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Electrophysiological estimate of human cortical magnification

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Abstract

Objective: The cortical magnification factor characterizes the area of human primary visual cortex activated by a stimulus as a function of angular distance from an observer's line of sight. This study estimates human cortical magnification using an electrophysiological method with excellent temporal resolution: visual evoked potential (VEP) dipole source localization.

Methods: For each of 60 independently modulated checkerboard patches within the central 18 deg of the visual field, location, orientation, magnitude, and time-course of the dipole current source that best described the VEP distribution across a multi-electrode array was obtained. At numerous eccentricities, cortical magnification was determined using two different techniques: (1) the distance between each pair of adjacent stimulus patches was matched to the corresponding distance between adjacent cortical sources; and (2) the area of each stimulus patch was matched to the magnitude of the corresponding cortical source (which was assumed to be proportional to cortical area).

Results: The estimates of human cortical magnification using our electrophysiological method were similar to previous estimates from psychophysics, cortical stimulation, and functional magnetic resonance imaging.

Conclusions: The concordance of results provided by these disparate technologies, with differing spatial and temporal limitations, supports their combination in studying the spatio-temporal dynamics of human brain function.

Keywords: Cortical magnification; Primary visual cortex; Human; Monkey; Visual evoked potential; Dipole source localization; Functional magnetic resonance imaging; Cortical stimulation; Psychophysics

1. Introduction

Points in visual space map onto the human primary visual cortex in a manner that preserves the spatial organization of the visual field, such that adjacent stimuli in space activate adjacent locations in the cortex. A major distortion of this cortical map involves an expansion of the representation of the central visual field whereby foveated objects at zero eccentricity activate a much larger area of primary visual cortex than the same size object located several degrees off the line of sight. Estimating cortical magnification as a function of eccentricity is a useful means to describe the overall visual-cortical architecture of the human primary visual cortex.

1.1. Parameters describing cortical magnification

When presented with a visual stimulus, an area of primary visual cortex is activated. Physiological studies in monkey have shown that the cortical distance corresponding to the portion of the visual field subtended by a stimulus is inversely proportional to stimulus eccentricity. This relationship can be expressed as:

$$M(E) = \Delta x/\Delta E = A/(E + E_2) \quad (1)$$

where M (in mm deg^{-1}), the cortical magnification factor, is a function of stimulus eccentricity E (Schwartz, 1980). Δx is the change in cortical distance (in mm) corresponding to a change in stimulus eccentricity ΔE (in deg). The constant E_2 (in deg) is the eccentricity at which a stimulus subtends half the cortical distance as it does when foveated (Levi et al., 1985) and A is a second constant (in mm), which represents the cortical scaling factor. E_2 can easily be determined if Eq. (1) is inverted to produce the relationship for inverse magnification, which is linearly related to eccentricity:

$$M^{-1} = \Delta E/\Delta x = (E + E_2)/A \quad (2)$$

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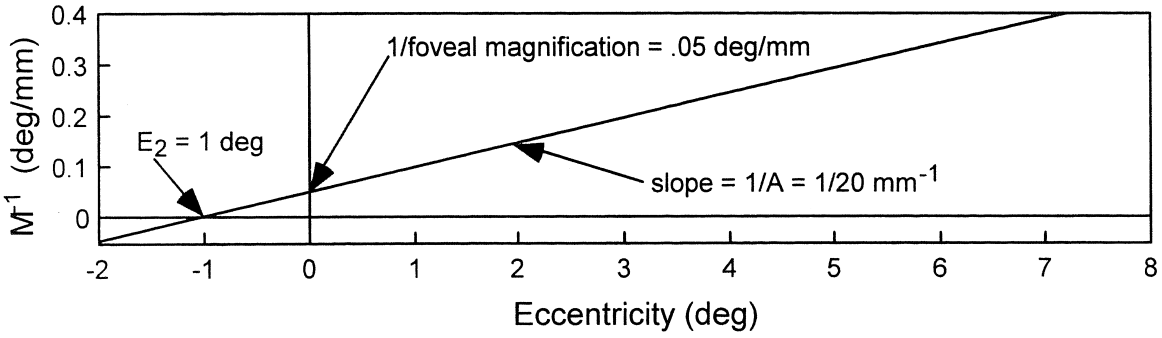

Fig. 1. A line describing inverse magnification as a function of eccentricity. In this example, $E_2 = 1$ and $A = 20$.

Fig. 1 shows a plot of inverse magnification vs. eccentricity for $E_2 = 1$ deg and $A = 20$ mm.

The linear relationship between M^{-1} and E is governed by the horizontal intercept $-E_2$ and slope $1/A$. Eq. (2) can also be interpreted in terms of changes in the cortical distance corresponding to percent change of effective eccentricity, $(E + E_2)$, if it is rewritten as:

$$\Delta E/(E + E_2) = \Delta x/A \tag{3}$$

For large eccentricities, E_2 is relatively small compared to E; thus, $\Delta x/A$ is approximately equal to the percentage change in eccentricity ($\Delta E/E$). For example, if $A = 20$ mm, then a 1 mm change in cortical distance corresponds to a 5% change of eccentricity. Eq. (2) can also be written in terms of the vertical intercept rather than the horizontal intercept:

$$M^{-1} = E/A + E_2/A \tag{4}$$

where E_2/A is the vertical intercept: foveal inverse magnification. For $A = 20$ mm and $E_2 = 1$ deg, the foveal magnification, at $E = 0$, is $M = A/E_2 = 20$ mm deg^{-1}, corresponding to an inverse magnification of $E_2/A = 0.05$ deg mm^{-1} (see Fig. 1).

1.2. Physiological studies in human

Primate cortical magnification has been investigated in three ways: (1) physiological studies in monkey; (2) psychophysical studies in human; and (3) physiological studies in human. Here, only the latter type of study is considered, while a more comprehensive review is undertaken in Section 4.

Using data provided by Brindley and Lewin (1968), Cowey and Rolls (1974) compared the cortical distance between pairs of stimulated electrodes placed directly on human visual cortex with visual field distance of the corresponding pairs of subjectively reported phosphenes in one subject. More recently, Sereno et al. (1995) presented stimuli at numerous eccentricities and measured the corresponding locations in human primary visual cortex using functional magnetic resonance imaging (fMRI). Visual inspection of their group cortical magnification estimate showed a steeper drop-off in cortical area per degree of visual field stimulation at increasing eccentricities than monkey. They argued that their results indicated an expanded cortical processing emphasis of the central visual field by humans. In contrast, Engel et al. (1997) argued that their previous fMRI data (Engel et al., 1994) showed a shallower drop-off of cortical magnification than those of Sereno et al. in agreement with the scaled monkey estimate (Horton and Hoyt, 1991).

The purpose of this paper is to provide an independent measure of human cortical magnification based directly upon neuronal activity. In addition, the parameters describing human cortical magnification using data from the present study and others are presented to compare results provided by psychophysics, cortical stimulation, fMRI, and visual evoked potential (VEP) dipole source localization.

2. Methods

When cortical areas are activated by a visual stimulus, voltages are generated on the scalp. For a given voltage topography, the location, orientation, magnitude, and time-course of the underlying brain activity can be obtained by modeling the active cortex as a dipole current source (Scherg, 1989) inside a 3-shell conducting sphere (Ary et al., 1981; Slotnick et al., 1999). The assumptions used in dipole modeling are simplistic and can result in erroneous results, especially when multiple dipoles are simultaneously active (Mosher et al., 1993; Jewett and Zhang, 1995). However, single dipole source localization results have been shown to be quite accurate when compared to known locations of stimulated intracranial electrode pairs (Cuffin et al., 1991) or compared to known locations of a single active area of cortex (Heinze et al., 1994; Mangun et al., 1998a).

The experimental methodology used here has been described in detail elsewhere (Slotnick et al., 1999), thus, the present discussion is limited to those details relevant to this particular study. Two males and one female (between the ages of 28 and 48) with normal or corrected-to-normal vision maintained central fixation during simultaneous stimulation of 60 stimulus patches across the central

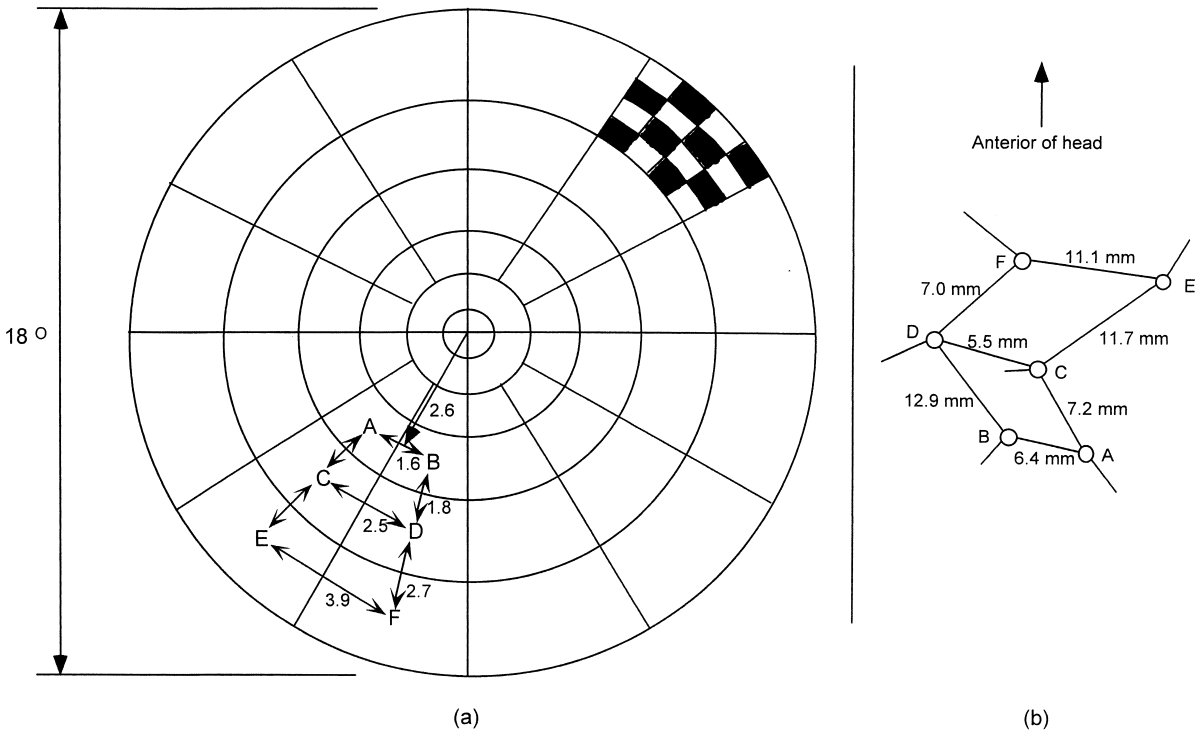

Fig. 2. Multi-stimulus array and dipole locations corresponding to six stimulus patches within the array. (a) All stimulus patches were made up of a 4×4 checkerboard configuration as illustrated by the patch in the upper right. Distances are in degrees of visual angle between patches labeled A–F. (b) Corresponding distances between dipoles in mm of cortex. Viewed from the top of the head with 20 deg rostral rotation about the axis connecting the pre-auricular points.

18 deg of the visual field. Each patch was modulated according to an orthogonal binary m-sequence, a pseudo-random series of 0s and 1s, where a 1 indicates state 1, as illustrated in the upper right patch in Fig. 2(a), and a 0 indicates state 2, the reverse of the illustrated patch (Baseler and Sutter, 1997). Modulation of each patch with an orthogonal m-sequence allows the computation of the multi-electrode VEPs corresponding to any given patch through cross-correlation of that patch's m-sequence with the response at any given electrode (Sutter, 1992). The mean patch reversal rate was 37.5 Hz (a 75 Hz frame rate). Such a high rate of pattern reversal has been shown to preferentially activate primary visual cortex in both fMRI (Schiefer et al., 1996, 1998) and VEP source localization studies (Slotnick et al., 1999). Patches were scaled by a cortical magnification factor using $E_2 = 0.75$ deg to activate an approximately equal area of cortex at all eccentricities.

VEPs were measured using a dense posterior electrode array of 43 or 48 electrodes placed on the back of the head. The electrode locations included the 10–20 positions with interpolated electrode placements to increase spatial sampling (Slotnick et al., 1999). Electrode CzP was used as a reference.

For each patch, the source location, orientation, magnitude, and time-course that best predicted the multi-electrode VEPs was found by assuming that the dipole was fixed in location and orientation while the magnitude was allowed to vary in time (Scherg, 1989) for 333 ms following stimulus onset. A one-shell head model was used (Brody et al., 1973) followed by an Ary correction (Ary et al., 1981), which corrects for the differences in source location between a one-shell and 3-shell head model. Only dipole locations were corrected because the correction for magnitude is negligible.

The average percent variance accounted for using a one dipole fit was 52% for subject TC, 51% for subject HB, and 39% for subject SD. Despite the simplicity of the single dipole model (i.e. a 425/1 data reduction), the resulting dipole locations followed a retinotopic organization as expected from the known classical architecture of primary visual cortex, indicating that the single dipole model was reasonable (Slotnick et al., 1999).

Two methods were used to estimate cortical magnification, the first based on dipole locations and the second based on dipole magnitudes. In the first method, the relationship $M^{-1}(E) = \Delta E/\Delta x$ (i.e. Eq. (2)) was used where Δx is the cortical distance between two dipoles (in mm) corresponding to the angular distance between two adjacent stimulus patches (ΔE). As discussed previously, a plot of inverse magnification vs. eccentricity is well fit by a linear function. The parameters describing cortical magnification, E_2 and A, can be determined by plotting the inverse magnification for each pair of adjacent patches/dipoles, and then obtaining the best-fit line to those points. $-E_2$ is given by the horizontal intercept and A is given by the inverse of the slope. At each

eccentricity, the median value of all inverse magnification estimates was used to eliminate the contribution of outliers. Isoeccentric pairs of stimuli that straddled the vertical meridian were omitted to avoid large inter-hemispheric dipole distances, as were radial pairs between patches in the two outer annuli because of evidence for spreading of cortical activity in unflanked stimuli (Kitano et al., 1991).

In the second method, estimates of E_2 were obtained based on dipole magnitude rather than dipole spacing. For any given patch, the visual field area (in deg^2) and the corresponding area of active cortex (in mm^2) can be determined. Visual field area is calculated given the inner and outer eccentricity and the transverse angle (Baseler et al., 1994). The area of active cortex is obtained by assuming that dipole magnitude is proportional to active cortical area. Taking the square root of visual field area divided by the square root of dipole magnitude produces a metric with the correct units for M^{-1} (deg mm^{-1}). Parameter A could not be estimated using this method because the scaling factor relating cortical response to scalp voltage amplitude is arbitrary. E_2 is determined by fitting the median value of inverse magnification for all patches at each eccentricity with a line as described in the previous method. Again, patches in the outer ring were not used to avoid possible cortical spreading artifacts (Kitano et al., 1991).

3. Results

In Fig. 3, M^{-1} is the angular distance between stimulus patches (ΔE) divided by the distance between the corresponding neural sources (Δx). To illustrate this point, a datum contributing to the rightmost point of Fig. 3, Subject TC, can be obtained by dividing $\Delta E = 3.9$ deg (i.e. the distance between stimulus patches E and F in Fig. 2(a)) by $\Delta x = 11.1$ mm (i.e. the distance between corresponding dipole locations E and F in Fig. 2(b)). For each subject, the best-fit line was obtained using the Marquardt nonlinear least-squares algorithm (Press et al., 1992) to obtain the parameters E_2 and A with estimates of standard error (see Fig. 3). These parameters are also shown at the bottom of Fig. 5 (circles). The technique utilizing dipole magnitudes (see Section 2) was also used to obtain estimates of E_2, which are presented in Fig. 4 and the bottom of Fig. 5 (squares).

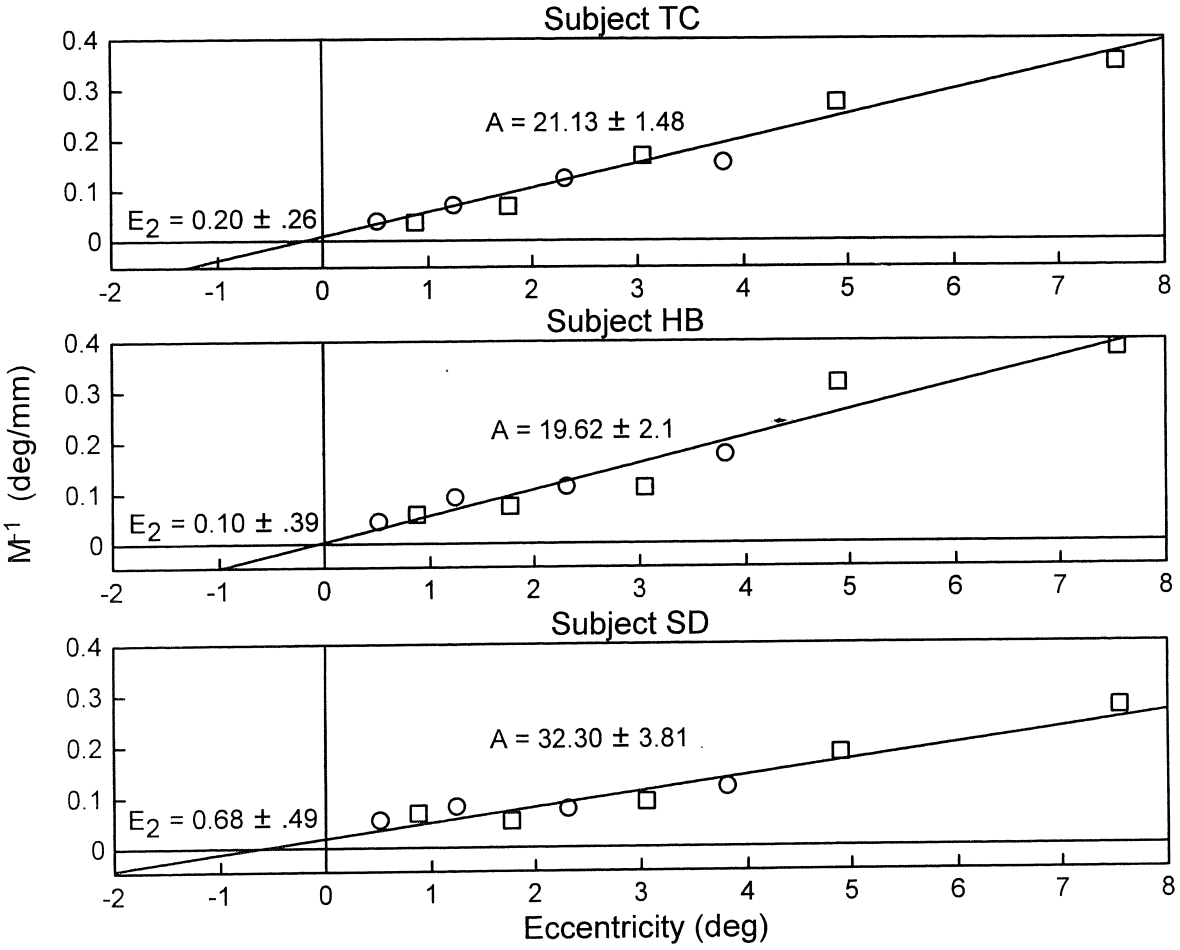

Fig. 3. Visual degrees between the centers of a stimulus patch pair divided by the cortical distance between corresponding dipoles as a function of stimulus patch eccentricity. Pairs in the radial direction are shown as circles and isoeccentric pairs are shown as squares.

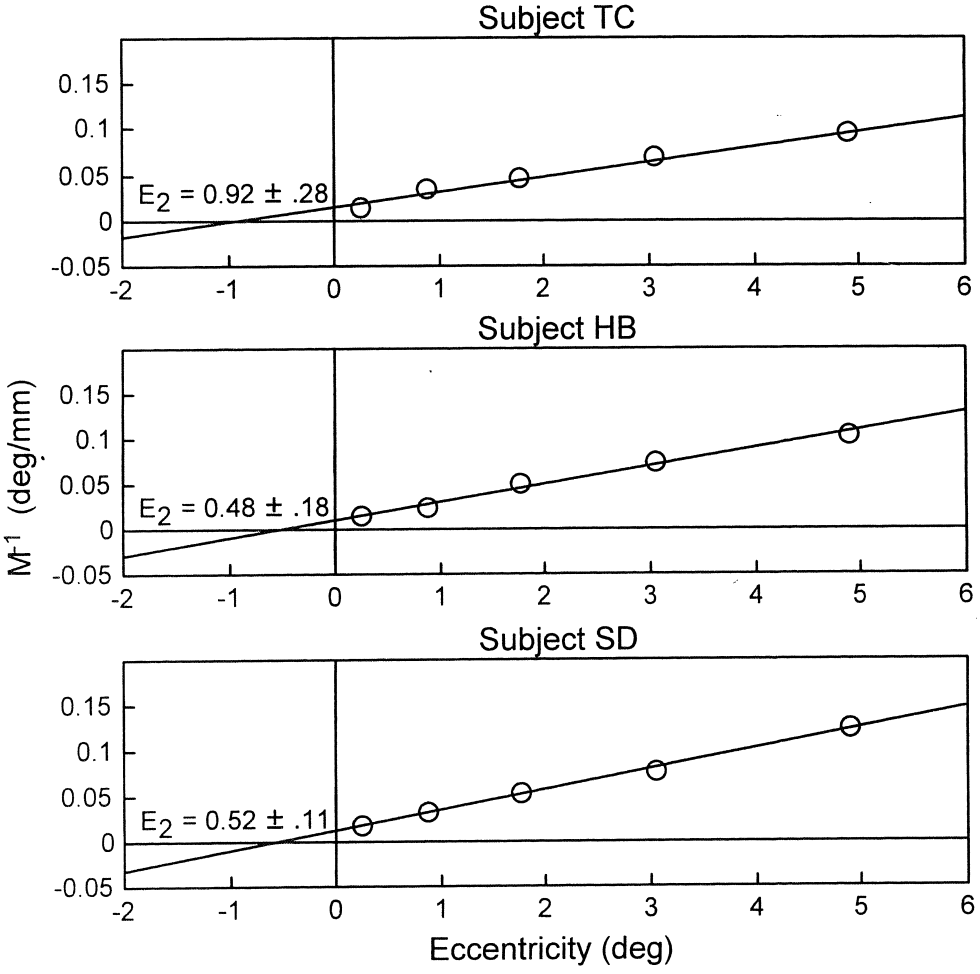

Fig. 4. Square root of visual field area for a given patch divided by square root of magnitude of the corresponding dipole as a function of eccentricity.

The standard errors of the parameter estimates, calculated from the residual variance of the fit, are small especially for E_2. Our estimates for E_2 based on dipole locations are 0.20 ± 0.26, 0.10 ± 0.39, and 0.68 ± 0.49. The estimates based on dipole magnitude are $E_2 = 0.92 \pm 0.28$, 0.48 ± 0.18, and 0.52 ± 0.11. The average value weighted by the inverse variance of all the values is $E_2 = 0.50 \pm 0.08$ deg. The estimates of A based on dipole locations are 21.1 ± 1.5, 19.6 ± 2.1, and 32.3 ± 3.8, with an average value weighted by the inverse variance of 21.7 ± 1.2 mm.

4. Discussion

Human cortical magnification has been estimated using a technique that combines multi-stimulus presentation and multi-electrode dipole source localization. This method, like the cortical stimulation and fMRI results discussed in Section 1, bases its results upon physiological changes in human brain. To view the present results in a broader context, cortical magnification estimates based upon physiological studies in monkey and psychophysical studies in human need also be considered.

4.1. Physiological studies in monkey

A number of studies have estimated cortical magnification in awake fixating monkeys using single-cell recording. These studies map the receptive field locations of numerous cells and use the correspondence between cortical location and visual field location. Typically, a linear regression is done to the data using an equation of the form:

$$M^{-1} = aE + b \tag{5}$$

which is identical to Eq. (4) with $a = 1/A$ and $b = E_2/A$. Since different monkeys have different sized brains, both a and b in Eq. (5) will co-vary depending on the size of the particular brain in which the measurements are made. Compared to an average sized brain, both a and b in a relatively large brain would be smaller, but the ratio $E_2 = b/a$ would be constant if the two brains differed by a scaling factor. As discussed by Levi et al. (1985), when comparing monkeys to humans, it is expected that a and b

vary with brain size, but E_2 could remain constant across species.

Horton and Hoyt (1991) assumed such a cross-species constancy of E_2 when they estimated human cortical magnification based on a number of physiological studies in monkey (i.e. $E_2 = 0.75$). To obtain their estimate of parameter $A = 17.3$ in human, they linearly scaled their monkey estimate of A by a correction factor, taking the cross-species difference in area of primary visual cortex into account.

Dow et al. (1981) carried out a detailed neurophysiological study of monkey cortical magnification and found the inverse magnification to be $M^{-1} = 0.12E + 0.040$, giving an $E_2 = b/a = 0.33$ deg. Both the accuracy of this estimate and its relevance to humans have been the subject of debate. The value of E_2 found by Dow et al. is lower than that estimated by others. Levi et al. (1985) argued that the low value is an artifact of Dow et al.'s procedure of using the combined data of two monkeys. If the data from each monkey are analyzed separately, then E_2 values of 0.77 ± 0.10 and 0.76 ± 0.25 are obtained (Levi et al., 1985), which are close to estimates of other studies.

Neurophysiological studies (Daniel and Whitteridge, 1961; Hubel and Wiesel, 1974) previous to Dow et al. did not acquire sufficient data close to the fovea, so although their estimate of slope (a) was accurate, their estimates of the horizontal intercept ($-E_2$) or vertical intercept (b) were inaccurate. The same problem (i.e. lack of data near the fovea) is found in attempts to estimate cortical magnification in humans.

4.2. Psychophysical studies in human

By assuming that a fixed cortical distance determines the limits of spatial resolution, it is possible to measure E_2 in humans by measuring resolution as a function of eccentricity. The notion of estimating cortical magnification became popular with the studies of Rovamo et al. (1978) and Rovamo and Virsu (1979). They found that the contrast sensitivity function (CSF) was constant at numerous eccentricities if stimulus spatial frequency was scaled using $E_2 \approx 2.5$ deg, the so called "invariance principle". In contrast, Levi et al. (1985) used a crowded vernier acuity task and found $E_2 = 0.8$ deg and argued that their task was appropriate for measuring cortical spatial limits whereas the CSF task was actually measuring retinal limits. Thus, although Rovamo and Virsu used the words "cortical magnification" they may have been investigating "optic nerve magnification" outside the fovea and optical blur within the fovea. One must be careful in selecting a psychophysical task that is truly limited by cortical spacing (Klein and Levi, 1987; Levi and Klein, 1990; Levi et al., 1988).

Weymouth (1958) showed that a large number of psychophysical resolution tasks demonstrated a linear relationship between acuity and eccentricity. He suggested that the minimal angle of resolution was in fact equal to ganglion cell density and fit thresholds (th) for a wide range of psychophysical tasks with the same linear function that we have been using to characterize cortical magnification:

$$\text{th} = aE + b \tag{6}$$

Note that psychophysical experiments are able to estimate E_2 but not A because cortical distance is unavailable. Levi et al. (1985) determined that Weymouth's coefficients a and b varied widely across different tasks. However, when the tasks were grouped according to whether they were resolution or hyperacuity tasks, a pattern emerged: the ratio $E_2 =$

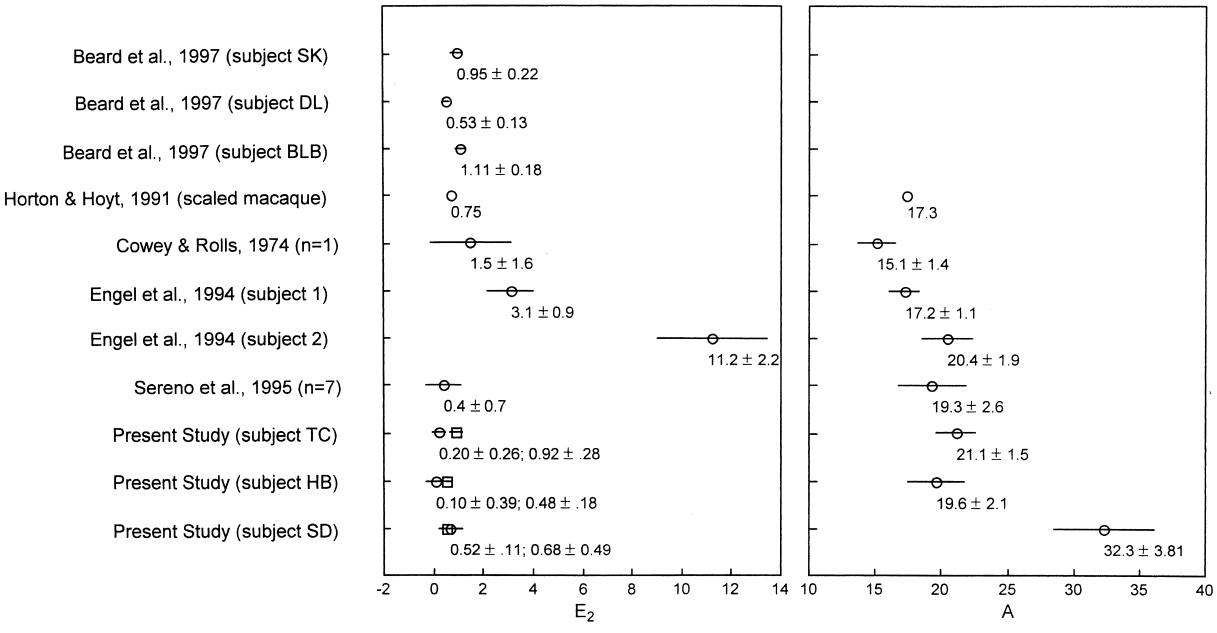

Fig. 5. Estimates of E_2 and A with standard errors using data from six studies.

b/*a* was approximately fixed at 2.5 deg for the resolution tasks and 0.75 deg for the hyperacuity tasks.

Levi, Klein and colleagues explored various factors that could produce erroneous magnification values (e.g. stimulus configuration, decision processes, eccentricity dependent differences in processing). Levi et al. (1988) and Levi and Klein (1989, 1990) showed that there could be confusion between limits based on eccentricity (relevant to cortical magnification) and limits based on separation of the components of the resolution task. They developed a task using isoeccentric stimuli to isolate separation effects from eccentricity effects. Beard et al. (1996) examined several methods for isolating the cortical spacing limits in psychophysical tasks. By manipulating stimulus asynchrony and polarity, they removed various artifacts that had distorted the cortically based estimates of E_2. Their E_2 values for three observers (ranging from 0.5 to 1.1 deg) are reported for comparison with other studies at the top of Fig. 5.

Fig. 5 displays the estimates of human cortical magnification parameters E_2 and A for six different studies loosely ordered from the least direct (i.e. psychophysics, which relies completely on subjective report) to the most direct measure of cortical magnification (i.e. based directly on neural activity, the present study).

Horton and Hoyt (1991) made reasonable estimates of E_2 and A for humans (fourth row of Fig. 5) based upon previously published reports on monkey (see Section 4.1 above). As these parameter estimates were not obtained experimentally, no standard errors could be calculated. However, the parameter values are reported for use in cross-species comparisons (e.g. the value of E_2 is used to answer claims made by both Sereno et al. (1995) and Engel et al. (1997) below).

The cortical magnification data of Cowey and Rolls (1974) were analyzed using the procedure described in Section 2 (i.e. a line was fit to the 53 data points of M^{-1} vs. eccentricity of Fig. 3(a) in Cowey and Rolls' paper). Cowey and Rolls could not determine whether the stimulated electrodes were placed on primary visual cortex or extrastriate cortex. If stimulating electrodes were placed on extrastriate cortex, estimates of E_2 would be distorted. The large standard error in the estimate of E_2 is likely due to somewhat noisy data and a lack of data near the fovea (i.e. all data were obtained at eccentricities $\sim$1.6 deg and greater). As discussed in Section 4.1, data must be collected near fixation, otherwise the standard error of the E_2 estimate will increase.

The estimates of E_2 and A using fMRI from the Engel et al. (1994) and Sereno et al. (1995) studies were calculated by Beard et al. (1996) using similar procedures described in Section 2. Engel et al. (1997) indicated that their estimates of cortical magnification were similar to those of Horton and Hoyt (1991). Fig. 5 shows that values of A for both subjects in the Engel et al. study are similar to Horton and Hoyt's estimate of A; however, the values of E_2 are quite different from Horton and Hoyt's estimate, more than an order of magnitude difference for subject 2. For both subjects, the standard errors for E_2 were large, which is likely due to a lack of data near the fovea (i.e. all data were obtained at eccentricities of $\sim$2 deg and greater).

Sereno et al. (1995) argued that their group estimate of E_2 (see Fig. 5) was lower than Horton and Hoyt's estimate, indicating that human cortex emphasizes central vision more than monkey cortex. Although their absolute level of E_2 is smaller than that provided by Horton and Hoyt, the estimates are similar if one takes standard errors into account. The larger standard errors of the Cowey and Rolls and Engel et al. E_2 estimates are likely due to lack of data near the fovea. The estimates of E_2 in the remaining studies, with lower standard errors, are similar (i.e. Beard et al., 1996; Sereno et al., 1995 and the present study). Although the estimated E_2 from Cowey and Rolls' data does have a large standard error, the value is close to that of studies with lower standard errors. This explains why results have generally confirmed Cowey and Rolls' cortical magnification estimates using scaled stimuli (Rovamo et al., 1978; Meredith and Celesia, 1982).

Rees et al. (2000) have recently shown cross-species similarity of function in visual area V5 by comparing results from monkey neurophysiology and human fMRI. As discussed here, a comparison of monkey E_2 estimates (Horton and Hoyt, 1991) with those of human E_2 estimates also indicates a cross-species similarity in the visual-cortical architecture of primary visual cortex. Moreover, similarity of human cortical magnification estimates has been shown using psychophysics, cortical stimulation, fMRI, and VEP source localization. The general convergence of results indicates that it may be reasonable to combine data obtained from different technologies, using the strengths of one methodology to compensate for the weaknesses of another. For example, although fMRI has excellent spatial resolution (in the mm range), one of its major limitations is the lack of temporal resolution due to dependence upon the hemodynamic response. Evoked potential source localization, which depends directly on neural activity, has sufficient temporal resolution (in the ms range) to follow the dynamics of cortical activation but does not have the spatial resolution of fMRI. The concordance of results found in this study indicates that it may be reasonable to combine fMRI and evoked potential source localization (Mangun et al., 1998b) thus providing the high spatial and temporal resolution needed to study the spatio-temporal dynamics of human brain function.

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