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Cortical Magnification Theory Fails to Predict Visual Recognition

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Abstract

The sense of form is poor in indirect view. Yet the *cortical magnification theory* asserts that the disadvantage can be made up by scaling the image size according to the spatial variation in the mapping of the retina onto the cortex (Rovamo et al., 1978, Nature 271: 54; Virsu et al., 1987, JOSA A 4: 1568). It is thus assumed that all visual information passes through a functionally homogeneous neural circuitry with the spatial sampling of input signals varying across the visual field. We challenge this notion by showing that character recognition in the visual field cannot be accommodated by any concept of sole size scaling but requires increasing *both* size and contrast of the target being viewed. This finding is formalized into a hyperbolic law of target size multiplied by log contrast being constant across the visual field. We conclude that the *scalar* cortical magnification theory fails for character recognition since the latter depends on multidimensional pattern representations in higher, i.e. striate and prestriate, cortical areas.The tenet of cortical magnification theory is that properties of the primary pathway, from the retina to the cortex, are fully responsible for any behavioural changes that occur between central and peripheral vision. Opposing to this are the claims according to which more complex visual processing depends on the interaction of filter mechanisms (Bennett and Banks, 1987; Rentschler and Treutwein, 1985) or receptive field types (Livingstone and Hubel, 1985) having different scaling properties.

The functional consequences of retino-cortical mapping may be studied in two ways. In the direct approach, spatial thresholds (e.g. grating resolution) are measured at various retinal loci (Cowey and Rolls, 1974; Daniel and Whitteridge, 1961; Koenderink et al., 1978a; Weymouth, 1958) and the resulting function is compared to the geniculate and cortical mapping functions (Drasdo, 1977; Drasdo, 1989; Perry and Cowey, 1985; Virsu et al., 1987; Van Essen et al., 1984; Wässle et al., 1989; Weymouth, 1958). In the indirect approach, the stimulus size is increased in order to compensate for the fall-off in performance found in indirect view (Cowey and Rolls, 1974; Daniel and Whitteridge, 1961; Drasdo, 1977; Drasdo, 1989; Koenderink et al., 1978a; Koenderink et al., 1978b; Perry and Cowey, 1985; Rovamo et al., 1978; Rovamo and Virsu, 1979; Virsu et al., 1987; Van Essen et al., 1984; Virsu and Rovamo, 1979; Wässle et al., 1989; Weymouth, 1958). When the increase in size is in inverse proportion to the cortical magnification M, it is called M-scaling.

M-scaling successfully equalizes performance for some visual functions, is controversional for others, and clearly fails for a third group of functions. Functions which can be scaled successfully are two-point separation in the near periphery (Aubert and Foerster, 1857), grating acuity/minimal angle of resolution (Wertheim, 1894; Weymouth, 1958; Daniel and Whitteridge, 1961; Cowey and Rolls, 1974; Drasdo, 1977; Rovamo and Virsu, 1979), Snellen acuity (Ludvigh, 1941), diameter of Panum's fusion area (Ogle, 1950), migraine scotoma size (Drasdo, 1977), and grating contrast sensitivity as a function of both spatial frequency (Hilz and Cavonius, 1974; Koenderink et al., 1978a; Rovamo et al., 1978; Virsu and Rovamo, 1979; Rovamo and Virsu, 1979) and temporal frequency (Virsu et al., 1982; Kelly, 1984). There is a debate over vernier acuity (pro scaling: Levi et al., 1985; Virsu et al., 1987, contra evidence: Hering, 1899; Bourdon, 1902; Weymouth, 1958; Westheimer, 1982), and orientation sensitivity (pro: Virsu et al., 1987, contra: Spinelli et al., 1984). The scaling concept fails for two-point separation in the far periphery (Aubert and Foerster, 1857), stereo acuity (Fendick and Westheimer, 1983), scotopic contrast sensitivity (Koenderink et al., 1978b), apparent grating movement (Hilz et al., 1981), numerosity judgment (Parth and Rentschler, 1984), bisection of a straight line (Levi and Klein, 1986; Virsu et al., 1987), positional relations of image components (Rentschler and Treutwein, 1985; Bennett and Banks, 1987; Saarinen, 1987), spatial phase resolution (Harvey et al., 1985), and masking by spatially correlated patterns (Hübner et al., 1985) (for reviews see Weymouth, 1958; Pointer, 1986; Virsu et al., 1987; and Drasdo, 1991).

The relationships between M and retinal eccentricity, proposed by various investigators (Cowey and Rolls, 1974; Daniel and Whitteridge, 1961; Drasdo, 1977; Drasdo, 1989; Rovamo and Virsu, 1979; Schwartz, 1980; Van Essen et al., 1984; Tolhurst and Ling, 1988), are essentially inverse linear functions of the form $M = (1 + aE)^{-1} M_0$, where E is retinal eccentricity in angular degrees from the fovea, and M_0 is the

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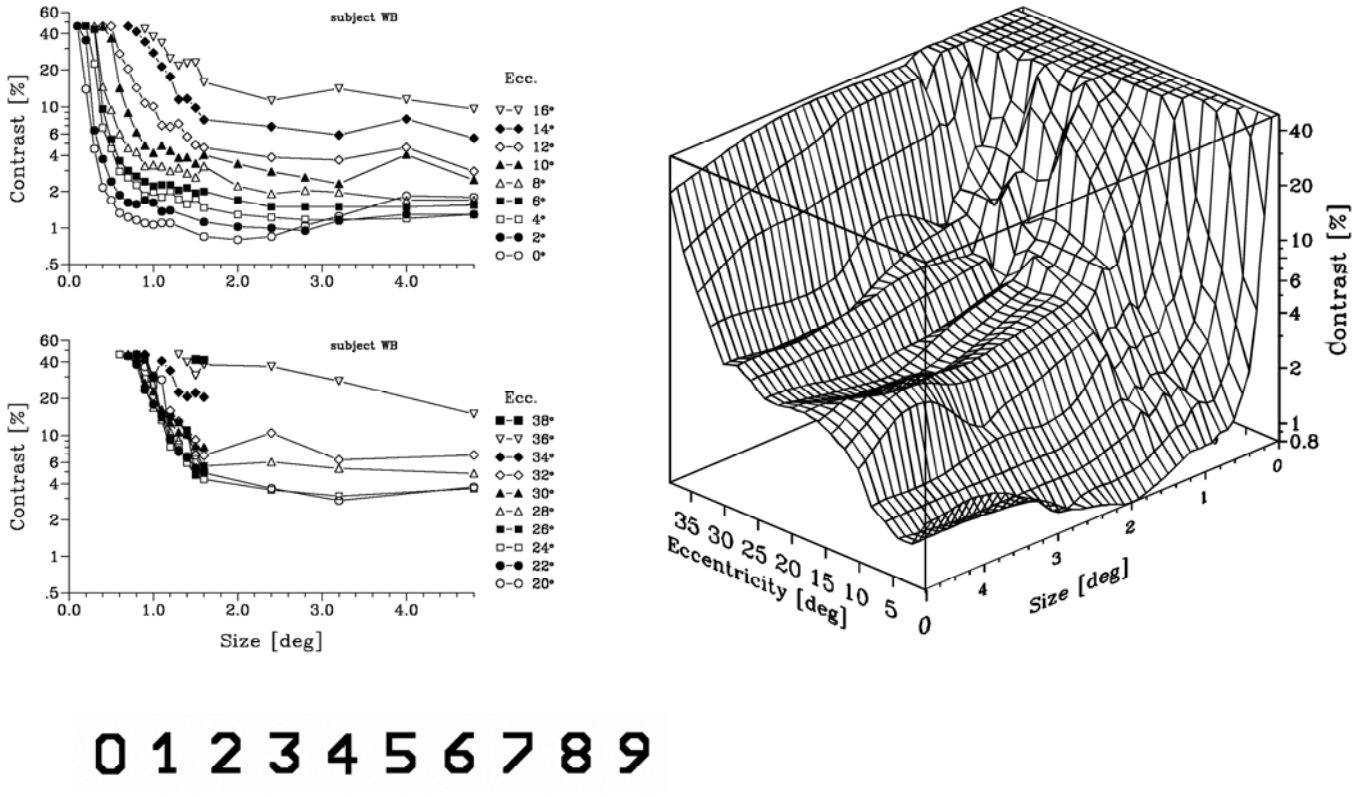

Fig. 1. Contrast threshold for recognition of digits (0 through 9) as a function of angular target size and retinal locus. Since we found no significant differences between thresholds in the left and right visual fields, this figure shows the mean results between the half fields. Contrast thresholds were measured using a computer-controlled maximum-likelihood sequential procedure (Harvey, 1986). This procedure effectively varies the contrast of the target from trial to trial in order to find the contrast giving 67 percent correct identification. 67% represents the point of maximum slope on a Weibull function which is a good descriptor of the underlying psychometric function. The criterion value is not critical, however, and use of a different value will only slightly change the obtained thresholds. No confusion matrix was recorded. We specify stimulus contrast using the Michelson definition: $(L_{max}-L_{min})/(L_{max}+L_{min})$. The background luminance of the video display was kept constant at 62 cd/m². White digits were presented in random order on the video monitor for 100 ms. The experimental setup was identical to that used in a previous study (Strasburger et al., 1991). Subjects fixated a dot located along the horizontal meridian; eccentricity was defined from this point to the target's centre. Viewing was binocular. Four subjects having normal vision were tested. The largest set of data (about 40,000 trials) was obtained from one subject. The main findings were confirmed with three additional subjects. The confidence interval, for each data point, is 0.13 log units, i.e. the error bars are smaller than the symbols. The inset shows the stimulus character set.

cortical magnification in millimeters per degree at the fovea[1]. Similar relationships have been reported for retinal ganglion cell density, receptive field center density, and other density measures along the retino-cortical pathway. Since these are of the same functional form as the preceding equation, with different coefficients (Drasdo, 1991), the arguments in the following also apply to these measures.

In the present study, we examine the validity of *M*-scaling for the *recognition* of numerical characters. On the one hand, this classification task is complex enough since it involves stimulus patterns with an intrinsically two-dimensional signal variation (see Zetzsche and Barth, 1990). Thus it is impossible to represent the numerals along a single feature dimension such as orientation, length, or curvature and the classification process has to rely on a feature space which has at least two dimensions. On the other hand, numerical character recognition is sufficiently simple in that it resembles the measurement of optotype acuity and involves only one sample for each of the ten signal classes.

As to the psychophysical procedure employed, we measured the threshold contrast that allowed for 67% correct identification of the ten digits 0–9. The stimulus size was kept constant thus avoiding an interaction between different target

[1] The formula is subject to slight modification due to the nonlinearities of $M^{-1}(E)$ found in anatomical (Daniel and Whitteridge, 1961) and electrophysiological (Van Essen et al., 1984) data at larger eccentricities. This correction is achieved by either adding a term of third-order in eccentricity *E* (Rovamo and Virsu, 1979), or by using an exponent of –1.1 in the foregoing equation (Tolhurst and Ling, 1988; Van Essen et al., 1984). The numerical differences between these two formulations are small.

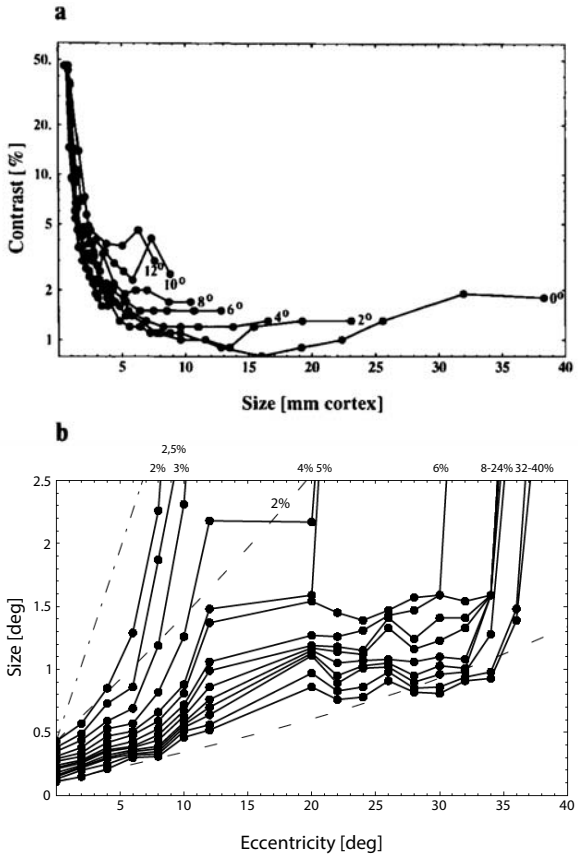

Fig. 2. Failure of *M*-scaling for the data show in Fig. 1. **(a)** Re-plot of Fig. 1 with size *M*-scaled analogous to Rovamo & Virsu's (1979) Fig. 4., using their nasal visual field function $M = (1 + 0.33\,E + 0.00007\,E^3)^{-1}\,M_0$, where E is retinal eccentricity in degrees and M_0 is the magnification in the central fovea, set equal to 7.99 mm of cortex per degree of visual angle. Each stimulus size plotted in this figure was transformed into cortical size by means of $S_c = S_t\,M$, where S_t is the target size in degrees of visual angle, S_c is the size of visual cortex onto which the stimulus projects, in millimeters of cortical extent, and M is the nasal magnification factor in mm/deg at a given retinal eccentricity from the previous equation. The center 12 degrees are shown. **(b)** Threshold target sizes, as a function of retinal eccentricity, for each of a series of threshold contrasts. These target sizes were obtained by interpolation from the data plotted in Figure 1. The dashed lines show predictions from the cortical magnification concept, for 2% and for 40% contrast. These are obtained by fitting $S = (1 + aE + bE^3)\,S_0$ (which follows from the *M*-scaling equation given in figure part *a* through $S = S_0\,M_0/M$) to the approximately linear portion of our data at a given contrast. In these functions, parameter a determines both the slope, aS_0, and the eccentricity-axis intercept, $-1/a$. All curves pass through S_0 on the size-axis. Since different estimates of a have been given in the literature, a was treated as a free parameter in the least-squares fit. The amount of curvature, i.e. the ratio b/a, was constrained to be that given in Fig. 2a (i.e. 0.00007/0.33), and the curves were constrained to go through S_0 at eccentricity 0. The linear coefficients obtained in these fits were $a = 0.227$ for the 2% curve and $a = 0.209$ for the 40% curve. These coefficients are similar to the value of $a = 0.33$ given by Rovamo & Virsu (1979) (see Part *a* of this figure).

sizes and changing scaling factors at different retinal loci. Such measurements were performed for a wide range of target sizes and retinal loci on the horizontal meridian. Viewing was binocular.

Figure 1 shows the recognition performance of one subject, WB, (mean of left and right visual field), as a function of target size and retinal locus. In direct view, lowest contrast thresholds (0.8%) were obtained with digits of 2 deg size, the thresholds increasing for larger and smaller targets. As target size decreases, contrast thresholds rise steeply until the maximum contrast (46%) possible with our equipment is reached. At high contrast, the target size would correspond to conventional visual acuity.

The data for eccentric view are different from those obtained in direct view in two respects: For high contrast conditions, the curves are shifted towards larger target sizes. This finding as such is in agreement with the idea of cortical magnification scaling. However, the curves are also shifted upwards, to higher contrast values. Size scaling therefore fails to match contrast-vs.-size curves from different retinal loci[2]. To illustrate this failure, we applied *M*-scaling to our data. For the central 12 degrees, Fig. 2a shows the data which were transformed accordingly. It can be seen how the data points are brought into register at high contrast but not at low contrast values.

This failure of *M*-scaling is further illustrated in Fig. 2b, where threshold target sizes are plotted as a function of retinal eccentricity for each of a series of threshold contrasts. At contrasts above, say, 6%, the curves extend far into the periphery in an approximately linear manner. Between about 20 and 30 deg there is a plateau, similar to the one described for the detection of light spots (Harvey and Pöppel, 1972). Further out, target identification becomes difficult or impossible. At low contrasts, this behaviour is much more pronounced, leading to an upward curvature at much smaller eccentricities. As a result of this fall-off of performance, the part of the visual field in which recognition is at all possible is sharply reduced. For subject WB, it spans no more than 8° at 2% contrast.

Figure 2b also shows predictions based on cortical magnification, for 2% contrast and for 40% contrast (dashed lines). The slope, a, obtained in both fits, is similar to the value given by Rovamo & Virsu (1979). At *high contrast*, the function based on cortical magnification fits the data reasonably well up to 34 deg eccentricity. Although it does not capture the plateau effect between 20 and 30 degrees, it explains 89.7% of the variance out to 34 deg. Further out, however, it fails to describe the subject's complete inability of target identification. For *lower contrasts*, the failure of target identification occurs at increasingly less eccentric retinal positions thus reducing the predictive range of *M* scaling to a smaller and smaller visual field. This relationship also fails to capture the more pronounced curvatures at lower contrasts.

[2] Formally, when $C = f_E(S)$ is the relationship between contrast and size at a certain eccentricity, there exists no transformation $g_E(S)$ such that $f_E(S) = f_0(g_E(S))$, simply because the range of function f_E varies with eccentricity E.

Fig. 3. **(a, b)** Hyperbola fits according to *Equation 1* to data replotted from Fig. 1. To fit our data to the hyperbolic function (1), we have performed a *constrained nonlinear regression* by explicitly minimizing the mean-squared deviation of log contrast. Data obtained in the blind spot were not considered in the fit. Furthermore, the increase in contrast threshold at large target sizes for 0 and 2 deg eccentricity was excluded and needs to be treated separately. Since equation parameters C_{off}, S_{off}, and k are correlated in the regression parameter space, it was necessary to separate the determination of k from that of the offsets C_{off} and S_{off}. The former constant determines the curvature of the hyperbolas. A value of k=0.25 resulted in excellent fits for the three central most curves (0, 2, and 4 deg), the explained variance (r^2) being 97.5%. k was then held constant across retinal locus, while the offsets C_{off} and S_{off} were allowed to vary. The resulting hyperbolas explained 98.4% of the total data variance. **(c, d)** Contrast and target size offsets resulting from these fits, as a function of retinal eccentricity. Data in the blind spot are shown as smaller points. The relationship shown in *d* can serve an a psychophysical estimate of the anatomical magnification factor *M*.

Table 1: Parameters for a full description of our data set (Equations 1 & 2).

Retinal Eccentricity		0 – 12 deg	14 – 18 deg	20 – 30 deg	30 – 40 deg
Sj. WB	a_1	–0.02	–0.02	0.73	–
	a_2	0.029	0.029	–0.0043	–
	a_3	–0.23	0.38	0.38	–2.25
	a_4	0.058	0.0068	0.0068	0.097
	k	–	0.25	–	–
Sj. KZ/MB	a_1	constr. to 0			
	a_2	0.033			
	a_3	constr. to 0			
	a_4	0.075			
	k	0.128			

The scaling transformations considered so far were restricted to the space domain. In the general case, thus, space domain transformations fail to produce invariance of character recognition over the visual field. A parsimonious and

complete description of the data can be obtained, however, when scaling is extended to include stimulus contrast. The data in Fig. 1, as a function of target size *S*, essentially follow the geometric locus of a hyperbola, described by the relationship

$$(\log C - \log C_{off}) \cdot (S - S_{off}) = k, \quad (1)$$

with

$$C > C_{off}$$

and

$$S > S_{off},$$

where C_{off} and S_{off} are the asymptotic contrast and size values. They are numerically similar to the minimum contrast and minimum size for each retinal locus and serve to offset the hyperbola away from the origin.

Other non-linear functions could also be fitted; the hyperbola is the simplest of all, though, and its use resulted in excellent fits. Examples of fitting the hyperbolas by means of constrained nonlinear regression are shown in Figs. 3a and b. The validity of relationship (1) has been tested by applying it to the mean data of two further subjects (KZ and MB; Strasburger et al., 1991) covering the range from 0° to 12° eccentricity. Using the same shape constant *k* as in Fig. 3, we arrived at a solution that accounted for 98% of the variance.

The offsets C_{off} and S_{off} resulting from these fits show a highly systematic pattern of variation with retinal eccentricity (Fig. 3c and 3d). The relationship, shown in the figure, can be described by piecewise linear functions:

$$S_{off} = a_1 + a_2 E \text{ and } \log C_{off} = a_3 + a_4 E. \quad (2)$$

Up to 12 degrees eccentricity, both S_{off} and log C_{off} vary linearly with eccentricity, at a slope of $a_2 = 0.029$ and $a_4 = 0.058$, respectively. The data fit a straight line especially well, the explained variance being 96.7% and 98.3%, respectively. The data of subjects KZ and MB lead to similar results (see Table 1). Up to 12 degrees, log contrast offsets and size offsets are also highly correlated to *each other* ($r = 0.993$).

Between 12 and 30 degrees eccentricity, contrast offsets C_{off} show a plateau, the slope (a_4) dropping to close to zero. For the size offsets S_{off}, the plateau starts beyond the blind spot and extends also up to at least 30 degrees eccentricity (slope $a_2 = -0.0043$). Beyond 30 degrees, contrast offsets increase steeply ($a_4 = 0.097$); size offsets become unreliable, since the contrast thresholds are close to the maximum contrasts in our setup. These parameters are summarized in Table 1.

Equations 1 and 2 together fully describe our data. They can be combined to derive a functional relationship, like that shown in Fig. 2b, between target size *S* and eccentricity, as a generalization of the *M*-scaling equation. It differs from the standard form in that it contains a non-linear term, the contribution of which is negligible at high contrast but at low contrast goes to infinity at a certain eccentricity.

The size offsets S_{off} at various eccentricities obtained in the fit (eq. 2a) can be considered to provide a direct description of the changes of spatial scale across the retina. The functional relationship depicted in Figure 3d thus gives a psychophysical estimate of the anatomical magnification factor *M*. Except for the plateau effect, it is in rough correspondence with the anatomical data.

We thus found variations in character recognition across the visual field which are incompatible with the (scalar) cortical magnification concept. This incompatibility is a consequence of the limited extent to which recognition contrast sensitivity can be improved by increasing target size and is not a matter of what the precise relationship between cortical magnification and retinal position is. *Explanations based on the topological mapping can, therefore, not account for our results.* This includes differences in the *M* factor between different cell types, e.g., between parvo and magno cells (compare Drasdo's (1989 Fig. 2 to the present Fig. 2b), and other explanations based on the spatial mapping from retina to cortex, including nonconformal maps (Mallot et al., 1990).

With optimal size scaling applied, recognition contrast thresholds still increase about 10-fold between the fovea and 32° eccentricity. The question arises whether such a variation can be due to the properties of the retino-cortical pathway. For an answer, three properties of this pathway need be considered: Variations in contrast sensitivity of ganglion cells, variations in the receptive field overlap factor or sampling density, and variations in positional uncertainty.

As to the first property, cells from the magnocellular pathway (M cells) have higher contrast sensitivity than parvo (P) cells (Derrington and Lennie, 1984; Hicks et al., 1983), the optimum M-cell contrast threshold being 1%, whereas P cells reach only about 10% contrast. It thus seems clear that the optimum contrast threshold for character recognition is mediated by M cells. Although M cells have, as compared to P cells, an about 8-times lower sampling density (Kaplan et al., 1990; Perry et al., 1984), it is sufficient to mediate optimum contrast thresholds at all retinal positions since these thresholds always go together with relatively large target sizes. The variation of the contrast sensitivity of primate M cells over the visual field is not documented in Hicks (1983) and Derrington (1984) but the overall similarity of primate M cells to cat X and Y ganglion cells (Kaplan et al., 1990) makes it likely that Fischer & May's (1970) result obtained in the cat also holds for the present case: These authors have shown that the contrast sensitivity of ganglion cells for small dots decreases with retinal eccentricity in inverse proportion to a simultaneous increase in receptive field size. Thus, for appropriately scaled stimuli the detection contrast sensitivity of ganglion cells becomes *independent* of retinal position. *Current models of visual processing are based on this premise (*Mallot et al., 1990; Bijl et al., 1992*)*. It also corresponds reasonably well to psychophysical findings concerning grating detection (Koenderink et al., 1978b; Virsu and Rovamo, 1979), where contrast sensitivity, after appropriate size scaling, varies by about a factor of two. However, detection presumably depends on the most-sensitive cells whereas recognition requires some kind of feature combination and

may therefore be limited by the least-sensitive contributing cells. All available evidence thus points to the conclusion that contrast sensitivity of ganglion cells is not the basis of peripheral recognition contrast thresholds.

The second property of the retino-cortical pathway that needs be considered is the varying sampling density or the overlap factor of receptive fields, i.e., the number of ganglion cells covering a point in visual space. This factor is incorporated in two recent models, one by Bijl et al. (1992) to describe the detection of Gaussian blobs, and one by Wilson (1991) to describe hyperacuity and masking. Bijl et al. (1992) assume a reduction in detection sensitivity proportional to the square root of the overlap factor. However, this leads to the prediction of a decrease in sensitivity for grating detection which only amounts to a factor of three between the fovea and 42 deg eccentricity, i.e., *much less* than we find for character recognition. The response pooling attained by the receptive field overlap will also be more effective for detection than for recognition so that, on the basis of overlap, one would predict an even *lower* peripheral sensitivity reduction in recognition.

The third possibility, the assumption of a varying precision of the spatial position code, is effective in the prediction of hyperacuity behaviour in Wilson's (1991) model. It cannot account for the decrease in optimum recognition contrast threshold that we found since it concerns the mapping: Sufficient enlargement of the stimuli at a fixed position will reduce the influence of positional jitter thereby removing any reduction in contrast sensitivity introduced by the latter.

To summarize, *recognition* of high contrast characters is, on the one hand, captured by cortical magnification, whereas recognition of low contrast characters is not. On the other hand, *detection* tasks generally seem to obey *M*-scaling or some other kind of spatial scaling law. From the latter observation we conclude that *detection* thresholds arise in the retino-cortical pathway and are fully determined by its sampling characteristics. Unlike detection performance, pattern *recognition* critically depends, at least in case of intrinsically more than one-dimensional stimuli, on the *combination* of several feature dimensions (Watanabe, 1985). The neural process of combination must be expected to introduce its own set of thresholds in the sense that the feature weights must be large enough along all relevant perceptual dimensions in order to preserve the full amount of information necessary for the subsequent recognition process. Clearly, these »combination thresholds« exist on top of those of the retino-cortical pathway and we interpret the observed recognition thresholds as their behavioural correlate. Furthermore, our results imply that these combination thresholds arise not in the retino-cortical pathway but in the primary visual cortex itself or at a functionally later stage. This view is supported by recent clinical and neurophysiological evidence. From observations with patients suffering from visual agnosia and from single-unit responses to illusory contours, Baumgartner (1990) has contended that cortical area V1 is "a detecting but not a perceiving device" and that "object perception begins not before V2". Fujita et al. (1992) showed that low-level features are combined in post-V1 areas to subserve the task of recognition. Thus we conclude that the conventional *scalar* cortical magnification theory fails for recognition tasks since they involve the processing properties *of striate and prestriate areas* which cannot be captured by a single scaling factor (see Rentschler and Treutwein, 1985; Bennett and Banks, 1987; Livingstone and Hubel, 1985).

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