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An Estimation and Application of the Human Cortical Magnification Factor

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Summary. Comparisons of the published data on the density D of receptive fields of retinal ganglion cells and on the cortical magnification factor M indicated that M^2 is directly proportional to D in primates. Therefore, the human M can be estimated for the principal meridians of the visual field from the density-distribution of retinal ganglion cells and from the density of the centralmost cones. Using the previously published empirical data, we estimated the values of the human M and express the values in four simple equations that can be used for finding the value of M for any location of the visual field. The monocular values of M are not radially symmetric.

These analytically expressed values of M make it possible to predict contrast sensitivity and resolution for any location of the visual field. We measured contrast sensitivity functions at 25 different locations and found that the functions could be made similar by scaling the retinal dimensions of test gratings by the inverse values of M. Visual acuity and resolution could be predicted accurately for all retinal locations by means of a single constant multiplier of the estimated M.

The results indicate that the functional and structural properties of the visual system are very closely and similarly related across the whole retina. Visual acuity, e.g., bears the same optimal relation to the density of sampling executed by retinal ganglion cells at all locations of the visual field.

Key words: Cortical magnification factor – Man – Visual resolution – Contrast sensitivity

Visual field is represented topographically in the primary visual cortex, but the scale of the map changes as a function of retinal location: the central parts of the visual field have a much larger representation than peripheral regions. The scale of mapping is described in mm of cortex per 1° of visual angle for various retinal locations by the linear *cortical magnification factor* M (Daniel and Whitteridge, 1961; Whitteridge and Daniel, 1961). Cortical magnification correlates visual

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acuity and resolution (Daniel and Whitteridge, 1961; Cowey and Rolls, 1974; Drasdo, 1977) and contrast sensitivity (Rovamo et al., 1978; Koenderink et al., 1978) with the structural properties of the visual system, and makes it possible to predict the visibility of various aspects of gratings independent of their size and location in the visual field (Virsu and Rovamo, 1979).

The previous comparisons between functional and structural properties of the human visual system have been accurate only for the lower nasal visual field since the values of M are not known for other locations of the visual field. In the present study we estimate the values of the human M for the principal meridians of the visual field and present the estimates in four simple equations. The equations predict the photopic contrast sensitivity and visual resolution for any location along the principal meridians as will be shown below. By means of linear interpolation, the four equations make general quantitative treatments of structural relations and functional properties of the visual system possible, irrespective of retinal location.

Estimation of the Human Cortical Magnification Factor

Since it is difficult to measure the values of the human M directly, except for a small part of the lower visual field (Cowey and Rolls, 1974), we estimated M indirectly in three steps. We established first the relationship between M and the retinal ganglion-cell density in primates. Secondly, we found a set of plausible functions to describe the density distribution of the human ganglion cells. Thirdly, we estimated the constant required for obtaining the values of M. Our analysis is based on the previously published empirical data and owes much to the work of Rolls and Cowey (1970) and Drasdo (1977), whose results underlie our estimation.

It has been suggested that in the cat (Tusa et al., 1978; Wilson and Sherman, 1976) and man (Drasdo, 1977) the areal cortical magnification M^2 is directly proportional to ganglion cell density, i.e., at any retinal location $M^2 = g\ D$, where D is the areal density of receptive fields of retinal ganglion cells in fields/degree^2 and g is a constant. The field density is the same as the cell density, except that the displacement of cell bodies in the fovea is taken into account in the field density. The direct proportionality between M^2 and D, or M and the square root of D, is anatomically plausible, for it follows if connections and cell mass are multiplied similarily at successive levels, disregarding the retinal locus from which the projections originate.

On the other hand, it has been claimed that in monkeys the central visual field has a much larger cortical representation than that implied by a direct proportionality (Rolls and Cowey, 1970; Malpeli and Baker, 1975; Myerson et al., 1977). Rolls and Cowey suggest that M, not M^2, is directly proportional to D. Since this has led to a considerable confusion in the literature (e.g., Hughes, 1977; 1978), we reanalyzed all the published monkey data available to us to check whether M or M^2 is directly proportional to D in monkeys (see Appendix I for details). Independent replicated work was found only for the rhesus monkey, and it is summarized in Fig. 1.

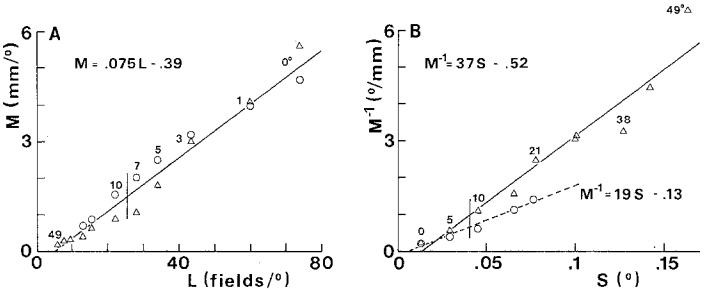

Fig. 1. Cortical magnification factor (M) and its inverse (M^{-1}) as functions of linear measures of receptive-field density of retinal ganglion cells in the rhesus monkey. The linear densities L of receptive fields and their separations S were obtained from the data of Rolls and Cowey (1970) for eccentricities larger than or equal to 10°; the data are based on the averages of ganglion cell densities measured along the nasal and temporal half-meridians in the rhesus monkey retina. The numbers next to the data points refer to various eccentricities. For eccentricities smaller than 10° (the crossover is indicated by a vertical bar) the receptive-field separations were estimated by means of linear interpolation assuming that the average field separation is 0.81' for the centermost cells. The values of M or M^{-1} depending on which one was more accurately reported were obtained from Hubel and Wiesel (1974, circles) and Daniel and Whitteridge (1961, triangles) by means of linear interpolation from the nearest data points available for each eccentricity; if several values were reported, they were averaged. The foveal value of 5.6 mm/° at E = 0° is a verbal statement by Whitteridge and Daniel (1961); for Hubel and Wiesel 4.7 mm/° was obtained by a direct extrapolation from the two most central values reported. The results of Hubel and Wiesel were collected from 2 rhesus monkeys and those of Daniel and Whitteridge from 3 baboons and 3 rhesus, 1 cynomolgus. and 1 vervet monkey. The least-squares lines fitted to the data and their equations are shown on the graphs

Figure 1A shows M as a function of L that refers to the linear density ($L = D^{0.5}$) or frequency of retinal ganglion-cell receptive-fields (fields/°). It is clear that the data are consistent with $M^2 = g\ D$, for the additive constant of the least-squares straight line can be considered to be zero within the variance occurring in the data. The linear fit extends to an eccentricity of 49°, beyond which ganglion cell data are not available.

Figure 1B plots the same data for M^{-1} as a function of the separation S of the receptive-field centers of the ganglion cells ($S = D^{-0.5}$) in order to show that no nonlinearity is hidden in the attenuated ends of the linear plots. The additive constants are insignificant again, indicating that M^{-1} is directly proportional to S. The latter plot reveals a distinct difference between the magnification data of Daniel and Whitteridge (1961; triangles) and of Hubel and Wiesel (1974; circles).

Our analysis differs from the previous ones in two respects. Firstly, we included the magnification data of Hubel and Wiesel (1974) measured from the rhesus monkey whereas the earlier comparisons (Rolls and Cowey, 1970; Malpeli and Baker, 1975) used only the data of Daniel and Whitteridge (1961) that average results from several species of monkey. Secondly, we took into account also the data of Polyak (1957) concerning the smallest separation (intercenter distance) of the most central cones in the rhesus monkey retina whereas the previous comparisons were based on the estimate of Rolls and

Cowey (1970) that averages the separation of cones in a 100 μm strip of retina. The cone separation plays a critical role in the comparison because the density of ganglion-cell receptive fields for the central 10° can be estimated only by means of the cone density due to the displacement of the foveal ganglion cell bodies. The minimal cone separation estimated by Cowey and Rolls is 1.08' and that based on Polyak's measurements is 0.54'; we used the averaged value of 0.81' for the intercenter distance in our comparisons.

Drasdo (1977) has recently estimated the human cortical M assuming that $M^2 = g\ D$. He pooled the empirical estimates of the human ganglion-cell density from several sources, corrected them for the optical magnification in the eye (Drasdo and Fowler, 1974), extrapolated to the foveal area of the ganglion cell excavation by means of the density of the centralmost cones, and fitted four empirical equations to the data to describe $D^{-0.5} = S$ for the principal half-meridians. M follows from the values of S because the constant g in $M^2 = g\ D = g\ S^{-2}$ is the ratio between the total striate area in the two hemispheres and the total count of retinal ganglion cells in one eye calculated from the cumulation implied by the equations for D.

The main reason why we find the values of M estimated by Drasdo unsatisfactory is that they do not agree with the best estimates available for the density D_o of the centralmost cones. This density is a critical parameter because it does not affect only the foveal values of M but also the peripheral values, because the total ganglion cell count implied by the equations has to be consistent with its empirical estimates.

We searched by means of successive approximations for a set of as simple as possible equations that would give the values of D in agreement with what is known about the density and total number of retinal ganglion cells, and the density of the centralmost cones. Unfortunately, the data on human ganglion cell density are not very complete or consistent (Hughes, 1977), and new data may necessitate a revision of the values of D and M estimated here. The numerical details of the estimation are presented in Appendix II.

We could not find a single equation to describe the human D at all locations of the visual field. Like Drasdo (1977), we obtained one equation for each principal half-meridian to summarize our present knowledge of D. They are presented below in a form that indicates directly M rather than D:

(1) Nasal: $M_N = (1 + 0.33\ E + 0.00007\ E^3)^{-1}\ M_o$, $(0 \leq E \leq 60°)$;
(2) Superior: $M_S = (1 + 0.42\ E + 0.00012\ E^3)^{-1}\ M_o$, $(0 \leq E \leq 45°)$;
(3) Temporal: $M_T = (1 + 0.29\ E + 0.000012\ E^3)^{-1}\ M_o$, $(0 \leq E \leq 80°)$;
(4) Inferior: $M_I = (1 + 0.42\ E + 0.000055\ E^3)^{-1}\ M_o$, $(0 \leq E \leq 60°)$.

E refers to eccentricity in degrees and M_o is the value of magnification (7.99 mm/°) for the most central fovea. The values for other meridians can be obtained from the equations with a reasonable accuracy by means of linear interpolations.

The equations give the linear receptive-field density L of retinal ganglion cells if $L_o = 123.8$ fields/°, the value of linear field density at $E = 0°$, is substituted for M_o. The pooled and corrected estimates of ganglion cell density indicated by Drasdo (1977) underlie our equations, which assume that Drasdo's estimates are accurate at about $E = 20°$ for each half-meridian, except that we

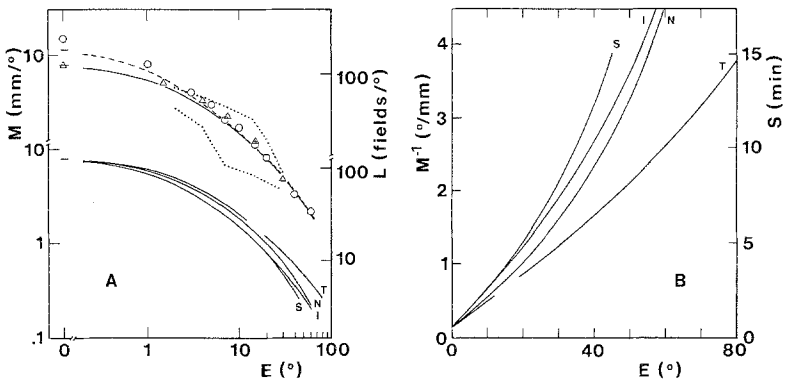

Fig. 2. The values of M and M^{-1} calculated from equations (1)–(4) and their comparison with earlier estimates. **A** The lower set of curves plots the human cortical magnification factor (M) and the linear density of retinal ganglion cells (L) as a function of eccentricity (E) for the various half-meridians of the visual field as indicated by the letters. The upper set of curves and data points (shifted upwards by 1 log unit) compares on the inferior half-meridian our values (continuous lines) with Drasdo's (1977) estimates (dashed line), with our previous estimates (triangles; Rovamo et al., 1978), and with the estimates of Cowey and Rolls (1974; circles). The dotted lines indicate the range between the highest and lowest values of M as measured in predominantly antero-posterior cortical directions by Cowey and Rolls (1974) from the phosphene data of Brindley and Lewin (1968). **B** The reciprocal magnification (M^{-1}) and receptive-field separation (S) calculated from equations (1)–(4)

increased slightly the difference between the ganglion cell densities of the nasal and temporal half-meridians so that our values match better the difference observed in these densities by Oppel (1967). All other deviations from the values estimated by Drasdo follow from the different value of D_o and the simpler form of equations.

The lower set of curves in Fig. 2A presents the values of M and L calculated from equations (1)–(4). The values for the inferior half-meridian are compared with earlier estimates of M in the upper frame. The reciprocal values M^{-1} and S are shown in Fig. 2B.

Our values of M do not deviate significantly from the earlier estimates outside the most central 10°. Drasdo's (1977) value for the centralmost cone density and consequently for M_o (11.5 mm/°) is too high. Cowey and Rolls (1974) extrapolated by means of acuity data a value of 15.1 mm/° for M_o, but this estimate is not reliable because it is based on Wertheim's (1894) psychophysical data.

Cowey and Rolls (1974) measured the values of M for a restricted range of eccentricities from the phosphene data of Brindley and Lewin (1968). Brindley and Lewin recorded where the sensations of light evoked by electrical stimulations of the human visual cortex appeared in the visual field. Since these are the most direct data available on the human M at the present, estimates of the human M should agree with these data.

The range of directly estimated values is delineated in Fig. 2A by the dotted lines, and our earlier estimates of M (Rovamo et al., 1978; Virsu and Rovamo, 1979) based only on inter- and extrapolation of the phosphene data are

indicated by the triangles. Including the value of M_o, our present estimates are consistent with the directly estimated values. The comparison supports the assumption that M^2 is directly proportional to D, for our equations agree with the best estimates available for the density of retinal ganglion cell receptive fields both in the fovea and periphery. The values of M estimated above are directly applicable to the monocular temporal crescent.

Methods

The methods of the psychophysical experiments were the same as in the preceding study (Virsu and Rovamo, 1979). The subject fixated a small point of green light binocularly in a dark room; a bite board aided steady fixation. Sinusoidal gratings were generated under computer control on a white cathode-ray screen. The screen was perpendicular to the visual axis if viewed directly and at the same distance as the fixation point; the screen was visible to one eye only. The average luminance of the screen was continuously 10 cd/m^2. The natural pupil used had a diameter of about 6.5 mm. Hence, the average retinal illuminance was about 330 trolands, which corresponds to 1060 scotopic trolands on our display. The adaptation level was photopic (Virsu and Rovamo, 1979).

Contrast sensitivity was measured at various eccentricities along the principal meridians of the visual field by determining the inverse of the threshold contrast for a series of spatial frequencies. Thresholds were determined by using a computer-controlled forced-choice method. In the detection task, the subject received two sound signals and had to decide during which signal a grating was presented. Another sound indicated the wrong choices. After each block of four consecutive correct responses, contrast was decreased by 0.1 $\log_{10}$ unit and every wrong choice led to a contrast increment by the same amount. The contrast required for a probability of 0.84 of correct response was estimated as threshold. The critical stimulus to be detected was a stationary vertical or a horizontal grating with a non-zero contrast for 0.5 s; the control stimulus was otherwise identical but had a zero contrast.

Discrimination of the direction of movement was required in some experiments. The method was otherwise similar but the subject received only one sound signal during which the blank screen was replaced by a drifting grating for 0.5 s. The subject had to decide whether the grating presented drifted to the left or to the right, if a series of vertical gratings was tested, and up or down, if horizontal gratings were shown.

Results

Contrast Sensitivity and M

An effective way to test the psychophysical predictions derived from M is to scale the retinal dimensions of stimuli so that they produce equivalent cortical representations as assessed by using M as the scale of mapping from the visual field into the striate cortex (Rovamo et al., 1978; Virsu and Rovamo, 1979). Scaling can be executed simply by viewing the same stimuli at different distances for each eccentricity: the viewing distance required is a constant multiple of M. This "partial M-scaling" makes the calculated cortical images of the grating stimuli quite similar at low and medium spatial frequencies, but it fails at high spatial frequencies because the optical degradation of retinal images affects the transfer of high spatial frequencies most.

In our earlier studies we estimated M for the inferior half-meridian from the phosphene data of Brindley and Lewin (Fig. 2A) and found that contrast

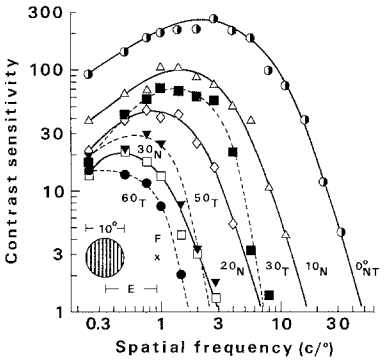

Fig. 3. A comparison of contrast sensitivity functions for the nasal visual-field half-meridian of the right eye (open symbols and continuous lines) and for the temporal half-meridian of the left eye (filled-in symbols and dashed lines). The values of eccentricity were measured as the angular distance of the fixation point from the middle of the gratings that subtended 10°. The nasal eccentricities were 0° (half-filled circles), 10° (triangles), 20° (diamonds), and 30° (squares). The temporal eccentricities were 0° (half-filled circles), 30° (filled squares), 50° (filled triangles), and 60° (filled circles). The foveal functions were similar for both eyes and are not drawn separately. The results were obtained with a detection task from the subject (VV). The circular gratings were viewed at a distance of 115 cm

sensitivity measured with M-scaled gratings was independent of eccentricity in the inferior visual field. The same values of M led to reasonable predictions of contrast sensitivity also in the nasal field but not in the temporal field. The reason for the failure in the temporal field is, of course, that the values of M for the temporal half-meridian differ considerably from the others in the periphery (Fig. 2B). This is in agreement with the well-known elliptic shape of the useful visual field, and with the variation of visual acuity (Wertheim, 1894) and sensitivity to spot stimuli (Harvey and Pöppel, 1972) at different locations in the visual field.

Figure 3 illustrates the radially asymmetric distribution of visual sensitivity in the visual field by comparing the contrast sensitivity functions measured with constant-size gratings at a few locations along the horizontal meridian. The measurements were done in the nasal visual field of the right eye and the temporal field of the left eye, which are both projected into the same (right) cortical hemisphere.

Visual performance deteriorates rapidly as a function of eccentricity when the size of the test gratings is retinally constant (Virsu and Rovamo, 1979). The point of Fig. 3 is that the performance differences are large also between different half-meridians at similar eccentricities. The contrast sensitivity function at a temporal eccentricity of 30° corresponds approximately to that of 15° nasal, and sensitivity at a nasal eccentricity of 30° is not better than at 50° temporally. The differences in acuity and resolution as assessed from the cut-off frequencies of the contrast sensitivity functions are not so prominent. The contrast sensitivity functions have a different shape for similar eccentricities on

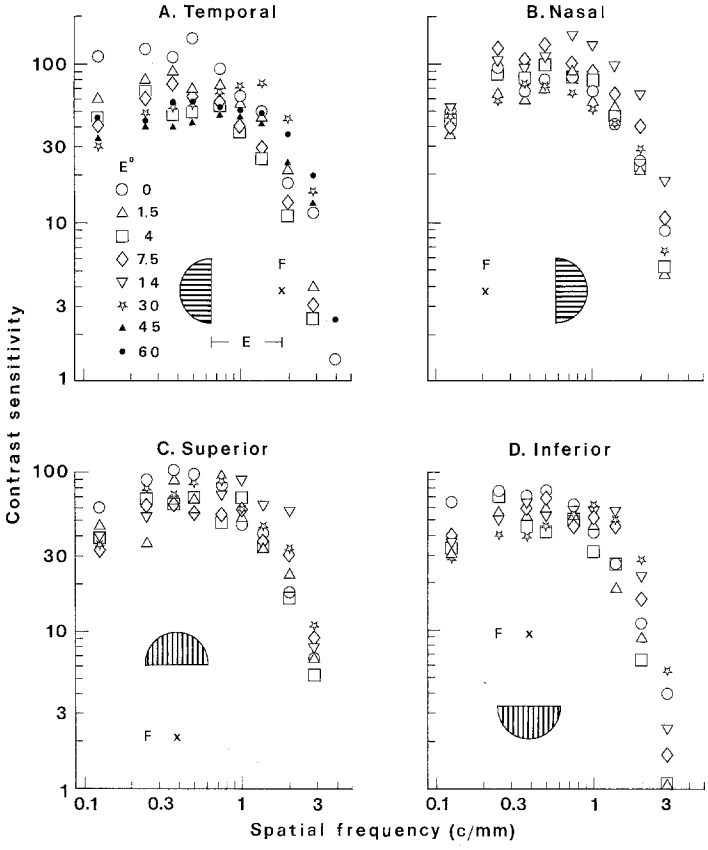

Fig. 4. The photopic contrast sensitivity functions for 25 locations of the visual field. The eccentricities were measured along the various half-meridians of the visual field as indicated on the graphs and in A for the different symbols. Contrast sensitivity was measured with a task that required discrimination of the direction of movement; the drift rate was a constant 4.1 Hz. The retinal dimensions of the gratings were scaled for equivalent calculated cortical representations. Contrast sensitivity is shown as a function of spatial frequency in the calculated cortical projection images (cycles/mm of cortex = c/° divided by M). The scaling factors for the various locations were obtained from M of equations (1)–(4). Scaling was as follows: viewing distance = 57.3 M cm; display radius = 7.99 M^{-1} degrees; and the lowest retinal spatial frequency measured = 0.125 M c/°. Subject JR; left eye. The data shown for the inferior meridian are the same as in Fig. 3B of the previous study (Virsu and Rovamo, 1979) because the values of M were practically the same there and in Eq. (4)

different half-meridians (compare the open and filled squares that denote the data for 30°).

In Fig. 4 we scaled the retinal dimensions of the test gratings so that they produced similar cortical representations on each half-meridian as calculated by means of M obtained from equations (1)–(4), and measured a contrast sensitivity function at 25 different locations of the visual field. The gratings covered practically the whole useful visual field of the left eye, for a next, more

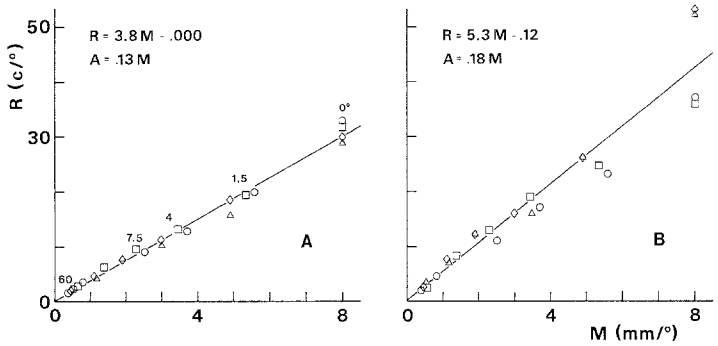

Fig. 5. Resolution and grating acuity as functions of M at 25 locations of the visual field. The highest visible spatial frequency at each location was estimated from the cut-off frequency of the corresponding contrast sensitivity function by extrapolating to contrast = 1. Acuity (A) is resolution (R) divided by 30 c/°. The data points refer to various eccentricities on the temporal (circles), nasal (squares), superior (diamonds), and inferior (triangles) half-meridians. Some of the eccentricities are indicated by numbers on the graphs. Eccentricity is maximally 60° and it was measured from the most central edge of the gratings (see the insets of Fig. 4). Some of the peripheral data points have not been plotted because of the overlap, but they were included in the computation of the least-squares lines shown on the graphs with their equations. **A** Subject JR, direction discrimination; the complete contrast sensitivity functions are shown in Fig. 4. **B** Subject VV, detection of stationary gratings. Viewing distance was 107 M cm, display radius 6.71 M^{-1} deg, and the lowest spatial frequency measured was 0.149 M c/°. The values of M were obtained from Eqs. (1)–(4)

peripheral grating for each half-meridian would have been only partially visible when the eye is in its rest position. Contrast sensitivity is plotted in Fig. 4 for different locations as a function of the cortical spatial frequency that is the retinal frequency divided by the value of M at each location; the value of E was measured from the most central edge of the semicircular grating.

All the contrast sensitivity functions measured with the "cortically" similar gratings are the same within a factor of $\mp$ 2, disregarding only the highest spatial frequencies that could not be scaled adequately due to the optical transfer properties of the eye (Virsu and Rovamo, 1979). A similar result was obtained from another subject for whom the same locations were mapped with a detection task and stationary gratings. Much of the residual variation of sensitivity that occurs with scaled gratings is independent of M. For example, the subject of Fig. 4 had a systematically higher sensitivity on the temporal and inferior sides of the fovea even though the values of M were the same (nominally E = 0°).

Resolution and M

Although a partial M-scaling performed by changing the viewing distance cannot equalize the contrast sensitivity at high retinal spatial frequencies, M can be used for predicting resolution and acuity thresholds for any location of the visual field. This is illustrated in Fig. 5, which presents the retinal cut-off

frequencies of the contrast sensitivity functions of two subjects as a function of M obtained from equations (1)–(4). It is evident that the grating resolution thresholds are predicted accurately by the same constant multiplier of M for any retinal location. The additive constants of the least-squares regression lines are negligible and zero within the experimental error. Thus, resolution $R = rM$ c/°, where r is a constant. This should be expected if the estimated values of M are correct: if M is zero, acuity and resolution should also be zeros. The converse is also true for our values of M: if M goes to infinity ($M^{-1} = 0$), the extrapolated acuity becomes infinite and the minimum angle of resolution (MAR) becomes zero.

Discussion

We derived the values of M from the receptive-field density (D) of retinal ganglion cells. The derivation was based on the direct proportionality between M and $D^{0.5}$ as illustrated in Fig. 1 for the rhesus monkey. The estimated values of the human M agree with the values measured for man in the lower visual field (Cowey and Rolls, 1974). The direct proportionality $M^2 = gD$ is supported also by the following assumptions often expressed or implied: (1) the density of afferent fibers entering the striate cortex is constant everywhere (Clark, 1941); (2) each retinal ganglion cell innervates a constant-size area of the striate cortex (Whitteridge and Daniel, 1961); (3) there is little excitatory convergence onto the cells of the LGN (Singer and Creutzfeldt, 1970; Levick et al., 1972) and visual cortex (Creutzfeldt et al., 1974; Lee et al., 1977); and (4) the whole striate cortex consists of a set of anatomically identical building-blocks (Hubel and Wiesel, 1974).

The estimates of M derived from D cannot be radially symmetric since the ganglion cell density distribution of the primate retina (Van Buren, 1963) is radially asymmetric. However, it is generally assumed that M is radially symmetric, i.e., independent of the visual-field meridians (Rolls and Cowey, 1970; Cowey and Rolls, 1974; Malpeli and Baker, 1975; Hubel and Freeman, 1977; Myerson et al., 1977). The assumption is supported by the direct cortical measurements performed by Daniel and Whitteridge (1961) in monkeys. Their results do not contradict the actual asymmetry of M, however.

Except for the monocular temporal crescent, each small region of the striate cortex receives projections from the optically corresponding locations of the contralateral nasal and ipsilateral temporal hemiretinae of the two eyes. Hence, for each location of the human or monkey striate cortex we can calculate two *monocular* cortical magnification factors M_n and M_t from the corresponding ganglion cell densities D_n and D_t of the nasal and temporal hemiretinae, respectively. To evaluate correctly the true dimensions and total area of the striate cortex we have to use the average of the projection areas M_n^2 and M_t^2 in the calculations. Therefore, we define the directly measurable classical cortical magnification factor M_c by equation $M_c^2 = (M_n^2 + M_t^2)/2 = g(D_n + D_t)/2$. Figure 1 verifies this relation for the rhesus monkey since it shows that M_c^2 is directly proportional to the density of ganglion cells obtained as the average of

the nasal and temporal field densities. A direct cortical measurement of M automatically averages the values of M_n and M_t yielding only one binocular value of M_c. The values of M_c are radially symmetric within the accuracy of direct measurements.

Our psychophysical results showed that the estimated values of the human monocular M indicated correctly how the size of monocularly presented gratings had to be adjusted (M-scaled) in order to equalize the contrast sensitivity functions for different locations in the visual field. In addition, our values of M were found to be directly proportional to grating resolution at various eccentricities (see also Virsu and Rovamo, 1979). By definition, the values of M are proportional to the linear density L of retinal ganglion cell receptive fields (fields/°). These relations indicate that the density of sampling performed by retinal ganglion cells relative to acuity and contrast sensitivity is the same at any location of the visual field, including the most central fovea.

It is generally assumed that the density of visual sampling executed by retinal ganglion cells relative to observed acuity is optimal in the central fovea in terms of the sampling theorem, but the optimal density of sampling has been disputed for the extrafoveal retina (Green, 1970; Hughes, 1977); an excess of retinal ganglion cells relative to acuity has to be postulated then in the periphery (Hughes, 1977). Our results show that no excess of retinal ganglion cells exists in man, for the density of sampling relative to acuity and resolution is the same at any location of the visual field. Our estimate of L for the centralmost fovea is consistent with the sampling theorem (see the Appendices), and therefore, it is consistent also elsewhere because resolution was found to be the same constant multiple of $M = (gD)^{0.5}$ for any retinal location. The proportionality constant in $R = rM = r'D^{0.5}$ conceals in itself the gradual change of optical attenuation that probably takes place as a function of eccentricity (Virsu and Rovamo, 1979). Since the bandwidths and maximum sensitivities displayed by the contrast sensitivity functions for M-scaled gratings (Fig. 4) are independent of visual-field location, we can assume that the sampling performed by visual cells has the same constant relation to $D^{0.5}$ and M at all retinal locations and spatial frequencies.

In addition to resolution and acuity thresholds, and MAR, various critical sizes and distances are either directly proportional or linearly related to M or M^{-1}. For example, Weymouth (1958) has plotted the vernier threshold, threshold of motion, diameter of the Panum area, and the mean variation in the settings of horopter rods as a function of eccentricity. They all increase with eccentricity following the same slightly concave course as M^{-1} in Fig. 2, and therefore, they are linearly related to M^{-1}. Weymouth did not possess the required neural data, but he suggested that at all retinal locations the spatial thresholds are linearly related to the separation of ganglion cell receptive fields. Our results confirm this assumption. The separation of cones, instead, is relevant to spatial thresholds only in the central retina (Weymouth, 1958) as could be expected on the basis of convergence onto the ganglion cells outside the fovea.

It seems to us that there is a much closer relation between the anatomical properties of the visual system and its performance characteristics than is

generally realized at the present. We hope that our results revive interest in accurate and comprehensive determinations of the structural constants that are necessary for finding the exact quantitative relationships between structure and function in the visual system. Although we believe that the relationships we propose are more accurate than those suggested before, it is clear that we are still far from having the final parameter values for various structural equations. We have tried to find the best possible estimates for D and M by combining data from many different sources, but the anatomical data available at the present are quantitatively very unsatisfactory and large differences occur between the results of different studies. Only new anatomical data can reconcile the differences and lead to final quantitative descriptions. New data are needed particularly on cell densities and magnifications at different levels of the primate visual system. They are necessary for finding both the construction principles and the functional principles of the visual system.

Appendix I: M and Ganglion Cell Density in Monkeys

Rolls and Cowey (1970) plotted M obtained from Daniel and Whitteridge (1961) against their own density estimates of retinal ganglion cells and cones. The result led to the incorrect but often cited conclusion that M is directly proportional to D because the cone-density estimates were too low and the values of M were not completely representative.

According to Polyak (1957, p. 269), the minimum cone separation of the rhesus monkey retina matches the human cone separation, being 1.78–2.67 μm when the limits of possible shrinkages are taken into account. Rolls and Cowey indicate that 0.246 mm on the macaque central retina corresponds to 1°. Polyak's measurements indicate then an averaged separation of 0.54', which is exactly a half of the value of 1.08', estimated by Rolls and Cowey (1970). Polyak studied the minimum separations using flat-mount preparations whereas Rolls and Cowey calculated averages from 100 μm long serial sections.

Polyak's estimate agrees with the visual acuity of 0.65' quoted by Rolls and Cowey for the macaque. If the cone separation is 0.54', linear density is 111 cones/°. According to common sense there should be one less stimulated cone between two more stimulated ones to make a discrimination possible, and the same is stated formally in the sampling theorem of the information theory. This purely mathematical theorem implies that a signal reaching frequencies W can be determined uniquely if, and only if, the sampling interval is not more than $(2\ W)^{-1}$ (see Hughes, 1977, for applications of the theorem). The sampling considerations imply that 111 cones/° can give a maximum acuity of 0.54', or maximum resolution of 55.5 c/°, if there is no optical deterioration in the retinal images. Taking the optical factors into account, Polyak's estimate would seem to agree with the observed acuity of 0.65'. If the cone separation is 1.08', the maximal non-attenuated acuity is also 1.08', which is much worse than the observed value. We regard Polyak's estimate as correct but plotted Fig. 1 with the average (0.81') in order to keep our conclusions as conservative as possible.

The magnification data of Daniel and Whitteridge (1961) average results from several species of monkey. The values of M measured by Hubel and Wiesel (1974) solely from rhesus monkeys deviate systematically from the averaged data of Daniel and Whitteridge (Fig. 1B). If the values of M are compared with the values of D corrected for the fovea as in Fig. 1, M^2 not M is found to be directly proportional to D.

Malpeli and Baker (1975) made their comparisons regarding the retinal and cortical magnification using the same data as Rolls and Cowey, and were misled in the same way. If the results of Malpeli and Baker regarding magnification in the macaque LGN are plotted against the macaque cortical M measured by Hubel and Wiesel, their conclusion that the representation of the central visual fields relative to peripheral fields increases from the LGN to the striate cortex has to be reversed, for if there is any reliable change, it is opposite to the one described by Malpeli and Baker.

An analysis of the data of Rolls and Cowey (1970) for the squirrel monkey indicates that they also agree with the principle of direct proportionality between M^2 and D for eccentricities from 10 to 50°. If the values of cone density in the most central fovea are corrected by the same factor as for the rhesus monkey, the linear fit extends to the zero eccentricity.

Myerson et al. (1977) claim that in the owl monkey the cortical representation of the central visual field is much larger than would be predicted from $M^2 = gD$. Being the only nocturnal monkey (Allman and Kaas, 1971), the owl monkey is visually so different from the other monkeys that it might deviate from the others in its cortical magnification principle. If it has evolved from a diurnal ancestor (Ogden, 1974), it could carry a disproportionally large foveal representation as a relic.

We do not, however, regard the evidence presented by Myerson et al. as conclusive. The study of Allman and Kaas (1971) that underlies the comparisons made by Myerson et al., and the similar comparisons made earlier by Webb and Kaas (1976), was not designed for the measurements of M and does not present all the revelant quantitative information. The values of M used in the comparisons were estimated indirectly from a model of cortex constructed by Allman and Kaas. If the values of M estimated from the original flat model by Webb and Kaas (1976) are plotted against the linear density L of retinal ganglion cells calculated from the areal densities measured by them, it becomes evident that if the central values of M were only 30% smaller, $M^2 = gD$ would agree also with the owl monkey data. The information given by Myerson et al. is not sufficient for deciding how they obtained a corresponding deviation by about 80%. The deviation would be slightly larger than 30% if a three-dimensional model is used in the estimation of M, but not 80%, and it would be still within the possible experimental error.

Talbot and Marshall (1941), for example, report that the first minute of arc at the fovea occupies 0.5 mm of cortex. According to this measurement the centralmost M has a value of 30 mm/° for the rhesus monkey since M is a derivative concerned with infinitesimal distances. Guld and Bertulis (1976) estimate 12 mm/° for the centralmost M in the vervet monkey. These values should be about 80% and 50% smaller, respectively, to agree with the values estimated by Daniel and Whitteridge (1961) and Hubel and Wiesel (1974).

The foveal values of the directly measured M tend to be overestimated because of the nearness of the secondary visual area (Zeki, 1978), projection scatter (Hubel and Wiesel, 1974; Albus, 1975), eye movements, and the ocular spread of light (Vos et al., 1976). The secondary visual area is a mirror image of the striate cortex in its projections. This makes it possible to overestimate M, for measurements are readily made between points in the primary and secondary visual cortex (Cowey and Rolls, 1974).

Appendix II: The Values of D_0 and M_0 for the Equations of M

Polyak (1957) states that "in the very center of the outer fovea, a minute, irregularly circular island, measuring not more than 100 μm across, is filled with 2,000 of the thinnest cones of practically uniform diameter." Assuming that the posterior nodal distance of he unaccomodated human eye is 16.7 mm, 1° corresponds to 291 μm and the cone density referred to by Polyak is 21,564 cones/deg^2. This agrees with his estimates on the separation (intercenter distance) of the centralmost cones, for he indicates a range of 1.78–2.67 μm, or 0.367–0.550', when the limits of a maximum and a minimum shrinkage noticed by him are taken into account. The mean separation of 0.458' implies a cone density of 17,162 cones/deg^2 for a rectangular packing. The packing of the cones is hexagonal, however, and therefore, the true density calculated from separation S is $(2/\sqrt{3})S^{-2}$, or 19,817 cones/deg^2 when S is 0.458'. This agrees with Polyak's areal count and suggests that the density is even within the centralmost 100 μm.

The human cone diameters and their intercenter distances estimated by Polyak tend to be smaller than those reported by others, as he himself points out. Österberg (1935) indicates a density of 147,300 cones/mm^2, or 12,474 cones/deg^2, on the basis of his cone counts in the central island. Because the direct density counts are available and they are the most relevant ones here, we will base our estimation of ganglion cell density D_0 in the very center of fovea on 17,018 cones/deg^2 that is the average of the direct counts by Polyak and Österberg. This hexagonally packed density implies an average cone separation of 0.494' and a linear density (frequency) of 121 cones/°, which are in agreement with most of the published estimates of cone size and separation.

According to Missotten (1974), there are 0.9 ganglion cells per 1 cone in the centralmost fovea. Because of the possible many-to-many connections, this result does not give the number of cones projecting to a single ganglion cell, but it implies that the centralmost ganglion cell receptive-field density D_o is 15,316 fields/deg^2. Since the packing of the receptive fields is more irregular than that of the cones as indicated by the ratio smaller than 1, linear density L_o can be calculated directly as the square root of the areal density D_o. We get L_o = 123.8 fields/°, which agrees with the cone frequency of 121 cones/°. Sampling theorem suggests then a maximal resolution of about 62 c/°, or a maximum acuity of 0.48′, which are consistent with the results obtained when the optical limitations of the eye are partially bypassed by using interference-fringe techniques (e.g., Campbell and Green, 1965).

In his estimation of D_o Drasdo (1977) assumed that it is equal to the centralmost cone density of 33,058 cells/degree^2. He refers to Polyak (1957, p. 269) as the source of this estimate, but actually Polyak indicates estimates that are about 37% smaller than value used by Drasdo.

Interpolation and numerical integration based on equations (1)–(4) of the main text with L_o = 123.8 fields/° substituted for M_o gives an estimate of 1.44×10^6 for the total number of retinal ganglion cells in one human eye as estimated for a spherical retina. Our estimate is perhaps more realistic than the 1.6×10^6 that is obtained if Drasdo's equations are applied in a similar spherical calculation (he quotes 1.5×10^6 that is evidently based on a planar calculation). About 1.1–1.3 million optic nerve fibers can be found in light microscopy (Potts et al., 1972), but this observed value may be lower than the true value since some of the smallest fibers are easily missed in light microscopy (Hughes, 1977).

To estimate the value of g in the equation $M^2 = gD$, we have to know also the total striate area of both hemispheres, because g is equal to the total striate area divided by the total ganglion cell count of one eye. In his estimation of M, Drasdo (1977) used an estimate of 6,000 mm^2 adapted from Cowey and Rolls (1974). The value represents a rounded average of 6,272 and 5,800 mm^2, based on the data of Filimonoff (1932) and the estimate of Cowey and Rolls, respectively. Later data by Stensaas et al. (1974) provide an estimate of 4,268 mm^2. Individual variance in total striate area is considerable (Filimonoff, 1932; Stensaas et al., 1974), but it affects the value of linear M by its square root, and therefore, quite moderately. In order to keep our estimates of M comparable to Drasdo's values, we use the same value of 6,000 mm^2 for the total striate area. Then the value of g is $6{,}000/1.44 \times 10^6 = 0.00417$. Since $M_o^2 = gD_o$ and D_o = 15,316 fields/deg^2, we can now calculate the value of M in the very center of the fovea: $M_o = (0.00417 \times 15{,}316) = 7.99$ mm/°.

Our equations do not apply to the monkey, but we can calculate the value of M_o for the rhesus monkey for comparison. Assuming a ratio of 0.9 between the centralmost ganglion cells and cones, and a change from hexagonal lattice to an irregular lattice, the ganglion cell receptive-field separation and the cone separation are practically the same 0.54′ obtained from Polyak (1957). For the rhesus monkey, D_o is then about 12,346 fields/deg^2. The total striate area is about 2,800 mm^2 (Daniel and Whitteridge, 1961), and the total number of retinal ganglion cells for one eye is about 1.08×10^6 (Rolls and Cowey, 1970). Constant g is then 0.00259 and M_o is 5.66 mm/°. This value agrees well with the direct estimates (Fig. 2 and its legend). It is consistent also with the cortical size relation between the monkey and man: the size ratio suggests that the monkey $M_o = (2{,}800/6{,}000)^{0.5} \times 7.99 = 5.46$ mm/°.

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