

Design Principles of Columnar Organization in Visual Cortex

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Visual space is represented by cortical cells in an orderly manner. Only little variation in the cell behavior is found with changing depth below the cortical surface, that is, all cells in a column with axis perpendicular to the cortical plane have approximately the same properties (Hubel and Wiesel 1962, 1963, 1968). Therefore, the multiple features of the visual space (e.g., position in visual space, preferred orientation, and orientation tuning strength) are mapped on a two-dimensional space, the cortical plane. Such a dimension reduction leads to complex maps (Durbin and Mitchison 1990) that so far have evaded an intuitive understanding. Analyzing optical imaging data (Blasdel 1992a,b; Blasdel and Salama 1986; Grinvald *et al.* 1986) using a theoretical approach we will show that the most salient features of these maps can be understood from a few basic design principles: local correlation, modularity, isotropy, and homogeneity. These principles can be defined in a mathematically exact sense in the Fourier domain by a rather simple annulus-like spectral structure. Many of the models that have been developed to explain the mapping of the preferred orientations (Cooper *et al.* 1979; Legendy 1978; Linsker 1986a,b; Miller 1992; Nass and Cooper 1975; Obermayer *et al.* 1990, 1992; Soodak 1987; Swindale 1982, 1985, 1992; von der Malsburg 1973; von der Malsburg and Cowan 1982) are quite successful in generating maps that are close to experimental maps. We suggest that this success is due to these principles, which are common properties of the models and of biological maps.

Recently it became possible to extract features of cortical cell behavior using optical imaging techniques (Blasdel 1992a,b; Blasdel and Salama 1986; Grinvald *et al.* 1986; Frostig *et al.* 1990; Ts'o *et al.* 1990; Bonhoeffer and Grinvald 1991). A map of the preferred orientations in the visual cortex of monkey obtained this way is shown in Figure 2a (Blasdel 1992b).

One of the obvious features of the map shown is its *periodicity* (Hubel and Wiesel 1968; Albus 1975): for most points, the preferred orientation is repeated in a certain distance, which we call λ . Generally, cells with all preferred orientations are found in an area of linear dimension λ around any point and visual space appears to be mapped in a repeating pattern onto the cortex. A region in which "all" features (e.g., preferred orientation, ocular dominance, color, velocity, etc.) of visual space are represented at least once is called a *hypercolumn* (Hubel and Wiesel 1968). Hypercolumns seem to be arranged roughly following a "module concept" (Szentagothai 1975) in which adjacent x, y -locations in the visual field are projected onto adjacent hypercolumns in the cortex. This leads to a complete representation of all features of one location in the visual space in a locally confined cortical module while representing adjacent locations in adjacent modules.

There are many ways to achieve a modular organization. It is neither required to arrange the features periodically with one predominant frequency nor is it necessary to have an orderly arrangement within the individual modules, by only making sure that each module has at least one feature detector of each characteristic. Therefore, periodicity does not seem to be an a priori concept of cortical design but rather a derived quantity. What then are the basic cortical design principles that, together with modularity, engender the observed periodicity of the maps?

We propose that these principles are (positive) local correlation, homogeneity, and isotropy, all with respect to a length scale λ , which is the only parameter in our framework. Let us introduce a coordinate system with coordinates¹ $\mathbf{x} = (x_1, x_2)$ in the cortical plane and let $\phi(\mathbf{x})$ be the preferred orientation of the column at location \mathbf{x} . Following Swindale *et al.* (1987) we define the complex orientation angle f by

$$f(\mathbf{x}) = e^{j2\phi(\mathbf{x})} \quad (1.1)$$

We introduced a factor 2 because the angles of preferred orientation take on values only between 0° and 180° (not 360°) and two angles differing by 180° are equivalent [see Swindale (1982) for details]. The preferred orientation at point \mathbf{x} is then represented by the complex number f , which can be interpreted as a vector of unit length in the complex plane. The correlation between the preferred orientations at two points is given by the scalar product of the respective vectors at these points. When we define the complex two-point autocorrelation function of $f(\mathbf{x})$ as,

$$C(\mathbf{y}) = \int dx_1 \int dx_2 f^*(\mathbf{x})f(\mathbf{x} + \mathbf{y}) \quad (1.2)$$

(see, e.g., Champeney 1973), it is seen that the real part of $C(\mathbf{y})$ corresponds to the mentioned scalar product,

$$\text{Re } C(\mathbf{y}) = \int dx_1 \int dx_2 \cos 2[\phi(\mathbf{x}) - \phi(\mathbf{x} + \mathbf{y})] \quad (1.3)$$

¹We use bold characters to designate vectors.

Isotropy implies the absence of systematic differences with respect to direction in the cortical plane. Therefore, $\phi(\mathbf{x}) - \phi(\mathbf{x} + \mathbf{y})$ depends only on $r^2 = y_1^2 + y_2^2$ and the autocorrelation function is circularly symmetric. We may therefore write

$$C(\mathbf{y}) = C(r) \quad (1.4)$$

We define a map as being *locally correlated* if, on average, variations of the preferred orientation on a length scale much smaller than λ are significantly smaller than those on a length scale λ . The autocorrelation function has then high values at small distances ($r \ll \lambda$). A system is *homogeneous* if all its locations are equivalent, that is, no systematic differences can be observed between different locations. Such a system is devoid of long-range correlations and therefore has a vanishing correlation function for long distances ($r \gg \lambda$).

Having expressed homogeneity, local correlation, and isotropy in terms of properties of the autocorrelation function, what are the consequences of modularity?² Within every module of linear dimension $\approx \lambda$, all preferred orientations are represented. Close to a given point ($r \ll \lambda$), orientations similar to that at the point itself preponderate. Since modularity requires that within the distance λ from this point (on average) *all* orientations have to occur with comparable frequencies, orientations other than the one at the given point have to occur with *above-average* frequency between the central peak and $r = \lambda$. From equation 1.3 and the lines following it, it is then seen that the autocorrelation function is characterized by a central positive peak, a surrounding negative "valley," and zero values for large distances.

A simple model for such a function is a difference of gaussians,

$$C(r) = e^{-(4r/\lambda)^2} - \frac{1}{4}e^{-(2r/\lambda)^2} \quad (1.5)$$

(the imaginary part of C vanishes identically in our model). This function, shown in Figure 1a, has a peak with width $\approx \lambda/4$ around $r = 0$, a minimum at $r \approx \lambda/2$, and decays to zero for $r \rightarrow \infty$.

According to the Wiener-Khinchine theorem (Champeney 1973), the power spectrum of the map is obtained from the Fourier transform of its autocorrelation function as $P(\mathbf{k}) = \iint e^{-i\mathbf{k}\cdot\mathbf{x}}C(\mathbf{x})d\mathbf{x}$. From equation 1.5, we therefore obtain

$$P(\mathbf{k}) = \frac{\pi\lambda^2}{16} \left\{ e^{-(\lambda\mathbf{k}/8)^2} - e^{-(\lambda\mathbf{k}/4)^2} \right\} \quad (1.6)$$

where $k^2 = k_1^2 + k_2^2$. This spectrum, shown in Figure 1b, has a large amplitude on an annulus with radius $\approx 2\pi/\lambda$ and small or vanishing

²Modularity here is understood in a restricted sense, that is, we suppose modularity only with respect to the distribution of preferred orientation. Swindale (1990) has given arguments against the realization of a strong form of modularity in cortex, in the sense that one module contains *all* represented features; see also Bartfeld and Grinvald (1992). These arguments do not exclude modularity in the more restricted sense used here.

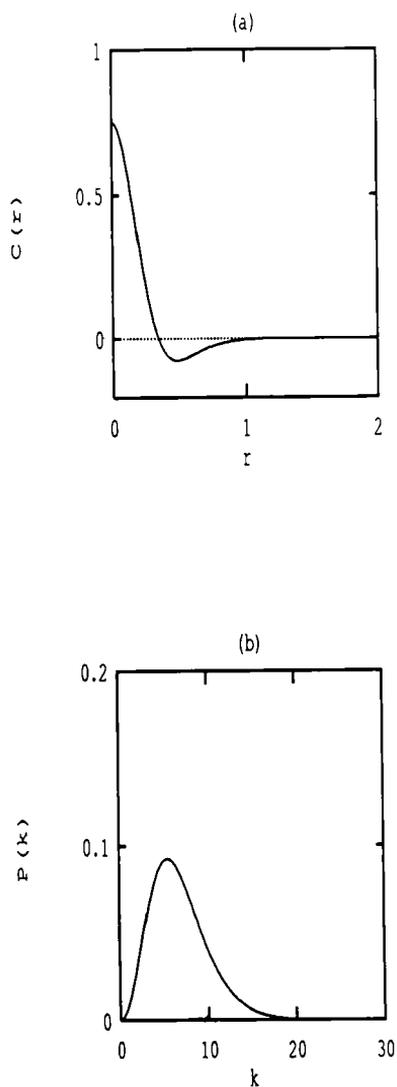
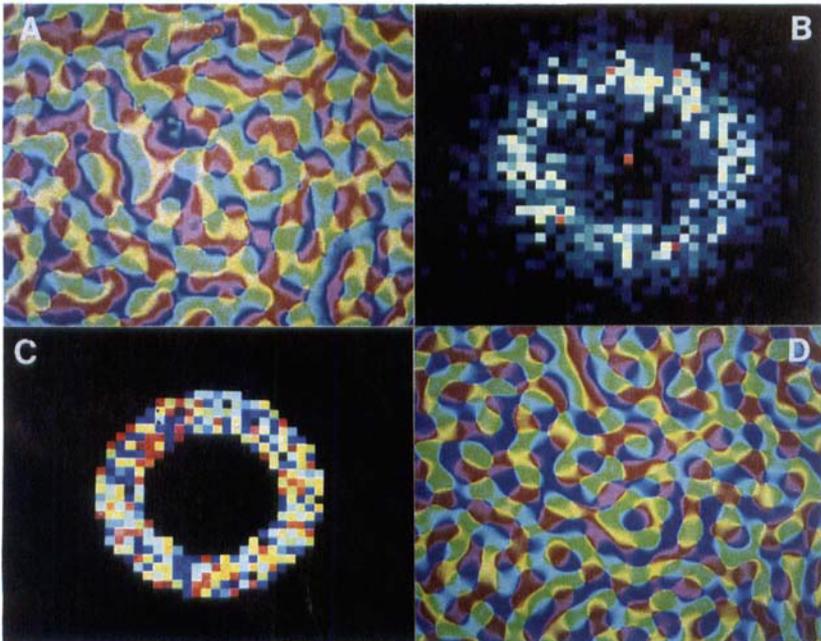


Figure 1: (a) Radial component of the model autocorrelation function (equation 1.5). The function is circularly symmetric around the origin. The horizontal axis is in units of λ . (b) Radial component of the power spectrum corresponding to the autocorrelation function shown in (a), as computed in equation 1.6. The horizontal axis in (b) is in units of $2\pi/\lambda$. Because the power spectrum is the Fourier transform of a function with circular symmetry, it is also circularly symmetric and therefore the function shown corresponds to an annulus around the origin.

amplitudes elsewhere. Similar power spectra have been observed experimentally for orientation column structures of monkeys (Obermayer *et al.* 1991, 1992). Local correlation leads to the absence of spectral components for frequencies much larger than the radius of the annulus (i.e., for spatial frequencies $\gg \lambda^{-1}$). Significant nonzero components for high spatial frequencies would lead to short-range variations in the map, which are generically not observed. Such variations do occur at isolated points, the so-called singularities (Swindale *et al.* 1987), but these singularities are necessary for topological reasons (they correspond to common zeroes of the numerator and denominator in equation 1.8 and only in very unusual cases are such common zeroes absent) and they are *not* caused by high frequencies in the spectrum of f . This can be seen clearly by the singularities in maps generated from Fourier spectra with vanishing high-frequency components (e.g., Fig. 2D).

Homogeneity leads to vanishing amplitudes of the low spatial frequency components in the spectrum inside the annulus because nonzero components for low spatial frequencies would lead to systematic differences (inhomogeneities) between distant hypercolumns, which are not



observed. Isotropy is reflected in the spectrum by the fact that the statistical distribution of the nonzero components in the same in all directions around the origin. Local correlation and homogeneity (i.e., missing high- and low-frequency components) will lead to a bandpass characteristic and consequently to a periodicity with only one predominant frequency.

In the preceding, we have shown that an annular spectrum is *necessary* for modular orientation maps that are homogeneous, isotropic, and locally correlated. Is an annulus spectrum also *sufficient* to produce realistic column structures? To test if this is the case or if more information is hidden in the details of the amplitudes or phases of the spectra of orientation column structures, we performed an inverse Fourier transform of simple annulus spectra (Fig. 2C), which have zero amplitudes everywhere except on an annulus of radius $\approx 2\pi/\lambda$. On this annulus, the amplitude has random values and the phases were either all set to zero

Figure 2: *Facing page*. Analysis of observed orientation preference map of monkey (A,B) and synthesis of model map (C,D). (A) Map of preferred orientations in area 18 of the macaque monkey measured with optical imaging by Blasdel (1992). Color circle for the preferred orientations: 0° = dark blue, 22.5° = purple, 45° = red, 67.5° = orange, 90° = yellow, 112.5° = green, 135° = light blue, 157.5° = sky blue, 180° = dark blue. (B) Power spectrum obtained from (A). Except for a DC component (orange pixel in the center of the annulus) that we attribute to a bias caused by the finite size of the map, the spectrum has significant power only on an annulus of a radius given by the inverse period of the preferred orientation in (A). (C) Model power spectrum. The power vanishes everywhere except on an annulus where it takes on random values (uniform distribution). (D) Model map of preferred orientations, color coding as in (A). Defining $F(k_x, k_y)$ as the Fourier transform of the complex angle f (see equation 1.1),

$$F(k_x, k_y) = \int \int dk_x dk_y f(x, y) \exp(-ik_x x) \exp(-ik_y y) \quad (1.7)$$

and from $\tan 2\phi = \text{Im}[f]/\text{Re}[f]$, we can trivially compute the preferred orientations $\phi(x, y)$ as follows:

$$\phi(x, y) = \frac{1}{2} \arctan \frac{\text{Im}[\text{IFT}(F(k_x, k_y))]}{\text{Re}[\text{IFT}(F(k_x, k_y))]} \quad (1.8)$$

In this equation, Re and Im describe the real and imaginary parts of their arguments, and IFT denotes the inverse Fourier transform (i.e., the inverse of equation 1.7). In order to show that the amplitude information presented in (C) is sufficient to generate a realistically looking map, we replace $F(k_x, k_y)$ in equation 1.8 by the square root of the power spectrum in (C), that is, we set all phases identically to zero (similar results were obtained by choosing random phases). The organization of the resulting map, shown partially in (D), is very similar to that of experimentally found maps (e.g., in A).

or to random values (with similar results). In Figure 2D, we show the cortical map that is obtained from this spectrum by a standard procedure (Swindale 1985) and that shows a striking resemblance to experimentally observed maps.

Furthermore, we found that this scheme is very robust: we obtain realistically looking maps for a wide range of variations in amplitudes, phases, and the width of the annulus, which can be varied by about a factor of 10 without significant disturbance of the maps. We also varied the form of the annular probabilistic distribution and found that artificial maps generated with an annulus constructed as a difference of gaussians (as in equation 1.6) yield realistic maps, as do annuli that are generated by a distribution generated as a gaussian whose mean value is the annulus radius and “rectangular” annuli with sharp borders as the one shown in Figure 2C. This robustness might explain why so many different developmental models are capable of producing “good-looking” maps: this is expected as long as their “products” (the maps they generate) are consistent with the basic properties of local correlation, homogeneity, modularity, and isotropy. Note, however, that in this study we are not concerned with the properties of developmental models but only with the properties of maps.

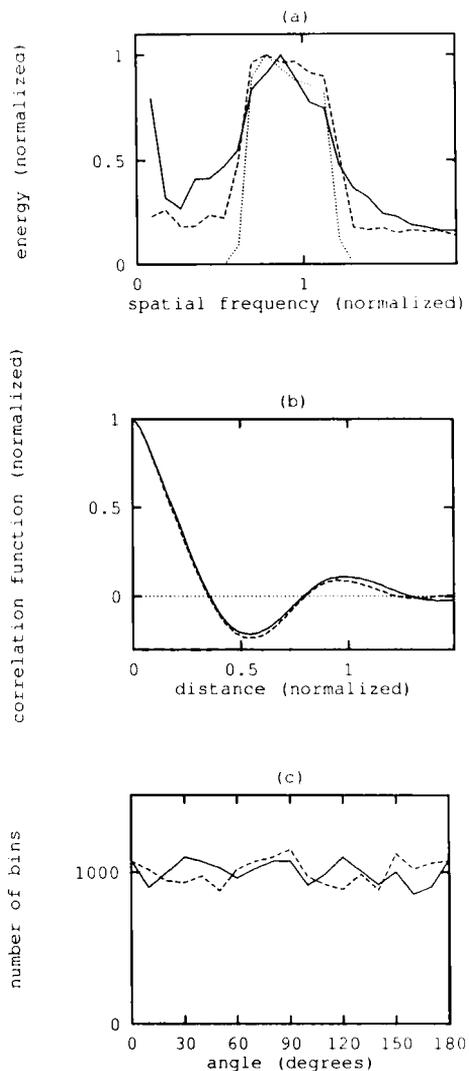
Nevertheless, care has to be taken to avoid the introduction of artifacts in this procedure. Rojer and Schwartz (1990) obtained orientation columns by bandpass-filtering two-dimensional noise. This procedure is mathematically equivalent to our Fourier transformation of a noisy annulus. Their method differs, however, from ours in the next step. Since preferred orientation is a vectorial quantity, they then differentiated the output of the bandpass filter and interpreted the obtained gradient as a vector field representing the map of preferred orientations. The obtained maps share many properties with measured orientation column maps: cells with similar orientation preference are clustered together and the maps have singularities as well as fractures. Closer inspection (Erwin *et al.* 1993) reveals, however, that the thus generated maps differ from experimentally observed data. For instance, certain types of physiologically quite frequently observed singularities can never occur in these maps. While loop singularities (“hairpin bend” shaped) with the opening to the left or right can occur, the same singularity cannot be obtained if they are turned by 90° , for example, if they have the opening to the top. Erwin *et al.* (1993) show that this deficiency is due to the fact that a gradient field is conservative which limits the class of patterns that can be generated when using gradient fields. The described singularity (loop open at top) would require a vector field with nonvanishing curl that is not conservative and can therefore never be obtained as the gradient of a scalar field. Experimentally observed orientation maps do not have this restriction and neither do the maps generated from annulus spectra by the procedure introduced by Swindale (1982) and used in this work (see caption of Fig. 2D).

Unfortunately, no complete scheme has yet been found for a quantitative characterization of cortical orientation maps. A first attempt toward the development of such a "fingerprint" has been made by Obermayer *et al.* (1992) who compared orientation and ocular dominance maps obtained from optical imaging data with maps generated from self-organizing feature maps. We have applied their methods to show that our simple model achieves quantitative agreement with experimental data. The power spectra of experimental and artificial maps are shown in Figure 3a, the circular autocorrelation function of the maps in Figure 3b, and the distribution of the orientations of the maps in Figure 3c. By all three³ measures, the model maps generated with our simple procedure are strikingly similar to experimentally obtained maps. Furthermore, we counted the density of singularities in the measured map and in the artificial map and found very similar values (3.3 singularities per squared hypercolumn length λ^2 in the real map and 3.4 in the artificial map).

Homogeneity, local correlation, and isotropy are properties of natural images (Field 1987), that is, properties of the input to the visual system, and it might be advantageous for an information-processing system if its structure reflects the properties of the input signals. For instance, if the incoming signals are, on average, homogeneous (no systematic variation across the visual field), similar signals have to be treated in all parts of the cortical representation of the visual field. It is therefore plausible that similar structures are to be found in different parts of the topographic map. Two remarks are in order here: (1) Neither the visual input (Switkes *et al.* 1978) nor the human visual system (Mitchell *et al.* 1967) are *completely* isotropic, and similar statements are probably true for homogeneity and local correlation. Our results should rather be taken as a general framework for leading-order effects than as a detailed model for particular features. (2) We neglect distortions by the "complex-logarithm transformation" of visual images that emphasizes the foveal region with respect to the periphery (Schwartz 1977).

Independent of the properties of visual input, one expects homogeneity to be a useful feature in any parallel system, since it allows replication of one module many times for parallel information treatment. Local correlation is found in all cortical areas reflecting the tendency of neurons to work in an environment in which they are surrounded by other neurons whose properties vary in a smooth, orderly manner (Legendy 1978). There seem to be less compelling reasons for strict isotropy except from conceptual and developmental simplicity, and, indeed, this property is not always found in perfect form. Ocular dominance columns in monkey and orientation columns in cat are better described by an anisotropic spectrum (Obermayer *et al.* 1991; Rojer and Schwartz 1990). It is possible

³Obermayer *et al.* (1992) introduced a fourth measure that characterized the interaction between orientation columns and ocular dominance columns. Since we do not model binocularity, this is not applicable to our maps.



that interactions between sensory features (like ocularity and orientation) induce corresponding interactions between the feature maps, which allow only one of these maps to be described by these simple principles.

Figure 3: *Facing page*. Statistical analysis of the real and artificial maps and spectra shown in Figure 2. (a) Normalized distribution of the energy of the spectra Figure 2B,C as a function of the radial spatial frequency. The DC component (i.e., at radius = 0) is omitted. The solid line belongs to the spectrum obtained from the experimentally measured map. The dotted line is directly computed from the annulus using the formula: $energy = \sqrt{(Re^2 + Im^2)}$, while the dashed line results from Fourier analysis of the artificial map Figure 2A. Note the significant background "noise" in the spectra, which is introduced by the numerical Fourier analysis. Due to the finite size of the map, most frequencies are not integer multiples of the map size and therefore do not correspond to sharp peaks in the spectrum but to rather broad structures. This background is also present in the spectrum of the experimentally determined map and highlights the question about the limits of resolution of Fourier methods applied to cortical maps. (b) Circular autocorrelation as defined in the text for the maps in Figure 2A,D computed and averaged at 500 randomly chosen map locations (solid line, experimental map; dashed line, artificial map). (c) Distribution of the preferred orientations for 18,000 randomly chosen map locations (solid line, experimental map; dashed line, artificial map).

In previous reports we have shown that rather unspecific isotropic connections similar to those observed in cortex (Bonds 1989) can produce complex, anisotropic behavior in cortical cells (Niebur and Wörgötter 1990; Wörgötter *et al.* 1992). The circular connections we used there were embedded in the cortical column structure, which was the major topic of the current study. Here we conclude that the complicated looking column system might be based on only a few design principles and that these very simple principles are sufficient to explain the essential features of the column system. It is certainly an oversimplification to neglect major anatomical details, but it appears that the combination of rather unspecific connections on an unspecifically designed column system could already explain the robustness of the cortical network during development and while suffering from damage. Very little structural information could be at the basis of highly complex performance.

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