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# Human Cortical Magnification Factor and its Relation to Visual Acuity

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**Summary.** The magnification factor (M) of the retina is the linear extent of visual striate cortex to which each degree of the retina projects. It has been suggested that magnification factor is directly proportional to visual acuity, but magnification factor measured in monkeys was compared with visual acuity in man. Here we first describe calculation of the magnification factor in man, and then compare it to human visual acuity.

We calculated M for the first 30 degrees of the lower visual field by using information provided by Brindley and Lewin (1968), who plotted the distribution of phosphenes evoked by stimulation of visual cortex in a human patient with electrodes implanted on the visual cortex. Since the inter-electrode distance was specified it was possible to calculate M for each of many pairs of electrodes by measuring the angular separation and mean eccentricity of the corresponding pairs of phosphenes. For the lower visual field, M was approximately 4 mm/degree at 2 degrees eccentricity and declined monotonically to 0.5 mm/degree at 25 degrees eccentricity.

The results indicated that the reciprocal of M is directly proportional to the minimum angle of resolution and, correspondingly, that the magnification factor is directly proportional to visual acuity in man.

By extrapolating this function for the whole of the visual field it was possible to estimate the area of striate cortex. The total extent of striate cortex estimated in this way agreed closely with previous direct measurements, suggesting that the measurements of M are accurate.

**Key words:** Visual acuity — Visual cortex — Magnification factor

## Introduction

Visual acuity in man is sharpest at the fovea and declines monotonically with eccentric presentation of the target. This decline has been quantitatively related to the reduction in cone and ganglion cell density in the periphery of the retina (Weymouth, 1958). It is also known that the cortical magnification factor of the retina — the linear extent of striate cortex to which each degree of the retina projects — is highest for the fovea and diminishes with increasing retinal eccentricity, but it has not yet been possible to relate this quantitatively to visual acuity. The problem is that cortical magnification factor has been accurately determined in monkeys (Daniel and Whitteridge, 1961; Cowey, 1964; Rolls and Cowey, 1970)

whereas acuity as a function of eccentricity has not. In man eccentric acuity has been accurately measured (see Weymouth, 1958) but cortical magnification has not. The only evidence that cortical magnification does decrease with eccentricity in man comes from studies of the size of the visual field defects following damage to the striate cortex (Holmes, 1918). If Holmes's rough measurements could be greatly improved it would be possible to relate visual acuity and cortical magnification factors in a single species. The only previous attempt to relate them used acuity data from man and magnification measurements from monkeys (Daniel and Whitteridge, 1961).

In 1968 Brindley and Lewin reported the results of implanting stimulating electrodes on the medial surface of the occipital lobe of a patient blinded by bilateral glaucoma. Although not all electrodes were effective, for most the stimulation of a given electrode produced the sensation of a spot of light (a phosphene). They were able to plot the distribution of these phosphenes in the visual field. Since the interelectrode distances were specified it should be possible to calculate magnification factor by also measuring the angular separation of the different phosphenes, and to relate the magnification factor to previously determined measurements of visual acuity. The present paper describes our attempts to do both. An abstract of this work has appeared (Cowey and Rolls, 1974).

## Methods

Thirty-five of the electrodes implanted by Brindley and Lewin produced low threshold phosphenes whose apparent position in the visual field could be plotted. Five of them produced more than one phosphene and although the multiple phosphenes from a single electrode always lay close together in the field we did not include them in our analysis. However, we know that had we included them by taking the mean position of each multiple the results we report would not have been substantially different.

The positions of the remaining 30 electrodes are shown in Fig. 1 A. We used these electrodes and the map of their phosphenes to calculate magnification factor in two slightly different ways.

1. The linear separation of various pairs of electrodes was measured, as was the angular separation between the corresponding phosphenes. The electrode pairs were chosen as follows. It is known that in monkeys the striate cortex is surrounded by a secondary visual area, which topographically is a mirror image of the retinal projection in striate cortex (Cowey, 1964; Cragg and Ainsworth, 1969; Zeki, 1969). If a similar arrangement exists in man and if the electrode array implanted by Brindley and Lewin straddled the boundary between striate cortex and a secondary visual area (as suggested by Brindley *et al.*, 1972) electrodes close together and on either side of this boundary would produce phosphenes which were close together and near the vertical meridian. Electrodes further apart but still equidistant from the boundary would also give phosphenes that were close together, but nearer the horizontal meridian. In order to minimize the problem that measurements between points in striate and secondary visual cortex would give an anomalous value for striate magnification factor, we measured between electrodes that were separated in a predominantly anterior-posterior direction on the brain. The solid lines joining the electrodes in Fig. 1 A show which pairs were used. Since the border of the striate cortex, representing the vertical meridian, follows the lips of the calcarine fissure in an anterior-posterior direction (Polyak, 1957) this method of measuring ensures that most of the electrode pairs will lie *either* in striate cortex *or* in the secondary visual area. For any pairs which do straddle this boundary the lines joining them will cross the border at an acute angle, i.e., the two electrodes are unlikely to lie on mirror image representations of identical points in space. We also avoided measurements across the calcarine fissure.

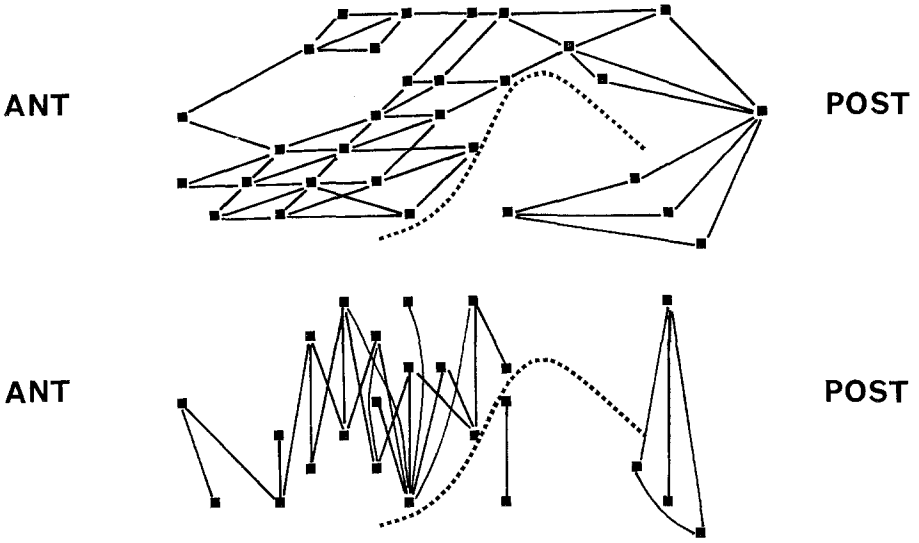


Fig. 1. A The positions on the medial surface of the right hemisphere of the electrodes used in calculating magnification factor, taken from Brindley and Lewin (1968). The lines joining electrodes show which pairs of electrodes were used in Method 1 of the text. The dotted line indicates the position of the calcarine fissure, as estimated by Brindley and Lewin. B The electrode pairs used in Method 2

Using this method we were able to calculate magnification factor for the phosphenes produced from 53 electrode pairings. It can be seen from Fig. 1 A that each electrode contributed to at least two pairings, and one of the electrodes contributed to six. The magnification factor was expressed as mm of cortex per degree of visual field at the mean eccentricity of each pair of phosphenes.

2. In the second method we deliberately chose electrode pairs which were separated in a predominantly vertical direction (see Fig. 1 B). If the retinotopic maps in areas 17 and 18 are mirror images of one another, as in monkeys, many of the electrode pairs will straddle the boundary between the two areas and thus stimulate cortical points representing similar regions of visual space. Method 2 should therefore give a large proportion of anomalously high, and incorrect, magnification factors, and such a result would be strong evidence for mirror image maps in areas 17 and 18.

## Results

The magnification factors calculated by Method 1 are shown by solid circles in Fig. 2. The magnification factor falls steadily from about 4 mm/degree at 2 degrees eccentricity to 0.5 mm/degree at 25 degrees eccentricity for the lower part of the visual field. As the nearest phosphene to the fovea was at 1.6 degrees eccentricity, the foveal magnification factor can only be inferred by extrapolation.

The calculations from method 2 are shown by open circles in Fig. 2. The magnification factors are clearly higher than those obtained from the first method, as expected if many of the electrode pairs straddled the border between areas 17 and 18 and if the two visual areas possess mirror image maps. The remaining results are all derived from method 1, which minimises this problem.

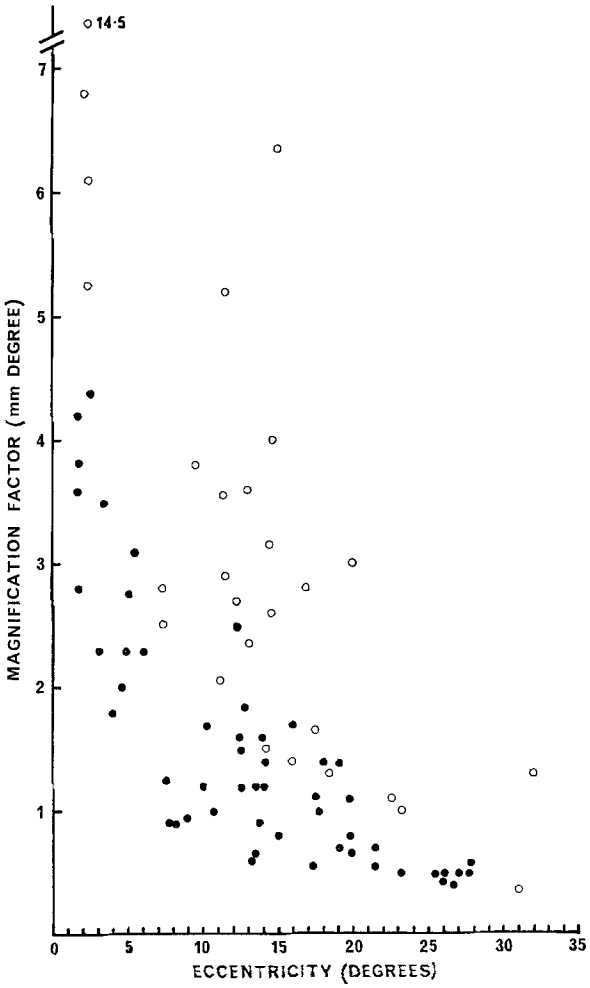


Fig. 2. Solid circles: Magnification factor as a function of eccentricity, calculated from the 53 pairs of electrode positions shown in Fig. 1A. Open circles: Magnification factors calculated by Method 2 using the electrodes shown in Fig. 1B

The decline in magnification factor with increasing eccentricity can now be compared with the corresponding decrease in visual acuity. We have used the acuity measurements from Wertheim (1894) because they were made over a wide range of eccentricities and in the lower part of the visual field, corresponding to the area in which phosphenes were produced in Brindley and Lewin's (1968) patient. Wertheim's data also appear to be reliable in that they are in agreement with other studies on man (see Weymouth, 1958), which show that the minimal angle of resolution increases approximately linearly with increasing eccentricity. The minimal angle of resolution and the reciprocal of magnification factor (i.e., degree of visual field/mm of striate cortex) are shown to increase similarly as a function of eccentricity in Fig. 3A. The relation between the reciprocal of magnification

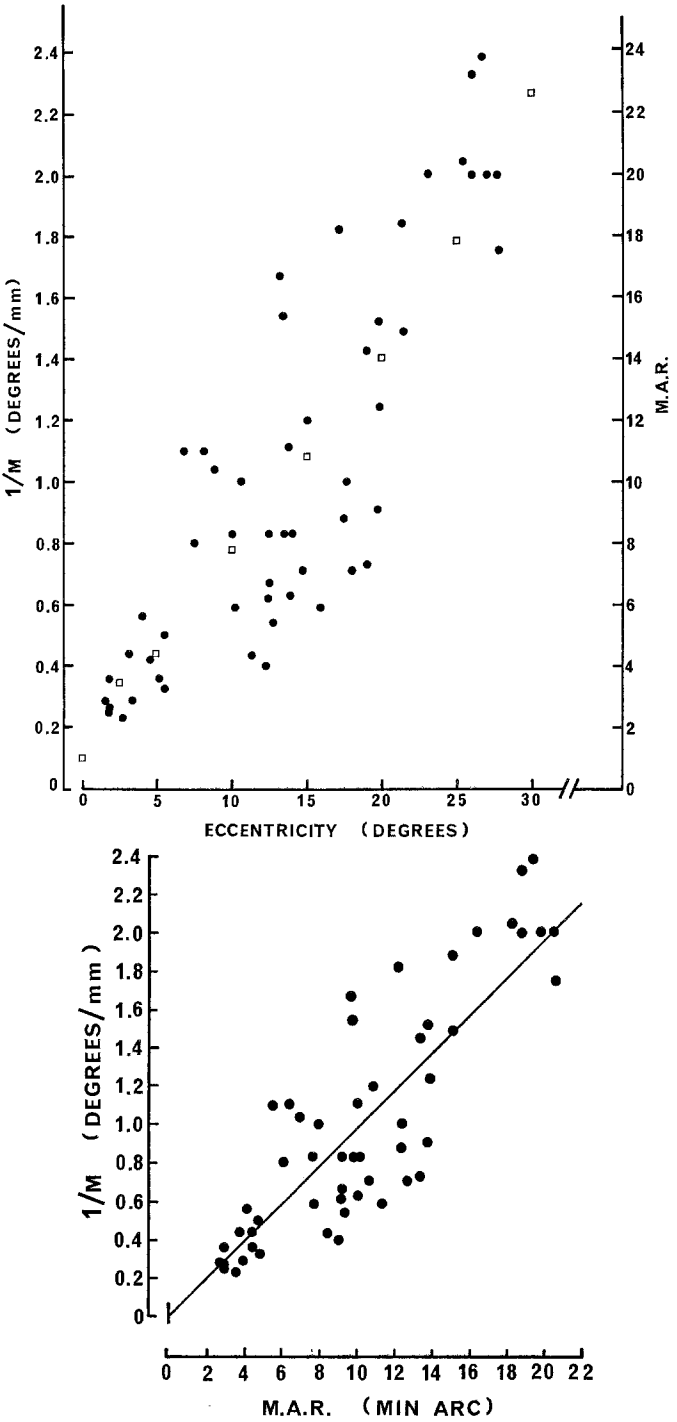


Fig. 3. A The reciprocal of the magnification factor, ● (degrees/mm cortex), and minimum angle of resolution, □, as a function of eccentricity from the fovea. The acuity data were taken from Wertheim (1894) for the lower visual field, where the phosphenes lay. B The reciprocal of the magnification factor (degrees/mm cortex) as a function of minimum angle of resolution (min of arc), using the data points of Fig. 3. The regression line was fitted by calculation, and the standard error at the intercept is shown

factor (1/M) and the minimal angle of resolution (M.A.R.) is shown more clearly in Fig. 3B by plotting 1/M as a function of M.A.R. The M.A.R. for each eccentricity point was found by interpolation from Fig. 3A. The regression line fitted to the data of Fig. 3B passes through zero (the standard error of the intercept is indicated), and the correlation coefficient is 0.85. Thus the data in Fig. 3B show that the reciprocal of cortical magnification factor is directly proportional to the minimal angle of resolution in man. This implies, and a similar regression analysis showed, that the cortical magnification factor (M) is directly proportional to visual acuity in man.

These results, which require confirmation over a wider range of eccentricities and on different meridia, suggest that in man cortical magnification factor is directly proportional to visual acuity. Alternatively, it may be stated that the reciprocal of magnification factor is directly proportional to the minimal angle of resolution. This indicates that the minimal angle of resolution, whatever its value in degrees, occupies the same length strip of striate cortex. The length of this strip is approximately 84 $\mu$, calculated by assuming a foveal visual acuity of 0.5 min arc and using data for 10° eccentricity in Fig. 2. The relation is consistent with the view that many types of analysis occur in the striate cortex, but that acuity information is present in proportion to the amount of cortex concerned with a given part of the visual field.

When magnification factors were calculated for the rhesus and squirrel monkeys in an earlier study (Rolls and Cowey, 1970) the measurements were checked by calculating the total area of striate cortex from the magnification factors and showing that this agreed with the actual area of the striate cortex. This check was repeated on the present data. The area of the striate cortex was calculated as follows. From Fig. 3B in which 1/M is plotted against 1/Acuity for the corresponding lower part of the visual field, the equation relating 1/M to 1/Acuity is shown by the regression line ($1/M = -0.035 + 0.101$ (1/Acuity)). Using this relation, 1/M for different eccentricities was calculated from Wertheim's (1894) acuity measurements averaged over the whole visual field, as appropriate when constructing a map of the whole visual cortex. Then the area of striate cortex was calculated from these values of M (shown in Table 1), using the method described by Daniel and Whitteridge (1961) and Rolls and Cowey (1970). The calculated striate arear for one hemisphere is 2900 mm$^2$.

Table 1. Magnification factor at different eccentricities. The value at each eccentricity was obtained from the relation between 1/M and M.A.R. for the lower visual field, shown by the regression line in Fig. 3B, and from the averaged acuity at each eccentricity along different meridia (acuity data from Wertheim, 1894). The calculated magnification factor is thus the mean for a given eccentricity along various meridia

| Eccentricity degrees | 0 | 1 | 3 | 5 | 7 | 10 | 15 | 20 | 30 | 40 | 60 | 70 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Magnification factor, mm/degree. . . . . | 15.1 | 8.3 | 4.16 | 3.08 | 2.1 | 1.75 | 1.16 | 0.82 | 0.49 | 0.34 | 0.224 | 0.159 |

## Discussion

As a check on the accuracy of the measurements of magnification factor the magnification factors were used to calculate the total area of striate cortex of one hemisphere. It is important to compare our estimate of 2,900 mm$^2$ with more

direct measures of the extent of striate cortex. In the most extensive study Filimonoff (1932) measured the extent of striate cortex in nine human brains and obtained a mean unilateral area of 2,613 $mm^2$ (range 2,208—2,877). Filimonoff's results were corrected for histological shrinkage by Sholl (1956), who obtained a mean area of 3,036 $mm^2$ (range 2650—3452). These estimates are close to those of Cunningham and Brodmann (both cited by Polyak, 1957: pp. 487—488), who obtained values of 3000 $mm^2$ and 3450 $mm^2$ respectively. The close agreement between the calculated and measured areas of striate cortex suggests (1) that the values of magnification factor shown in Table 1 are accurate and (2) that 1/M is directly proportional to minimum angle of resolution not only as far as 30° eccentricity but also to 70° eccentricity, as was assumed in calculating the area of striate cortex.

Two further and related points require comment. The first is that most of the pairs of phosphenes used to calculate magnification factor lay at different eccentricities along radii. Evidence that magnification factor for a given eccentricity has the same value when measured along a semicircle of latitude within the same region of the visual field is that 10 of the values shown in Figs. 2, 3 and 4 were measured in this way and they did not differ systematically from the other 43. The second point is that all but 4 of the phosphenes lay in the left lower octant of the visual field. There is therefore no direct evidence on the value of magnification factor in other parts of the visual field. However, in calculating the total extent of the striate cortex we assumed that magnification factor varied along different meridia only in proportion to the slight differences in visual acuity along different meridia reported by Wertheim (1894). If the variation was greater than this the estimates of the extent of striate cortex obtained by direct measurement and from our calculations of magnification factor should not have been so close. The best evidence therefore is that, as in monkeys (Daniel and Whitteridge, 1961; Cowey, 1964) magnification factor depends mainly on eccentricity from the fovea and not on direction.

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