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# Coverage and the design of striate cortex

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**Abstract.** Hubel and Wiesel (1977) suggested that ocular dominance and orientation columns in the macaque monkey striate cortex might be bands of uniform width that intersected orthogonally. They pointed out that if this were the case, there would be an equal allocation of cells of different orientation preference to each eye and to each point in visual space. However, orientation and ocular dominance columns have a more complex structural organization than is implied by this model: for example, iso-orientation domains do not intersect ocular dominance stripes at right angles and the two columnar systems have different periodicities. This raises the question as to how well the striate cortex manages to allocate equal numbers of neurons of different orientation preference to each eye and to each region of visual space, a factor referred to here as coverage. This paper defines a measure of uniformity of coverage, $c'$, and investigates its dependence on several different parameters of columnar organisation. Calculations were done first using a simplified one-dimensional model of orientation and ocular dominance columns and were then repeated using more realistic two-dimensional models, generated with the algorithms described in the preceding paper (Swindale 1991). Factors investigated include the relative periodicities of the two columnar systems, the size of the cortical point image, the width of orientation tuning curves, whether columns are spatially anisotropic or not, and the role of the structural relationships between columns described by Blasdel and Salama (1986). The results demonstrate that coverage is most uniform when orientation hypercolumns are about half the size of ocular dominance hypercolumns. Coverage is most uneven when the hypercolumns are the same size, unless they are related in the way described by Blasdel and Salama, in which case coverage gets only slightly worse as the size ratio (ori/od) increases above 0.5. The minimum diameter of cortical point image that ensures reasonably uniform coverage is about twice the size of an ocular dominance hypercolumn i.e. about 1.5–2.0 mm.

## 1 Introduction

Hubel and Wiesel (1974b, 1977) suggested that the macaque monkey striate cortex is designed in such a way as to ensure a uniform allocation of orientation preferences to each point in visual space, and to each eye. They showed that visual information present within a small region of visual space could potentially excite cells present within a relatively small region of cortex 1–2 mm in diameter, a region subsequently referred to as the cortical point image (Van Essen et al. 1984; Dow et al. 1981). The size of the point image was shown to depend both on individual receptive field size, and on the random scatter in receptive field position about a local mean that is encountered when recordings are made from cells in the same cortical column. Because ocular dominance and orientation columns both have repeat periods that are smaller than the cortical point image, a complete range of ocular dominance values i.e. excitation strengths from either eye, and of orientation preferences would be expected to be present at all locations in the visual field. Provided that all combinations of eye and orientation preference are present, and equally frequent within the point image for all visual field locations, vision would be expected to be equally good through either eye. This is presumably an important requirement if vision is to survive as best it can the loss of one eye, a not infrequent occurrence, and may also be necessary for other reasons, for example to ensure adequate matching of the images in the two eyes for the purposes of stereopsis.

Hubel and Wiesel (1977) pointed out that this requirement would be met if orientation columns were parallel slabs of uniform thickness that intersected ocular dominance stripes at right angles, and it is easy to see that this arrangement would guarantee a uniform allocation of orientations to each eye, provided that the cortical point image was equal in size to, or larger than, whichever set of columns had the larger spacing. However, more recent structural studies of orientation columns have shown that they are morphologically complex, and although they form locally parallel domains, these are not of uniform thickness, and do not intersect ocular dominance stripes at right angles (Hubel et al. 1978; Blasdel and Salama 1986). Furthermore, ocular dominance columns are not always simple stripes, but may have a relatively complex morphology in which stripes may curve or branch; in addition, the two sets of columns have different periodicities, and are now thought to be structurally related in a complex way (Blasdel and Salama 1986). These features make it much less easy to determine the extent to which a uniform combination of eye and orientation preference is achieved in the cortex, and the role played by factors such as the size of the cortical point image and the relative periodicities of the two sets of columns. It might be supposed (Cynader et al. 1987) that if orientation and ocular dominance columns had a similar periodicity, interference 'beats' would be produced leading to an absence of some combinations of eye and orientation preference in relatively large areas. But it is not clear to what extent this would be a problem in the macaque monkey, even if the columns did have the same periodicity, given the local variability in both patterns in stripe width and the angles at which the stripes intersect.

This problem can be investigated computationally given the availability of morphologically realistic models of both orientation and ocular dominance columns described in the preceding paper (Swindale 1991). It is possible to define a measure of the uniformity of coverage, and to investigate how this measure might depend on the geometrical properties of the columns, the size of the cortical point image, and the structural relationships discovered by Blasdel and Salama. The results of the calculations can be understood in terms of the behaviour of a simplified one-dimensional model of the visual cortex, and suggest that many aspects of cortical morphology may be designed to ensure uniform coverage.

## 2 Methods

### *2.1 Definition of a measure of coverage*

The measure of coverage used here is based on the total amount of neural activity, $A$, evoked in the striate cortex by a contour of a particular orientation $\theta$ present at a particular visual field location $(\varphi, \psi)$ in one of the two eyes, $e \in \{L, R\}$. The hypothesis being investigated is that the cortex is designed in such a way as to minimize local variation in $A(\theta, \varphi, \psi, e)$, i.e. its dependence on $\theta$, $\varphi$, $\psi$ and $e$. A simple measure of non-uniformity, analogous to the $d'$ measure of statistical uncertainty used in information theory, can be obtained by taking the ratio between the standard deviation of $A$ and its mean value. This will be referred to here as coverage uniformity and denoted by the symbol $c'$.

$A(\theta, \varphi, \psi, e)$ can be derived as follows: let $n_e(x, y)$ represent ocular dominance at a position $(x, y)$ on the cortical surface, on a scale from 0 to 1, with 1 representing maximum input strength from a particular eye. Let $\theta_c(x, y)$ represent preferred orientation as a function of cortical position, and let $\Omega(\theta - \theta_c)$ be an averaged orientation tuning curve i.e. total neural response at any given location as a function of the difference between a stimulus orientation $\theta$ and the preferred orientation $\theta_c$. For simplicity, assume that the map of visual field space on the cortex is isotropic, and that the magnification factors relating $\varphi$ and $\psi$ to $x$ and $y$ are both unity i.e that $x$ maps to $\varphi$ and $y$ maps to $\psi$. If the distribution of activity in the cortex evoked by simulation of a point in visual space $(\varphi, \psi)$ is the cortical point image $P_c(x, y)$, then,

$$\begin{aligned} A(\theta, \varphi, \psi, e) = \int & n_e(x - x', y - y') \\ & \times \ \Omega\{\theta - \theta_c(x - x', y - y')\} \\ & \times P_c(x', y') \cdot \mathrm{d}x' \cdot \mathrm{d}y'. \end{aligned} \tag{2.1}$$

Coverage uniformity is then defined as

$$c' = \text{standard deviation}(A)/\text{mean}(A) \tag{2.2}$$

Note that when $c'$ is large, coverage is bad i.e. $A$ is uneven. Figure 1 illustrates some of the stages involved in calculating coverage.

### *2.2 Orientation tuning*

For the calculations to be described here, the orientation tuning curve $\Omega(\theta - \theta_c)$ was assumed to be a gaussian function of orientation:

$$\Omega(\theta - \theta_c) = \exp\{-h(|\theta - \theta_c|_{180})^2/2\sigma_\Omega^2\} \tag{2.3}$$

where

$$h(\theta) = \theta \qquad \theta \leqslant 90^\circ$$

$$h(\theta) = 180^\circ - \theta \qquad \theta > 90^\circ,$$

$\theta$ is the stimulus orientation, and $\theta_c$ is the preferred orientation of the region of cortex in question. Quantitative studies of orientation tuning curves in the monkey (Schiller et al. 1976) suggest that a gaussian is a reasonable approximation for single cells, provided tuning is relatively narrow. Since it is the summed tuning curves from a number of cells in the same column that is relevant to the present calculations, and there is likely to be scatter in both the widths and the center positions of the individual curves, the approximation to a gaussian seems even more likely to be correct. The effect of changing the width $\sigma_\Omega$ of the tuning function was explored in the calculations; values typically used were in the range 12° to 32°. The measurements of Schiller et al. (1976) showed that the most common value of $\sigma_\Omega$ in a large population of cells in macaque striate cortex, including both simple and complex types, was about 24°. For simplicity, the value of $\sigma_\Omega$ was assumed not to vary with position in the cortex, despite the evidence that it varies in the upper layers.

### *2.3 The cortical point image*

The cortical point image, $P_c(x, y)$ was assumed to be a gaussian function of distance,

$$P_c(x, y) = \{1/(2\pi\sigma_x \cdot \sigma_y)\} \cdot \exp(-x^2/2\sigma_x^2 - y^2/2\sigma_y^2) \tag{2.4}$$

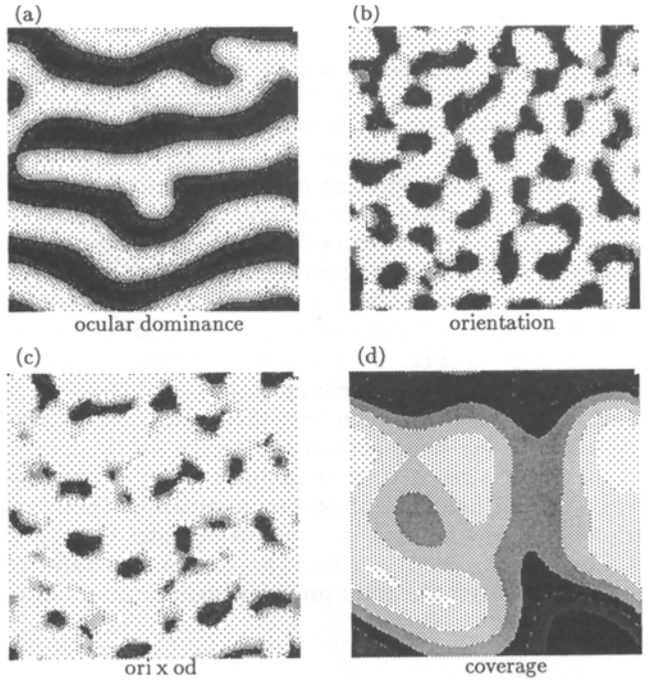

**Fig. 1a–d.** Illustration of the method used to calculate coverage: the calculation is for the two-dimensional case, with periodic boundary conditions. The initial patterns of ocular dominance and orientation selectivity were produced using the algorithms described in the preceding paper. All four panels are hypothetical maps of neural activity, the intensity of shading (i.e. blackness) being approximately proportional to the amount of activity. **a** Shows the activity evoked in a small area of cortex by all orientations seen through one eye, derived from the pattern of ocular dominance columns as described in the text; **b** shows the activity evoked in the same area of cortex by a single orientation seen through both eyes, and is derived from the pattern of orientation columns. Note that the size of the responsive areas is dependent on the width of the orientation tuning curve, which in this case was defined by (2.3), with $\sigma_\Omega = 24°$. Panels **a** and **b** can be compared with the activity patterns found in deoxyglucose experiments (e.g. Fig. 2 in Tootell et al. 1988a and Fig. 8a in Hubel et al. 1978). Panel **c** shows the product of **a** and **b** i.e. the activity evoked by a single orientation seen through one eye. Panel **d** is a transformation of panel **c** into retinotopic coordinates and the density of shading at each point is proportional to the total activity evoked in the cortex by a single orientation seen through one eye at a single visual field location. This transformation is effected by convolving the image in **c** with the cortical point image (2.1), under the assumption that cortical magnification factor is locally uniform and isotropic. The lowest and highest intensities of shading in **d** correspond to coverage values (i.e. values of $A$) of about 1.05 and 1.48 respectively. In this simulation the periodicity ratio (ori/od) was 0.71, ocular dominance columns were anisotropic (i.e. elongated in one direction), orientation columns isotropic (i.e. no preferred direction), and there was no coupling between the two sets of columns

where $\sigma_x$ and $\sigma_y$ describe the spread in the $x$ and $y$ directions respectively. Accurate measurements of this quantity do not exist; if however the cortical magnification factor is known it can be calculated as an inverse of the distribution of visual field locations, weighted for response strength, that can activate cells in a given cortical column. Hubel and Wiesel (1974b) estimated that this cortical region is roughly circular with an overall diameter of about 2–3 mm, and that this size is largely independent of retinal eccentricity. Assuming that their estimate of overall diameter is about 4 times larger than the standard deviation of an underlying gaussian distribution this would imply that $\sigma_x$ and $\sigma_y$ are in the range 0.5 mm–0.8 mm. Later work suggests that $P_c$ varies slightly in size over the cortex (Dow et al. 1981; Van Essen et al. 1984) being larger in the foveal representation than elsewhere; overall however the more recent measurement suggest that values of $\sigma_x$, $\sigma_y$ in the range 0.25 mm to 0.6 mm would be appropriate. It should be noted in addition that $\sigma_x$ and $\sigma_y$ are likely to vary with depth in the cortex, being the smallest in layer IVC$\beta$ (Tootell et al. 1988b), and, since receptive field size is involved, may even depend on factors that affect neuronal response threshold such as behavioural arousal or selective attention.

### *2.5 Calculations*

The calculations explored the effects on $c'$ of changing the ratio between the wavelengths $\lambda_\theta$ and $\lambda_n$ of the orientation and ocular dominance columns respectively. As the wavelengths are the repeat periods of the columns, $\lambda_\theta$ corresponds to the size of an orientation hypercolumn, and $\lambda_n$ to the size of an ocular dominance hypercolumn, as defined by Hubel and Wiesel. In order to explore the influence of wavelength ratio per se, and not the effect of simply making one set of columns smaller (which always makes coverage more uniform), the geometric mean of the two wavelengths was kept constant. Thus as one set of columns was made larger, the other set was made smaller, while $\sigma_x$ and $\sigma_y$ were kept constant. Increments and corresponding decrements in wavelength were kept equal on a logarithmic scale, and ratios covered the range 0.25 to 4.0. Coverage was calculated (2.1 & 2.2) for 9 different values of $\theta$, 20° apart.

Two kinds of model cortex were studied: *a)* a simple one-dimensional model in which both ocular dominance and orientation were periodic and perfectly regular functions of distance, and *b)* more realistic two-dimensonal models of orientation and ocular dominance columns, generated using the algorithms described in the previous paper (Swindale 1991). In the latter case the effect of coupling the two sets of columns in the manner described in the previous paper was also studied. This introduces a tendency for regions of rapid orientation change to lie close to the centers of ocular dominance stripes, although as shown in the preceding paper this effect is itself dependent on the relative periodicities of the columns. The effect of causing one or both sets of columns to be spatially anisotropic i.e. extended in a given direction, was also studied, since this anisotropy is often present in at least one set of columns.

The ocular dominance values provided by the model alternate between +1 and −1 (corresponding to ocular dominance groups 1 to 7) with few intermediate values, and thus do not accurately represent the gradual changes with distance in the physiological responsiveness to one eye that occurs in the cortex (Hubel and Wiesel 1968). For example in the monkey, monocular regions (ocular dominance groups 1 and 7) generally only occur in regions in the centers of ocular dominance stripes. In order to model the physiological pattern of ocular dominance more accurately, the values provided by the model were smoothed by convolution with a radially symmetric gaussian function, with a width chosen to produce a roughly uniform distribution of ocular dominance values, similar to that found in the monkey (Hubel et al. 1977). After smoothing, responses to one eye varied roughly sinusoidally, and fell close to zero only in the centers of ocular dominance stripes (Fig. 1a). The width of the smoothing function was scaled to the period of the ocular dominance bands and this ratio remained the same in all the calculations described here. Anisotropic bands were generated by changing the value of $\beta$ (Eq. 3.2 in Swindale 1991). For any given set of parameters ($\lambda_n$, $\lambda_\theta$, $\sigma_\Omega$, $P_c$, and $\beta$) an average measure of coverage uniformity was usually calculated for three different sets of model patterns, generated using a different seed for the random number generator (which is responsible for the variations in structure between one simulation and the next). Because large numbers of different patterns had to be generated, care was taken to ensure that the random number generator was a good one (Sedgewick 1988) with a shortest cycle in excess of 40,000 numbers. Unless otherwise described, parameter values for the initial calculations of ocular dominance and preferred orientation are the same as those used in the preceding paper to generate Fig. 4.

## 3 Results

### 3.1 *A one-dimensional model*

The behaviour of a simplified one-dimensional model of the cortex was first investigated. Ocular dominance was assumed to vary sinusoidally as a function of position $x$, i.e

$$n_R(x) = \tfrac{1}{2} + \tfrac{1}{2}\sin(2\pi x/\lambda_n) \qquad (3.5a)$$

$$n_L(x) = \tfrac{1}{2} - \tfrac{1}{2}\sin(2\pi x/\lambda_n) \qquad (3.5b)$$

and orientation to change linearly with distance

$$\theta_c(x) = |180x/\lambda_\theta|_{180} \qquad (3.6)$$

where $\lambda_n$ and $\lambda_\theta$ are the spatial wavelengths of ocular dominance and orientation respectively. Calculation of coverage proceeds as follows (2.1): the one-dimensional response $R_\theta(x)$ to a given orientation $\theta$ seen by both eyes, ie

$$R_\theta(x) = \exp\{-h(|\theta - \theta_c|_{180})/2\sigma_\Omega^2\}\,. \qquad (3.7)$$

This a series of gaussian curves, of width $\sigma = \sigma_\Omega \lambda_\theta/180$, separated by a distance $\lambda_\theta$. The response to a given eye is a sinusoidal function with a period $\lambda_n$ (3.5), and the net response to a given orientation in a given eye is in the product of these two functions. This product is then convolved with the one-dimensional point image, a gaussian of width $\sigma_x$, to give evoked activity as a function of position in visual space:

$$A(x \rightarrow \varphi, \theta, L) = \{R_\theta(x) \cdot n_L(x)\} * P_c(x) \qquad (3.8)$$

This calculation is then repeated for the other eye, and for a range of values of $\theta$ (which simply introduce different phase relations between $R_\theta$ and $n$) and $x$, to give a set of coverage values. The standard deviation of these values is then divided by the mean to give $c'$.

Results of calculations of this kind are shown in Fig. 2a and b, which shows how coverage uniformity varies as a function of the wavelength ratio between the two sets of columns ($\lambda_\theta/\lambda_n$). In Fig. 2a this has been calculated for four different sizes of the cortical point image, and in Fig. 2b for four different values of orientation selectivity. The graphs show that coverage is always least uniform when orientation and ocular dominance have the same periodicity; except for the largest point image sizes it is most uniform when orientation has a period half that of ocular dominance. There are also subsidiary minima in $c'$ at period rates ($\lambda_\theta/\lambda_n$) of 1.5 and 3.0, as well as a local maximum at a ratio of 2.0, except when the point image is small or orientation

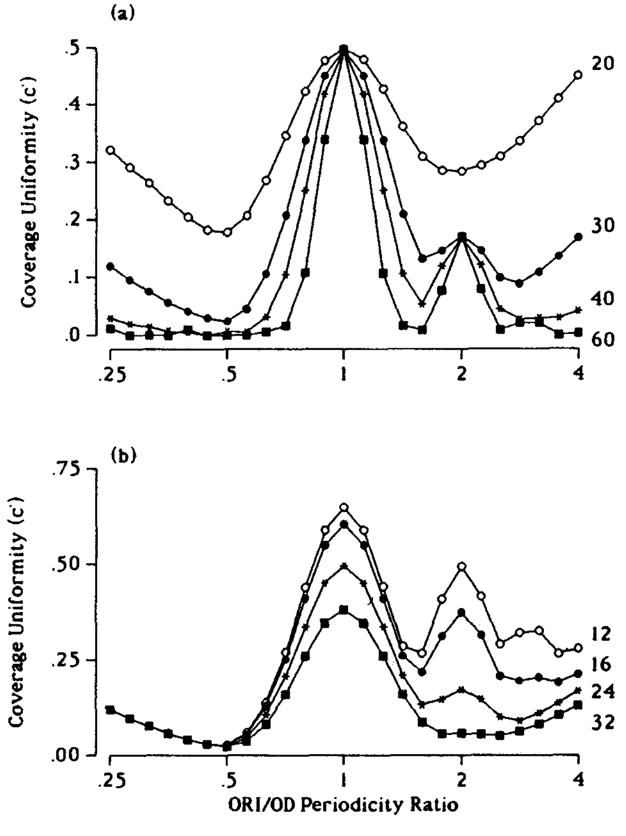

**Fig. 2. a** Coverage uniformity ($c'$) graphed as a function of wavelength ratio (ori/od) for four different point image sizes for the one-dimensional model. Orientation tuning was kept constant and had a value $\sigma_\Omega$ (2.3) = 24°. The numbers on the right give the value of $\sigma_x$ (2.4) of the point image in array units. At a ratio = 1.0 both columns had a period = 50 array units. Column periods $\lambda_\theta$ and $\lambda_n$ were varied reciprocally around a geometric mean value of 50. Thus at wavelength ratios of 0.25 and 4.0. periods were in the ratio 25 : 100 and 100 : 25 respectively. **b** Coverage uniformity as a function of wavelength ratio for four different values of orientation tuning. Values on the right give $\sigma_\Omega$ in degrees; point image size was constant and had a value $\sigma_x$ = 30 array units

tuning is broad, in which case there is a local minimum at a ratio of 2.0. As would be expected, increasing the size of the point image improves coverage uniformity at all frequency ratios, except at unity, and also narrows the range of ratios around unity for which $c'$ is larger than some specified value (Fig. 2a). For relatively large sizes of point image there is a relatively large range of frequency ratios below unity, as well as others above it, for which coverage is almost completely uniform. Increasing the width of orientation tuning has relatively little effect on coverage at ratios less than about 0.5, but improves coverage for ratios larger than this, the largest improvements occurring at ratios close to 1 and 2.

The behaviour of this one-dimensional model can be explained in general terms as follows: multiplication of the two periodic functions $n(x)$ and $R_\theta(x)$ (3.8) gives a function in which both the original periodicities are present, as well as a d.c. component, and sum and difference periods. Convolution with $P_c(x)$ is equivalent to multiplication of this function in frequency space by a gaussian centered on the origin (i.e. zero frequency) with a width inversely proportional to the width of $P_c$. $P_c$ is generally wide enough (and thus narrow in frequency space) to substantially attenuate the original frequencies a well as the sum terms, but reduces the difference frequency term by a much smaller amount. It is this term that makes the largest contribution to the variance of $A$ and thus to $c'$. Note that when the periods of $n(x)$ and $R_\theta(x)$ are equal, the difference frequency is zero and its magnitude is unaffected by the width of $P_c$, as Fig. 2a illustrates. Note also that because $R_\theta(x)$ is not sinusoidal, additional energy terms are present in its frequency spectrum at integer multiples of $1/\lambda_\theta$. This introduces additional difference frequencies into the product with $n(x)$ which under some conditions can cause additional peaks in $c'$ at frequency ratios of 2 and 3 (Fig. 2).

### 3.2 *Two-dimensional cortical models*

The calculations just described show that uniform coverage is severely compromised when very regular patterns of orientation and ocular dominance have a similar periodicity, but it is not certain that coverage would be similarly compromised in the cortex, given the lesser degree of regularity of the patterns that are found there. To test this, the calculations done on the one-dimensional maps were repeated, with little essential change, on the two-dimensional models generated using the algorithms described in the previous papers. Figure 1 illustrates how the calculations were carried out.

*3.2.1 No coupling.* In this set of calculations, orientation and ocular dominance stripes were structurally independent i.e. the relations described by Blasdel and Salama (1986) were absent, and $\alpha$ (3.5; Swindale 1991) $= 0$. Much of the behaviour of the one-dimensional model is manifested in this situation, although there is overall a much smaller range of variation of values of $c'$ with coverage never being as uniform, or as non-uniform, as in the one-dimensional case.

Figure 3a shows calculations of $c'$ across a four-fold range of frequency ratios (i.e. $\lambda_\theta/\lambda_n$) for three different sizes of cortical point image. In these calculations both sets of columns were isotropic i.e. bands could run in any direction and the angle of intersection between individual iso-orientation domains and ocular dominance stripes was thus random. As in the one-dimensional case, coverage was always most uniform at a periodicity ratio of about 0.5, i.e. when orientation column wavelength was half that of the ocular dominance stripes. The increase in $c'$ at a periodicity ratio of 1 was much less pronounced than in the one-dimensional case however. Increasing the size of the cortical point image made coverage more uniform at all wavelength ratios including unity.

An interesting result of the one-dimensional calculations (Fig. 2a and b) is that coverage uniformity is not a symmetric function of periodicity ratio: thus for example, coverage would be more uniform if orientation and ocular dominance columns have periods of 0.5 mm and 1 mm respectively, than if the reverse were the case and the periods were 1 mm and 0.5 mm. This lack of symmetry is evident also in the results obtained from the two-dimensional model columns: coverage is generally more uniform at frequency ratios below unity than at the reciprocal ratio above it. This bias towards low ratios is most evident when the point image is small (Fig. 3a) and when orientation tuning width is narrow (Fig. 3b).

*3.2.2 Effect of column anisotropy.* Figure 3c shows the effect on coverage uniformity of changing the overall direction of elongation of either the ocular dominance or the orientation columns, or both. In all of these conditions coverage seems to be most uniform at frequency ratios ($\lambda_\theta/\lambda_n$) of about 0.5. The figure shows that there is little effect on coverage of making only one set of columns run in a single direction, but if both sets of columns run in the same direction, coverage at frequency ratios close to unity is impaired. When the columns run in orthogonal directions (the condition which is closest to Hubel and Wiesel's original model of the relation between the columns) the coverage deficit at frequency ratios close to 1 is absent, but coverage is still more uniform when the orientation hypercolumns are smaller than the ocular dominance hypercolumns.

*3.2.3 Effect of coupling.* Figure 4 shows the effect on coverage of introducing structural relations between orientation and ocular dominance columns similar to those discovered by Blasdel and Salama (1986). This was done for the case where neither set of columns has a preferred direction of elongation: the effect is to make coverage more uniform at frequency ratios close to unity. There is little effect on coverage at ratios above 2 or below about 0.7.

*3.2.4 Effect of point image size and shape.* Figures 2a and 3a show, not surprisingly, that increasing the size of the point image improves coverage uniformity, $c'$, at all frequency ratios; Fig. 5a shows in more detail how $c'$

depends on point image at a single frequency ratio, close to that found in the monkey. For the purpose of comparison with experimental estimates of point image size, this has been expressed here in cortical mm, assuming that an experimental measure of diameter is likely to equal about $4\sigma$ of the underlying distribution, and that ocular dominance column periodicity equals 800 µm. The figure shows that coverage uniformity decreases rapidly (i.e. $c'$ increases) as point image size decreases below a value of about 1.5 mm, about twice the period of the ocular dominance columns.

In the calculations so far described, the point image has been assumed to be radially symmetric (i.e. $\sigma_x = -\sigma_y$), although this is known not to be the case in area 18 of the cat (Cyander et al. 1987). The latter authors suggested that if one or both sets of columns is elongated in a particular direction, the point image might be narrowed in one or other direction without impairing coverage uniformity. Figure 5b illustrates that elongating the point image in either the $x$- or the $y$-direction, keeping the total area constant, has only a slight effect on coverage uniformity when both sets of columns run the same direction. This suggests that for a given total area, point image shape has much less of an impact on coverage uniformity than does total area, even when both sets of columns run in a similar direction.

## 4 Discussion

### 4.1 Independence and proportionality

An important assumption about the behaviour of visual cortical neurons is built into (2.1), which defines the calculation of coverage. This is that a cell's response to some combination of eye, orientation and stimulus position can be expressed as a separable product of functions describing the response to each of these three variables. Only if this is the case is it possible to define a preferred eye, orientation and receptive field position (and maps for these properties) that are independent of each other. This assumption seems to be at least approximately correct although it has not been explicitly tested in physiological studies. For example neither a cell's ocular dominance, nor the shape of its orientation

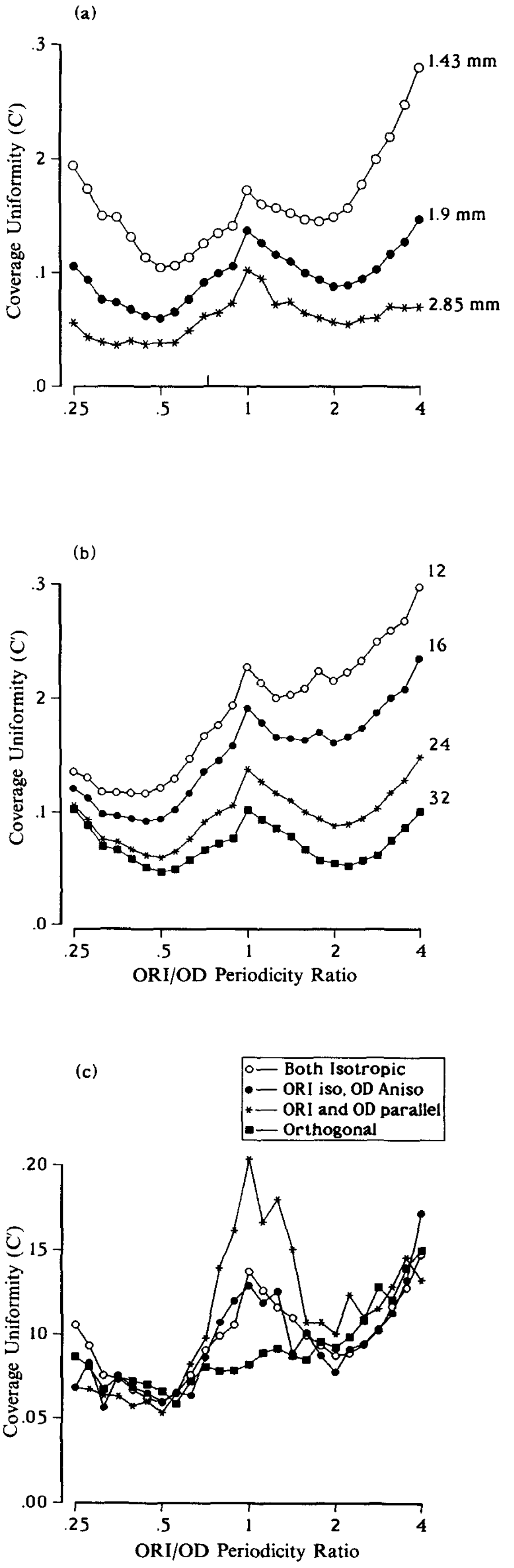

**Fig. 3.** **a** Graphs of coverage uniformity as a function of wavelength ratio (ori/od) for three different point image diameters, for the two-dimensional simulations. For these simulations, there was no coupling between orientation and ocular dominance columns ($a = 0$; (3.5) Swindale 1991) and both sets of columns were structurally isotropic, i.e. bands could run in any direction ($\beta = 1.0$, (2) Swindale 1991). At a periodicity ratio of one, both columns had a period $\lambda = 12$ array units. Numbers on the right give the diameter of the cortical point image in millimeters. In this and subsequent figures each plotted symbol is the average coverage value derived from three different patterns. The tick mark above the $x$-axis marks a ratio of 0.73, similar to the period ratio found in the macaque monkey. **b** Graphs of coverage uniformity as a function of wavelength ratio for four different values of orientation selectivity ($\sigma_\Omega$), given in degrees on the right of each graph. Values are calculated from the same set of patterns analysed in **a**, and the point image had a constant diameter of about 1.9 mm. **c** Graphs of coverage uniformity for various cortical designs. For these calculations $\sigma_\Omega = 24°$, and the point image = 1.9 mm in diameter. See text for further description

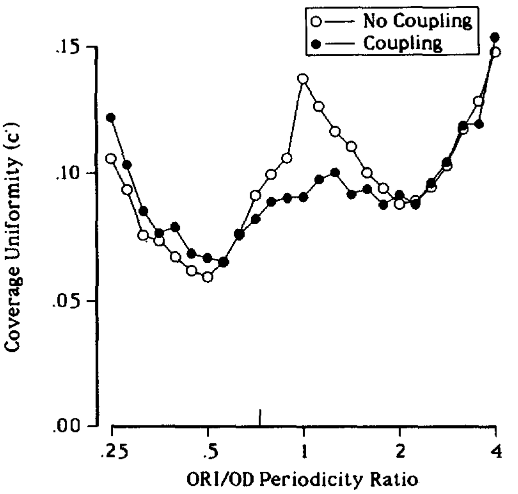

**Fig. 4.** The effect of coupling orientation and ocular dominance columns on coverage uniformity. For these calculations both sets of columns were isotropic (no preferred direction of elongation), and coupling was produced by setting $a$ (Eq. 3.5, Swindale, 1991) = 20. Point image size and orientation selectivity were the same as for Fig. 3c. The tick mark on the $x$-axis marks a periodicity ratio = 0.73, about the same as in the macaque monkey

tuning curve have been reported to depend on position within its receptive field, nor has ocular dominance been reported to change with the orientation of stimulus. Some forms of dependence have been reported: preferred orientation can differ in the two eyes by a few degrees (Blakemore et al. 1972; Nelson et al. 1977), as can receptive field position (Barlow et al. 1967). These effects are small however, and, when averaged over the cells in a single column, may not have a significant effect on the conclusions obtained here.

The further assumption of proportionality in responses (i.e. that the net response can be written as a simple product of separable functions) has not, to the author's knowledge, been explicitly tested, although this would be well worth doing. It is reasonable to expect that points on an orientation tuning curve will be scaled down in magnitude if measurements are made in the periphery of the receptive field, or if the less responsive eye is stimulated, but it is not certain whether this and similar interactions can be expressed as a multiplicative scaling, or whether there is some other relationship. At present however there are no obvious reasons for thinking that a non-multiplicative scaling of responses would lead either to improved coverage, or to conclusions that are substantially different from those drawn here.

### *4.2 Is coverage a significant constraint on cortical design?*

Coverage uniformity, as defined here, is a measure of one source of uncertainty in the amount of neural activity evoked in the cortex by a contour of a particular orientation lying in a particular receptive field position in one eye. As such, $c'$ quantifies a potential source of noise, additional to other sources, in the cortical response to an oriented stimulus. Typical values of $c'$ calculated for model parameters similar to those found in macaque striate cortex were in the range 0.05 to 0.1.

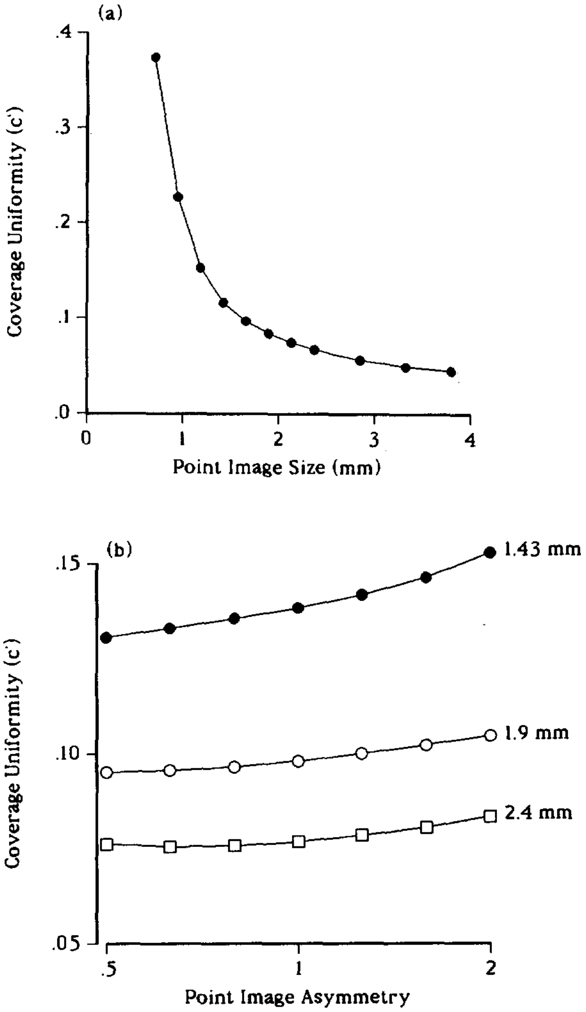

**Fig. 5.** **a** The effect of point image size on coverage uniformity at a single wavelength ratio ($\lambda_\theta/\lambda_n$) = 0.71, approximately the same as in the macaque monkey. Ocular dominance columns were anisotropic, and orientation tuning width was also similar to that in the monkey ($\sigma_\Omega = 24°$). To facilitate comparison with the experimental data, point image size is expressed as a diameter = $4\sigma_x$, assuming that $\lambda_n$ = 13.47 array units is equivalent to 800μm in the monkey. **b** The effect of point image asymmetry on coverage uniformity for the case where both sets of columns run parallel to each other. The $x$-axis shows the degree of asymmetry, expressed as $\sigma_x/\sigma_y$ (2.4). The results of three sets of calculations are shown; in each the ratio was varied keeping the geometric mean of $\sigma_x$ and $\sigma_y$ constant, and thus the total area of the point image. The mean size is indicated on the right hand side of each graph. Note that the effects on coverage uniformity are smaller than the effects of changing total point image area

Although these alues are small (indicating a standard deviation in coverate value equal to 5% to 10% of the mean) the total range of values encountered is somewhat larger: e.g. Fig. 1d shows how coverage (i.e. the value $A(\theta, \varphi, \psi, e)$, 2.1) varies with the visual field position $(\varphi, \psi)$ for a single orientation seen through the right eye. Although $c'$ in this case had a value of 0.08, the values in Fig. 1d range between extremes of 1.05 and 1.48, a variation of ±17% about the mean.

Some factors might operate to reduce $c'$. For example groups of cells could vary in their responsiveness, or the strength of their connections with subsequent cells in the visual pathways, in such a way as to make the net response to a given stimulus more predictable. Alternatively, it may be the case that the nature of cortical processing is such that large variations in coverage value can be tolerated, provided the value remains above some threshold level. Since it is difficult to guess what this threshold might be, one cannot be sure whether any of the design conditions considered here would produce coverage values that fell below such a threshold.

The calculations of $c'$ have been carried out on patterns that visually resemble those found in the monkey, but it is possible that there are unrecognized structural differences between the real and model patterns which would have the effect of altering the coverage estimates. One way of checking for this would be to calculate coverage values from the voltage sensitive dye patterns using the methods described here, and to compare the results with the predicted values.

The estimates of $c'$ are likely to be smaller than the ones that are functionally significant, because factors additional to those considered here are likely to influence the response of a given cortical location to a particular stimulus. Thus for example the length of an edge, or its colour or velocity of motion are all factors that might influence the response of any particular cell. If selectivity along any of these (or other) dimensions has a columnar representation additional to that for orientation and ocular dominance then the stimulus space to be considered in the calculation of $c'$ should be expanded along each of these additional dimensions. The results of such a calculation would necessarily yield larger values of $c'$, although the role of the factors studied here would be expected to remain essentially the same. There is evidence that selectivity for direction of movement in the cat visual cortex has a columnar representation that is at least partially independent of that for orientation preference (Tolhurst et al. 1981; Payne et al. 1981; Swindale et al. 1987) as well as evidence for a systematic representation in the monkey (Blasdel, personal communication). There is also evidence that colour preference (Michael 1981; Livingstone and Hubel 1984; Tootell et al. 1988c) has a columnar organization. No attempt was made to include these dimensions in the present calculations partly because it is not clear yet how these columnar systems are organised in the monkey, and plausible models of them have not been devised. It seems unlikely that including these additional factors would change the general conclusions drawn here, since obtaining uniform coverage values along a subset of dimensions in stimulus space is presumably a prerequisite for obtaining uniform values over all the relevant dimensions.

In general, the assumption that values of $A$ (2.1) should be unform along all the dimensions that are represented in a map is unlikely to be correct. For example it is believed that horizontal and vertical orientation preferences predominate in some areas of striate cortex (Blakemore et al. 1981) and this suggests that there is some functional advantage in having coverage values that are higher for these orientations than others. Obviously, for more complex stimulus spaces including for example colour, temporal and spatial frequency, not all possible combinations of these variables can or need be represented. Coverage uniformity should then be calculated relative to some 'ideal' value of $A$ that varies with location in stimulus space in a systematic way determined by functional considerations.

### *4.2 Psychophysical correlates of uneven coverage*

The possibility that the visual cortex does not achieve a uniform representation of stimulus attributes across the visual field is supported by psychophysical findings of irregular variations with eccentricity in contrast sensitivity for simple stimuli, such as gratings of particular orientations (Regan and Beverly 1983) and for positional hyperacuity thresholds (Jiang and Levi 1991). In addition, more severe defects, including complete blindness to motion in depth within irregularly shaped regions of the visual field have been observed in apparently normal observers (Hong and Regan 1989).

### *4.4 Is the visual cortex designed to optimize coverage uniformity?*

A number of features of visual cortical structure seem designed to avoid large values of $c'$, if not to optimize it. For example it is striking that in all species studied, ocular dominance and orientation columns have different periodicities. In the monkey, the period of ocular dominance columns has variously been given as 848 μm (Hubel et al. 1977), 770 μm (Hubel et al. 1978) and 880 μm (LeVay et al 1985), although the latter authors report that the period decreases with visual field eccentricity. Orientation column periodicity has been given as 570μm (Hubel et al 1978) and 640 μm or less (Hubel and Wiesel 1974a). Averages of these measurements yield a periodicity ratio (orientation/ocular dominance) of 0.73. As the ocular dominance columns get narrower towards the periphery of striate cortex it would be interesting to know whether there is a similar change in the repeat period of orientation columns. In the cat, Fourier powers spectral measurements in area 17 give an orientation periodicity of 1.0–1.1 mm (Löwel et al. 1987) and an ocular dominance periodicity of 800 μm (Löwel and Singer 1987), a ratio of 1.3. Similar values were obtained by Diao et al. (1990) in a study of physiological maps made in area 17 close to the border with area 18. In area 18, the periodicities are 1.25 and 1.86 for orientation and ocular dominance respectively (Cynader et al. 1987), a ratio of 0.67, with similar values obtained in area 18 in the separate study by Diao et al. (1990). These differences show that although a range of periodicity values is available to both sets of columns, the ratios between them are always significantly different from unity.

A slight reduction in orientation column width, accompanied by an increase in the size of ocular dominance stripes to give a periodicity ratio closer to 0.5 would improve coverage uniformity: the fact that this does not happen suggests an interaction with some other constraint that puts a lower limit on orientation column spacing (for example an orientation discrimination task might require the detection of some minimum change in the locus of cortical activation, and this would be related to column periodicity). This or some other constraint on column periodicity is presumably important because simply decreasing the size of either or both sets of columns, while keeping point image size constant will increase coverage uniformity, as would assigning orientation and eye preference at random to cells in any particular cortical location.

### *4.5 Coupling*

It is shown here that linking orientation and ocular dominance columns in a manner that is probably similar to that demonstrated by Blasdel and Salama (1986) reduces the increase in $c'$ found at periodicity ratios close to unity (Fig. 4), although it has little apparent effect on $c'$ at other ratios (e.g. below about 0.7 and above 2.0). Since the periodicity ratio in the monkey is about 0.73 this means that the present analysis does not provide an obvious functional explanation for coupling. However it might be unwise to conclude from this that the role of coupling is unrelated to improving coverage uniformity. One possibility is that coupling could be significant when calculation of coverage is expanded to include more stimulus dimensions than are considered here. Another is that the orientation/ocular dominance periodicity ratio in the monkey is not fixed but deviates. For example ocular dominance columns decrease in size from fovea to periphery by a factor of two (LeVay et al. 1985), and unless orientation columns change similarly in size, the periodicity ratio between the two is certain to fall into a range where coupling would significantly improve coverage uniformity. It is also possible that there are local variations in the sizes of both sets of columns and this would have the same effect of causing periodicity to have values for which coupling would help ensure uniform coverage.

### *4.6 Point image size*

An obvious role of point image size, which as defined here is a consequence of both receptive field scatter (Hubel and Wiesel 1974b) and receptive field size, is to ensure even coverage, and for a sufficiently large point image this can be guaranteed for almost any condition, presumably at the expense of a decrease in the accuracy of visual localization and related functions. Because there is unlikely to be any advantage, beyond obtaining uniform coverage, of having the point image be large, it is reasonable to suppose that the point image is no larger than is required by the coverage constraint, and Fig. 5a illustrates that this is probably the case. For parameter values similar to those in the macaque, $c'$ increases rapidly as point image size decreases below a value of about 1.5 mm i.e. about twice the period of the ocular dominance columns. This is similar to current estimates of point image size in the monkey. The fact that point image size decreases with eccentricity (Dow et al. 1981; Van Essen et al. 1984) may be related to the decrease in the size of ocular dominance columns in the visual periphery (LeVay et al. 1985), and a consequent decrease in the absolute values of $A$ (2.1), indicating less complete analysis of visual information there.

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## References

Barlow HB, Blakemore C, Pettigrew JD (1967) The neural mechanisms of binocular depth discrimination. J Physiol (Lond) 193:327–342

Blakemore C, Fiorentini A, Maffei L (1972) A second neural mechanism of binocular depth discrimination. J Physiol (Lond) 226:725–749

Blakemore CB, Garey LJ, Vital-Durand F (1981) Orientation preferences in the monkey's visual cortex. J. Physiol (Lond) 319:78P

Blasdel GG, Salama G (1986) Voltage-sensitive dyes reveal a modular organization in monkey striate cortex. Nature 321:579–585

Cynader MS, Swindale NV, Matsubara JA (1987) Functional topography in cat area 18. J Neurosci 7:1401–1413

Diao Y-C, Jia W-G, Swindale NV, Cynader MS (1990) Functional organization of the cortical 17/18 border region in the cat. Exp Brain Res 79:271–282

Dow BM, Snyder AZ, Vautin RG, Bauer R (1981) Magnification factor and receptive field size in foveal striate cortex of the monkey. Exp Brain Res 44:213–228

Hong X, Regan D (1989) Visual field defects for unidirectional and oscillatory motion in depth. Vision Res 29:809–819

Hubel DH, Wiesel TN (1968) Receptive fields and functional architecture of monkey striate cortex. J Physiol (Lond) 195:215–243

Hubel DH, Wiesel TN (1974a) Sequence regularity and geometry of orientation columns in the monkey striate cortex. J Comp Neurol 158:267–294

Hubel DH, Wiesel TN (1974b) Uniformity of monkey striate cortex: a parallel relationship between field size, scatter, and magnification factor. J Comp Neurol 158:295–306

Hubel DH, Wiesel TN (1977) Functional architecture of macaque monkey striate cortex. Proc R Soc Lond B 198:1–59

Hubel DH, Wiesel TN, LeVay S (1977) Plasticity of ocular dominance columns in monkey striate cortex. Phil Trans R Soc Lond B 278:131–163

Hubel DH, Wiesel TN, Stryker MP (1978) Anatomical demonstration of orientation columns in macaque monkey. J Comp Neurol 177:361–380

Jiang B, Levi DM (1991) Spatial-interval discrimination in two-dimensions: effect of eccentricity. Invest Ophthalmol 32:1269

LeVay S, Connolly M, Houde J, Van Essen DC (1985) The complete pattern of ocular dominance stripes in the striate cortex and visual field of the macaque monkey. J Neurosci 5:486–501

Livingstone MS, Hubel DH (1984) Anatomy and physiology of a color system in the primate visual cortex. J Neurosci 4:309–356

Löwel S, Singer W (1987) The pattern of ocular dominance columns in flat mounts of the cat visual cortex. Exp Brain Res 68:661–666

Löwel S, Freeman B, Singer W (1987) Topographic organization of the orientation column system in large flat-mounts of the cat visual cortex: a 2-deoxyglucose study. J Comp Neurol 155:401–415

Michael CR (1981) Columnar organization of color cells in monkey's striate cortex. J Neurophysiol 46:587–604

Nelson JI, Kato H, Bishop PO (1977) Discrimination of orientation and position disparities by binocularly activated neurons in cat striate cortex. J Neurophysiol 40:260–283

Payne BR, Berman N, Murphy EH (1981) Organization of direction preferences in cat visual cortex. Brain Res 211:445–450

Regan D, Beverley KI (1983) Visual fields described by contrast sensitivity, by acuity, and by relative sensitivity to different orientations. Invest Ophthalmol Vis Sci 24:754–759

Schiller PH, Finlay BL, Volman SF (1976) Quantitative studies of single-cell properties in monkey striate cortex. II Orientation specificity and ocular dominance. J Neurophysiol 39:1320–1333

Sedgewick R (1988) Algorithms. Addison-Wesley, Reading Mass

Swindale NV (1991) A model for the coordinated development of columnar systems in primate striate cortex. Biol Cybern (this volume)

Swindale NV, Matsubara JA, Cynader MS (1987) Surface organization of orientation and direction selectivity in cat area 18. J Neurosci 7:1414–1427

Tolhurst DJ, Dean AF, Thompson ID (1981) Preferred direction of movement as an element of organization of cat visual cortex. Exp Brain Res 44:340–342

Tootell RBH, Hamilton SL, Silerman MS, Switkes E (1988a) Functional anatomy of macaque striate cortex. I. Ocular dominance, binocular interactions, baseline conditions. J Neurosci 8:1500–1530

Tootell RBH, Switkes E, Silverman MS, Hamilton SL (1988b) Functional anatomy of macaque striate cortex. II Retinotopic organization. J Neurosci 8:1531–1568

Tootell RBH, Silverman MS, Hamilton SL, De Valois RL, Switkes E (1988c) Functional anatomy of macaque striate cortex. III Color. J Neurosci 8:1569–1593

Van Essen DC, Newsome WT, Maunsell JHR (1984) The visual field representation in striate cortex of the macaque monkey: asymmetries. anisotropies and individual variability. Vision Res 24:429–448

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