase procedure. A two-down, one-up staircase control criterion was used (Levitt, 1970), and six reversals on each staircase were required for termination of a block of trials. A practice period of two reversals preceded each block. The stimulus duration was 100 msec, the inter-stimulus interval 500 msec, and the total trial duration 5 sec. Auditory feedback indicating correctness was given following each response. Failures to respond, which occurred infrequently, were treated as errors.

Each session consisted of four blocks, each block presenting a different increment area. The order of the blocks was counterbalanced across sessions. For each stimulus size, two staircases were run in each of two sessions.

IDEAL-OBSERVER ANALYSIS

The present ideal-observer analysis is based on the theory of ideal observers (Rose, 1942; de Vries, 1984; Barlow, 1977; Peterson, Birdsall & Fox, 1954; Green & Swets, 1974). The classic approach, represented in the above references, is to compute the performance of an ideal observer operating prior to any sensory processing. Our approach involves pushing the analysis further along in the visual pathway by calculating the performance of an ideal-observer operating at the level of photon absorptions in the receptors (Geisler, 1984, 1987, 1989; Geisler & Davila, 1985). The performance of this ideal observer shows precisely how pre-neural mechanisms and photon noise limit the information available for discrimination at the level of the photoreceptors. The calculation of ideal performance in the present area summation paradigm consisted of several steps that we briefly summarize here. For a more detailed discussion of the general methods see Geisler and Davila (1985) and Geisler (1989).

The first step was to construct an accurate representation of the stimuli. This was given by the spatial and temporal dimensions of the stimuli, and the spectral power density of the Tek 690SR green primary/gun (Cowan, 1985). The second step was to convolve the stimuli with the optical point-spread function for the 3-mm pupil. The point-spread function was estimated from the 3-mm line-spread function reported by Campbell and Gubisch (1966). Specifically, their line-spread data were fitted with a sum of two Gaussian functions (see Fig. 1), and then converted into a point-spread function assuming that foveal optics are radially symmetric. This convolution, and the others described below, were computed by multiplication in the Fourier domain.

The third step was to compute the mean number of photon absorptions in each of the three classes of cone. First, the retinal intensity distribution that resulted from the first two steps was convolved with a receptor aperture function. The receptor aperture was taken to be 34 sec in diameter—the average diameter of a foveal cone inner segment. Next, the spectral power distribution of the primary/gun was converted to quantum units, normalized to an area of one quantum, multiplied by the transmission function of the ocular media (Wyszecki & Stiles, 1982) and by the individual cone absorption spectra Estevez (1979) (as reported in Wyszecki & Stiles, 1982), and then integrated. The result was a one-dimensional matrix that transformed an intensity of the primary in quantum units into photon absorptions in each cone class. This transformation was applied to the result obtained by convolution with the aperture function to obtain the effective retinal distribution of photon absorptions for each cone class in the Fourier domain. These distributions were then inverse Fourier transformed and evaluated at the receptor locations, which were assumed to lie in a triangular array. The above

![Fig. 1. Line-spread function of the eye for a 3-mm pupil. The symbols are data from Campbell and Gubisch (1966). The smooth curve is the weighted sum of two Gaussian functions; \( \sigma_1 = 0.417 \) min, \( \sigma_2 = 1.42 \) min, \( w = 0.409 \). (w is the relative weighting on the two Gaussian functions.) The point-spread function was obtained from the smooth curve by assuming that the eye is isotropic and by normalizing the volume under the function to 1.0.](image)
Pre-neural and neural summation

Calculations were carried out for both stimuli (a and b) in the discrimination task. The result was two lists of numbers, \(a_1, a_2, \ldots, a_n\) and \(b_1, b_2, \ldots, b_n\), giving the mean numbers of absorptions in each cone for each stimulus.

The final step was to compute the discrimination performance of the ideal observer. Although the above calculations give the mean numbers of absorptions in each cone, the actual number of absorptions in a trial is random in accordance with the Poisson density. If there are no sources of stimulus variability other than the Poisson randomness of light, then \(d'\) for the ideal observer in a two-alternative forced choice experiment is given by:

\[
d' = \frac{\sum (b_i - a_i) \ln(b_i/a_i)}{\left[\sum (b_i + a_i) \ln^2(b_i/a_i)\right]^{1/2}}.
\]

To compute thresholds for the ideal observer, all of the above calculations were repeated until the test intensity producing a \(d'\) of 1.00 was found. (This value of \(d'\) corresponds to 70% correct in the 2AFC task.)

RESULTS

The threshold energies for the light-background conditions (symbols) and for the ideal observer (solid curves) are plotted as a function of target area in Fig. 2. The dark-background thresholds and ideal-observer predictions are shown in Fig. 3. To generate these predictions a small amount of dark-light (photon-like events in the receptor) was assumed. The exact value is not important because it does not affect the shape of the predicted curve.

In the double-logarithmic plot of Figs 2 and 3, a horizontal line corresponds to Ricco's law. The ideal observer is, of course, more sensitive than the real observers. Thus, in order to compare shapes, the predicted curves were shifted vertically by adjusting the density of a neutral filter placed in front of the ideal observer until the ideal predictions gave a best fit to the data by a minimum \(\chi^2\) criterion.

As anticipated, threshold energies were relatively constant over a range of the smallest stimulus areas, and then increased with further increases in area. It is immediately obvious from Fig. 2 that the region of relatively constant threshold energy under the light-background conditions is very similar for both real and ideal observers, even though the thresholds for real observers represent the spatial summation of the entire visual system and those for the ideal, only the pre-neural mechanisms. For the

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Fig. 2. Threshold energy on a 10 cd/m² background as a function of target area for four human observers. The threshold energies are the product of the test luminance (cd/m²), duration (sec), and area (min²). The display was viewed through a 3 mm artificial pupil. The error bars indicate ± 2 SEM. The solid curves represent the performance of an ideal observer whose sensitivity is limited only by preneural factors and quantal fluctuations. For the purposes of comparing shapes, the ideal observer predictions were shifted vertically (for each subject) by placing a neutral density filter in front of the ideal observer. The average density across the four subjects was 2.26, which corresponds to a relative efficiency of 0.0055, with a vertical threshold shift of 1.13 log units.
Fig. 3. Threshold energy on a dark background as a function of target area for two human observers. The threshold energies are the product of the test luminance (cd/m²), duration (sec), and area (min²). The display was viewed through a 3 mm artificial pupil. The error bars indicate ± 2 SEM. The solid curves represent the performance of an ideal observer whose sensitivity is limited only by pre-neural factors and quantum fluctuations. For the purposes of comparing shapes, the ideal observer predictions were shifted vertically (for each subject) by placing a neutral density filter in front of the ideal observer.

dark-background conditions the agreement is not quite so good.

To quantify the comparison between real and ideal observers, we calculated Ricco's areas. Two straight line segments, one of which was constrained to be horizontal, were fit to each real observer's data and independently to the ideal observer's predictions, using the minimization program STEPIT.* The intersection of the line segments was used as the measure of Ricco's area, the region of full summation.

Figure 4 shows the fits for each subject in the light background condition. The χ² values of the best-fitting lines were 13.4, 7.08, 62.5 and 47.6 for subjects JB, MG, WG and JE respectively.

*J. P. Chandler, STEPT Package With STEPIT and SIMPLEX, Quantum Chemistry Program Exchange, QCPE Program no. 907. Indiana University Department of Chemistry.

Fig. 5 shows the fits for the two subjects in the dark background condition.

Table 2 presents the estimates of Ricco's area and associated confidence intervals. The confidence intervals were estimated from the threshold standard errors of the individual data points, using the routine FIDO. Note that for the light-background conditions the pre-neural Ricco's area falls within the 95% confidence interval for two of the four subjects, and is slightly larger than the upper bound of the interval for one subject and slightly smaller than the lower bound for the other subject. The average value of Ricco's area across all four subjects is 5.5 min² which agrees exactly with that of the ideal observer. For the dark-background conditions the measured values of Ricco's area are slightly larger than the ideal for subject JE and clearly larger for subject WG.

In Table 2, the estimates of Ricco's area for the ideal observer vary across subjects. The reason is that Ricco's area is not a parameter of the ideal observer (in fact, for the ideal observer, Ricco's law does not hold exactly over any range of areas); rather, Ricco's area must be estimated from the ideal-observer thresholds. In order for the comparison of real and ideal Ricco's areas to be as fair as possible, ideal Ricco's areas were estimated by using exactly the same sets of areas that were tested on the subjects. The different sets of areas yielded slightly different ideal Ricco's areas.

Not only do both the ideal and real observers obey Ricco's law over a similar range of small test areas, but they also both obey Piper's law (threshold energy proportional to the square-root of test area) for larger test areas. Subjects JB and MG obeyed Piper's law up to a test area of 1024 min² (a width of 32 min) and subjects WG and JE up to a test area of 256 min² (a width of 16 min).

In the above analysis, we ignored absolute sensitivity in order to examine area summation. However, it is also of interest to compare the absolute sensitivity of the entire visual system with the limits to sensitivity imposed by quantum fluctuations and the pre-neural subsystem alone.

A simple way to do this is to take the ratio of the real observer’s increment threshold at each stimulus size to that of the ideal observer at the same points. These ratios are plotted in Fig. 6 for the light-background conditions. The average ratio of real to ideal threshold across all subjects was 13.477. This is approx. 0.4 log units higher than the optimal values we found in
Pre-neural and neural summation

Fig. 4. Straight-line fits used to estimate Ricco's area. The segments were fit with a minimum $\chi^2$ procedure (STEPIT), with the constraint that the first segment have a slope of 0. Exactly the same procedure was applied to the ideal observer predictions. The average size of Ricco's area ($5.5 \text{ min}^2$) across the four subjects was the same as that of the ideal observer.

an earlier increment-detection task (Geisler & Davila, 1985), and represents an average relative efficiency ($d'_{\text{opt}}/d'_{\text{real}}$) of 0.0055. However, the earlier study used a barely visible pedestal upon which the increment stimulus was superimposed. Therefore, the difference between the results appears to be a demonstration of the familiar pedestal effect (cf. Foley & Legge, 1981).

The most striking aspect of the plots in Fig. 6 is the nearly constant ratio of real to ideal performance (constant efficiency) for all but the largest test area. This suggests that pre-neural factors may account for much of the variation in threshold with test area, at least for targets up to 256 min$^2$ (16 min on each side).

Figure 6 also shows the ratios of real to ideal threshold for the dark-background conditions. The relative efficiency is still quite constant, although not as constant as under the light-adapted conditions. Also note that the absolute values of the ratios (the vertical positions of the curves) are not as meaningful here because they depend on the amount of dark-light assumed in generating the ideal predictions.

DISCUSSION

The contribution of pre-neural factors to Ricco's area

In the introduction we noted that pre-neural factors have not in general been taken into account in estimates of Ricco's area. Only Lamar et al. (1947) and Lamar, Hecht, Hendley and Shlaer (1948) quantitatively considered diffraction effects, but they did not consider the effects of optical aberrations or the receptor aperture. Also, their results were not expressed as a pre-neural component to the Ricco area measure.

The present finding is that the contribution of pre-neural factors is quite sizeable. In fact, pre-neural factors appear to completely dominate the obtained summation areas. The average value of Ricco's area in light-background conditions is $5.5 \text{ min}^2$ which is exactly that predicted by the ideal observer. There are individual differences, but they could easily be explained by our use of normative data to characterize the pre-neural components, and by the limitations of estimating areal summation by fitting straight line-segments to the data and ideal observer. Furthermore, we were conservative in estimating Ricco's area. For example, for subjects WG and JE we included the thresholds for the largest patch size in fitting the straight lines, even though these points were out of the range which complied with Piper's law (see below) and thus tended to increase the estimates of Ricco's area. Thus, it appears that the neural contributions to Ricco's area in the fovea at photopic levels are small (or negligible) compared to those of the pre-neural mechanisms.
Ricco's area as evidence for receptive-field-center size

Anatomical studies of the primate retina (e.g. Boycott & Dowling, 1969) have found that midget ganglion cells serving the foveal region appear to receive input from only one cone via one midget bipolar cell. This vertical route is assumed to be the one responsible for the central, summatory portion of the ganglion cell's receptive field, while the horizontal route, involving horizontal and amacrine cells, is assumed to be responsible for the surround. Thus, anatomical evidence for one-on-one connections between cone receptors and bipolars, and between bipolars and ganglion cells, suggests that many of the center mechanisms in the foveal retina do not sum information over cones.

From single unit recordings in the macaque monkey, estimates have been made of receptive-field center size for retinal ganglion cells (De Monasterio & Gouras, 1975; De Monasterio, 1978) and for cells in the lateral geniculate nucleus (Derrington & Lennie, 1984; Kaplan & Shapley, 1982). De Monasterio and Gouras found rather large receptive-field center sizes (modal foveal size about 3.6 min arc, which is equivalent to 4–5 cone dia.). On the other hand, Derrington and Lennie obtained estimates of the center size as small as two cone diameters by measuring contrast sensitivity to moving gratings. Neither study corrected for optical effects. Indeed, Derrington and Lennie suggest
that optical rather than receptive field factors were likely to be the limiting factor in macaque neuron's resolution capacity. Thus, the physiological results appear to be consistent with the anatomical results. Of course, summation could still occur at a level beyond the retina, before the processing that leads directly to detection and discrimination decisions.

The present experiment and analysis show that the size of Ricco's area (under light-adapted conditions) is consistent with the single-cone hypothesis. Nonetheless, two alternative hypotheses must be considered. The first is that the center mechanisms of post-receptor neurons sum over more than one cone, but that center mechanisms overlap enough spatially to represent the photon absorptions in each cone without loss of information. To illustrate this argument, consider a row of cones and a row of second-order units which are equal in number, and which sum outputs of adjacent cones in an overlapping fashion. Suppose further that each absorbed photon produces one spike in the second-order unit. By appropriately adding and substracting the responses of the second-order units, the distribution of photon absorptions in the cones can be completely recovered up to a single constant (the photon absorptions in one of the cones). The existence of this recovery process, which is an example of deconvolution (Rosenfeld & Kak, 1982), implies that no detection information is lost due to summation. However, the recovery process can only work if no noise is added to the output of second-order units. For example, if some spikes from the second-order units were lost in random transmission to higher-order units, much like photons are lost in transmission through a neutral density filter, then there would be unresolvable spatial uncertainty about which cone was responsible for a given spike. This loss of spatial information would not occur if the second order units summed over one cone (even if the same number of spikes were lost in transmission). Because substantial noise in post receptor units is almost certain to exist, it seems likely that any neural summation by center mechanisms would be detectable in an areal summation paradigm. This conclusion is supported by the fact that the increase in center-mechanism size with eccentricity is correlated with changes in Ricco's area measured psychophysically (Wilson, 1970; Inui, Mimura & Kani, 1981).

Another alternative hypothesis is that the areal-summation paradigm is insensitive to moderate magnitudes of neural summation. Two calculations were carried out to examine this hypothesis. In one test we added a second stage of spatial summation that was identical to that produced by the optics of the eye. Recall that in the single-channel framework, the transfer function for the whole visual system (VTF) is the product of the optical, aperture, and neural transfer function:

\[ VTF = OTF \times ATF \times NTF. \]

Thus, if we set the NTF equal to the OTF we have

\[ VTF = OTF^2 \times ATF. \]

When the OTF in the ideal-observer was squared, it increased the predicted Ricco's area by 4 min² from 6 to 10 min². (These predicted Ricco's areas are based on line-segment fits to the ideal thresholds at the particular target areas tested on subject JB.) This magnitude of neural summation would have been easily detected by the current experiment. Specifically, the obtained mean Ricco's area of 5.5 min² is significantly less than 5.5 + 4 min² (t = 3.87, d.f. = 3, P < 0.025). Thus, the receptive-field center sizes in the fovea (with optics factored out) must be smaller than the line-spread function in Fig. 1.

To test more quantitatively the ability of the areal-summation paradigm to detect neural summation, we compared the fits of the ideal-observer predictions to the threshold data assuming various amounts of summation. Ideal-observer predictions were generated for cone aperture sizes of 1, 2, 3 and 4 cone diameters. For each cone diameter a minimum \( \chi^2 \) fit of the predicted curve was obtained using STEPIT. As before, the only free parameter was the value of a neutral density filter placed in front of the ideal observer. This parameter translated the predicted curves up and down in the log-log

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*The minimum \( \chi^2 \) fits for each subject were obtained with the data point for the largest test area omitted. Most of the subjects deviated strongly from the ideal predictions at this test area. (Recall that at this test area, two of the subjects' data no longer follow Piper's law.) Including these points would have inflated the chi-square values in a misleading way because the largest test area is so far removed from the crucial region surrounding the blur in the areal-summation curve. For two of the subjects (WG and MG) the \( \chi^2 \) values for the fit of the ideal observer were smaller than those for the pair of line segments; for the other two subjects the straight-line fits were better. The Ricco's areas estimated with the largest test area omitted are slightly smaller than those in Table 2.
Table 3. Variation in minimum \( \chi^2 \) values

<table>
<thead>
<tr>
<th>Assumed summation in cone diameters</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
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<tr>
<td>JB (33.9)</td>
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<tr>
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<td>41.6</td>
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<tr>
<td>AVE (31.24)</td>
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<td>24.0</td>
<td>35.4</td>
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From the above calculations we conclude that use of the areal-summation paradigm, in conjunction with the ideal observer(s), can detect modest amounts of neural summation but cannot detect small amounts. Thus, even though the present results provide no evidence for neural summation greater than a single cone diameter, and hence are consistent with the more sensitive contrast-sensitivity measurements of Banks et al. (1987), they cannot alone reject the hypothesis of a neural summation of up to two cone diameters.

Piper's law

In agreement with the ideal observer, all four subjects were found to display approximately Piper's law for test widths of up to 16-32 min arc. The ideal observer displays Piper's law because it sums photons across the whole test area. In other words, it adjusts the summation area to match the retinal stimulus. At smaller stimulus diameters, the ideal observer displays Ricco's law because the effective retinal stimulus does not contract beyond a minimum size set by the optics of the eye and the receptor aperture. The fact that the human observers displayed Piper's law suggests that they are also summing responses over an area proportional to the target area. Because of the fairly uniform size of parvocellular center mechanisms and the relative scarcity of magnocellular receptive fields in the primate fovea (Derrington & Lennie, 1984), it is unlikely that the summation responsible for Piper's law is occurring prior to the cortex. At the cortical level, the summation might be due to either the wide range of center mechanism sizes, or perhaps to a more flexible higher-level process.

The existence of center mechanisms of various sizes at the early cortical level does not contradict the present hypothesis of a subsystem with center mechanisms the size of a single cone. Because of the enormous explosion in the number of neurons between the LGN and the input layers of the visual cortex, there is plenty of room for a complete subsystem with small center mechanisms.

Spatial summation at low photopic background levels

For the two subjects tested, Ricco's area increased from an average of 6 min² under light-adapted conditions to 10 min² under dark-adapted conditions. This is smaller than the increases found by Glezer (1965) and Lie (1981). The difference might be explained by the following facts: (a) Lie (1981) used natural pupils which would result in larger point-spread functions and poorer accommodation under the dark-adaptation conditions; (b) we were careful to select lenses that would optimize the subject's ability to maintain accommodation throughout the experimental run. The other major difference between our study and the earlier studies is that we used forced-choice procedures;
however, it seems unlikely that this would have an effect on the difference between Ricco’s area under light- and dark-adapted conditions.

The increase in Ricco’s area under dark-adaptation conditions suggests that under those conditions, the neural mechanisms in the fovea are summing over more than one cone. One plausible hypothesis is that there is a change in the population of neurons mediating detection as light level is decreased. At high mean luminances, units whose center mechanisms are driven by a single cone (or a single row of cones) dominate, but as luminance is lowered, units with larger center mechanisms begin to contribute to detection sensitivity. For example, it is possible that the relatively sparse magnocellular neurons (which have large center mechanisms) make an important contribution to detection at low mean luminances because of the high gain of their center mechanisms (Derrington & Lennie, 1984; Kaplan & Shapley, 1982), but that their gain is reduced more severely than that of parvocellular neurons as background luminance is increased, in order to prevent saturation. This would cause the parvocellular neurons to contribute more to detection of spots under light-adapted conditions, resulting in a smaller Ricco’s area.

SUMMARY

Using an ideal-observer analysis that takes into account the spatial-summation effects of pre-neural factors, we have predicted the sizes of foveal Ricco summation areas expected from pre-neural factors alone. These predicted values are so similar to the Ricco’s areas measured for real observers that they suggest that Ricco’s area estimates are dominated by pre-neural effects, rather than being primarily measures of neural summation as has often been supposed. However, we have also shown that the areal summation paradigm is not sensitive enough to detect summations of up to 2 cone diameters. Taken together with anatomical evidence and other recent psychophysical evidence (Banks et al., 1987), the present findings support the notion of a neural subsystem in the foveal region that preserves, for higher visual centers, the discrete information from individual foveal cones. Ricco’s area increases by a factor of 1.7 under dark-adapted conditions, suggesting that neurons with larger center mechanisms might be contributing to detection of test spots under these conditions.

Acknowledgements—We thank John Beam, Josh Elmore and Mark Garrison for their patient work and unfailing good-humor as observers. Gordon Hanka wrote many of the subroutines used for stimulus generation, and Larry Stern assisted with data collection and manuscript preparation. Gail Geisler drafted the figures. This research was supported by NIH grant EY 02688 from National Eye Institute.

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