Quantifying the variability of patterns of orientation domains in the visual cortex of cats

Matthias Kaschube[a,b,*], Fred Wolf[a], Theo Geisel[a], Siegrid Löwel[b]

[a]*Max-Planck-Institut für Strömungsforschung, D-37073 Göttingen, Germany*
[b]*Leibniz-Institut für Neurobiologie, D-39118 Magdeburg, Germany*

Abstract

In the visual cortex, orientation domains are arranged in complex patterns, assumed to exhibit a high degree of interindividual variability. In the present study, we quantitatively analyzed this variability using 2-deoxyglucose (2-DG) labeled patterns of orientation domains in area 17 of cat visual cortex. We calculated wavelengths, correlation-lengths, anisotropy parameters and band-parallelism parameters within the entire area 17 and analyzed their statistical relationships. All parameters vary considerably among different individuals and appear to be statistically independent. These analyses identify sensitive quantitative indicators for the overall similarity and dissimilarity of cortical orientation maps and confirm their strong interindividual variability. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

It is often assumed that during development the pattern of orientation preferences in the visual cortex emerges spontaneously by activity-dependent self-organization (see e.g. [8,10–13]). Nevertheless, an innate predetermination of the patterns cannot be ruled out at present [4,10]. In principle, an activity-dependent self-organization of orientation preference implies that even in genetically closely related animals the patterns may differ strongly. Thus, the interindividual variability of the patterns [3,5] is expected to provide important information about the role of innate and

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* Correspondence address: Max-Planck-Institut für Strömungsforschung, D-37073 Göttingen, Germany.
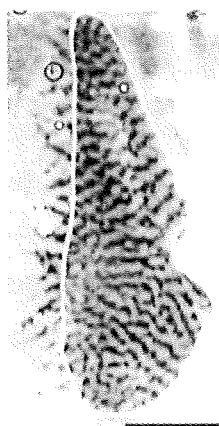
Fig. 1. [^{14}C]2-deoxyglucose (2-DG) labeled orientation domains in area 17 of cat visual cortex. Autoradiographic labeling is coded in gray scale. Dark regions correspond to domains activated by moving whole-field square wave grating stimuli of one orientation. The boundary of area 17 is indicated by the white line. Scale bar, 1 cm.

activity-dependent factors in determining the pattern layout. A necessary prerequisite for evaluating the degree of similarity or dissimilarity between patterns is the quantitative characterization of their overall interindividual variability. In the present study, we quantitatively analyzed the variability of patterns of orientation domains in area 17 of cat visual cortex. Our results identify sensitive quantitative indicators for the overall similarity of cortical orientation maps. In previous studies, the wavelength was used to quantify the variability of orientation patterns [9]. Here we show that the wavelengths vary little compared to other parameters, which appeared to be more appropriate in evaluating the degree of similarity between orientation patterns.

2. Methods

We analyzed patterns of orientation domains activated by moving whole-field square wave grating stimuli of one orientation. The patterns were obtained by [^{14}C]2-deoxyglucose (2-DG) autoradiography of large flat-mounts of visual cortex. Visual cortical flat-mounts were previously prepared from 31 hemispheres of adult cats [5–7]. The 2-DG patterns represent the layout of activated orientation domains within the entire area 17. Fig. 1 shows one example. The autoradiographs were first digitized by scanning them with an effective resolution of 18.9 dots per mm cortex using 256 grey-values per dot. For every autoradiograph a region of interest covering area 17 was defined.

In all investigated hemispheres, the orientation domains form regularly spaced patches exhibiting a preference to be organized in bands. In the center region of the area, the bands are preferentially oriented in parallel to the cortical representation of the horizontal meridian. The precise orientation of the bands is not constant and

varies systematically in different regions within area 17. There are also regions where the patterns appear rather isotropic and lack a band-like organization. We used various methods to analyze global and local properties of the 2-DG patterns: global properties were assessed using correlation functions and power spectra; local properties were assessed by a wavelet analysis.

For every pattern the two-dimensional correlation function

$$C(r) = \langle I(x) I(x + r) \rangle_x$$

was estimated. Here and in the following $I(x)$ represents the normalized autoradiographic labeling as a function of position x within cortex and $\langle \cdot \rangle_x$ denotes averaging over the entire area 17. For every pattern the correlation-length λ was estimated by fitting a model function

$$c_M(r) = \cos(2\pi r / \Lambda) \exp(- r/\lambda)$$

to the measured correlation function in the direction maximizing λ. The correlation-length λ measures the average regularity of the pattern: λ is proportional to the range over which the positioning of domains can be predicted statistically. We also calculated the power spectra

$$P(k) = \hat{C}(k),$$

where $\hat{C}$ denotes the Fourier transform of C. From P we estimated the wavelength Λ:

$$\Lambda = 2\pi \left(\frac{\int_0^\infty dk\, k \int_0^{2\pi} d\theta\, P(k, \theta)}{\int_0^\infty dk \int_0^{2\pi} d\theta\, P(k, \theta)} \right)^{-1}.$$

The wavelength Λ measures the average distance of adjacent domains preferring similar orientations.

To analyze local properties, a two-dimensional continuous wavelet transform [1,2] was calculated for every pattern. This transform is given by

$$\tilde{I}(l, x, \theta) = \int_{\mathbb{R}^2} I(x') \psi^*_{lx\theta}(x')\, d^2x',$$

where $x, x' \in \mathbb{R}^2$, x is the position of the wavelet $\psi_{lx\theta}$ in cortical coordinates, $l \in \mathbb{R}_+$ is its scale and $\theta \in [0, \pi)$ is its orientation. $\psi_{lx\theta}$ is defined through a mother wavelet $\psi(x')$ by

$$\psi_{lx\theta}(x') = \frac{1}{l} \psi\left(\Omega^{-1}(\theta) \frac{x' - x}{l} \right)$$

with $\Omega(\theta)$ being the rotation matrix. For $\psi(x')$ to be an admissible mother wavelet it is required that

$$\int_{\mathbb{R}^2} \psi(x')\, d^2x' = 0.$$

The anisotropy of the pattern suggests the choice of an anisotropic wavelet. We therefore used the anisotropic normalized Morlet wavelet

$$\psi(x) = e^{ik_\psi \cdot x} e^{-|x|^2/2},$$

where k_ψ determines the number of oscillations within the Gaussian envelope. From the coefficients $\tilde{I}(l, x, \theta)$ we calculated a local scale parameter $\bar{l}(x)$ defined as the mean value of l over the energy distribution:

$$\bar{l}(x) = \frac{\int_0^\pi d\theta \int_0^\infty dl \, |\tilde{I}(l, x, \theta)|^2 / l^3 \, l}{\int_0^\pi d\theta \int_0^\infty dl \, |\tilde{I}(l, x, \theta)|^2 / l^3},$$

with $|\tilde{I}(l, x, \theta)|^2 / l^3$ being the space-scale energy density. $\bar{l}(x)$ is the dominant scale at x. It therefore determines the wavelength $\Lambda(x)$ by

$$\Lambda(x) = \bar{l}(x) \Lambda_\psi,$$

where Λ_ψ denotes the mean wavelength of the mother wavelet ψ.

Based on the dominant scale we further calculated the anisotropy parameter

$$s'(x) = \frac{\int_0^\pi d\theta |\tilde{I}(x, \theta)|^2 \, e^{i2\theta}}{\int_0^\pi d\theta |\tilde{I}(x, \theta)|^2},$$

where the dependence of the dominant scale is being suppressed. The factor 2 in the exponent is due to the 180° symmetry of the wavelet $\psi(x)$. The phase of the complex number $s'(x) = |s'(x)| e^{i2\phi(x)}$, $\phi(x)$, gives the orientation perpendicular to the bands. Its modulus $|s'(x)|$ is a measure for the anisotropy of the pattern. For an isotropic pattern $|s'(x)|$ is close to 0, while for a band-like anisotropic structure $|s'(x)|$ is significantly larger than 0.

Moreover, regions of high $|s'(x)|$ that exhibit rapid variation in $\phi(x)$ should also be seen as being isotropic. To account for that s' was smoothed according to

$$s(x) = K(x) * s'(x)$$

with K being the window $K(x) = \cos^2(\pi/2R)(|x|)$ for $|x| < R$ and $K(x) = 0$ else. The radius R of the filter was typically taken as twice the overall wavelength Λ.

From $s(x)$ we calculated the mean anisotropy of the pattern

$$\alpha = \langle |s(x)| \rangle_x$$

and the band parallelism

$$\nu = \frac{|\langle s(x) \rangle_x|}{\alpha}.$$

3. Results

3.1. Global properties of orientation domains

In the visual cortex of cats, the pattern of orientation domains is not isotropic, its anisotropy and the overall variability of the pattern layout can be quantified by correlation functions and power spectra as defined above.

The correlation functions $C(r)$ were generally anisotropic with the largest correlations occurring parallel to the cortical representation of the vertical meridian. Fig. 2
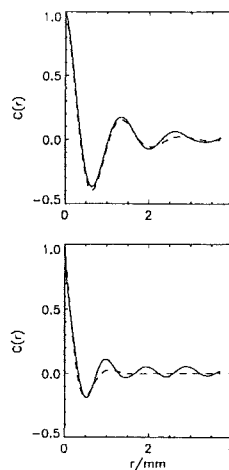
Fig. 2. Correlation functions $C(r)$ for two 2-DG patterns. The solid lines represent the calculated functions; the broken lines represent the fitted functions.
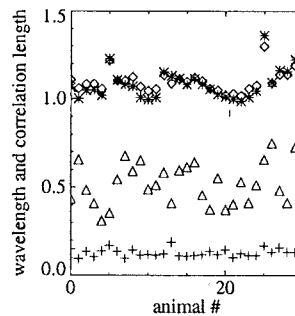

Fig. 3. Correlation length λ and wavelength Λ for the 31 investigated patterns. Wavelengths derived from power spectra are represented by diamonds. Wavelengths derived from wavelet transform are represented by the stars. Both methods lead to similar results. Standard deviations of the local wavelengths $\Lambda(x)$ are given by crosses. Standard deviations appear to be lower than 0.2 mm. Correlation lengths are represented by triangles.

shows two typical correlation functions, taken as slices of $C(r)$ in the direction of the smallest overall wavelength. The solid lines represent the measured correlation $C(r)$, while the broken lines represent the fitted function $c_M(r)$. Positive peaks at 1Λ, 2Λ and 3Λ are present in the correlation function.

Fig. 3 shows the wavelengths and their corresponding correlation lengths for all analyzed patterns. Wavelength and correlation length varied considerably among the patterns. The wavelengths were distributed homogeneously between 1.0 and 1.3 mm. The correlation lengths were distributed homogeneously between 0.3 and 0.8 mm.
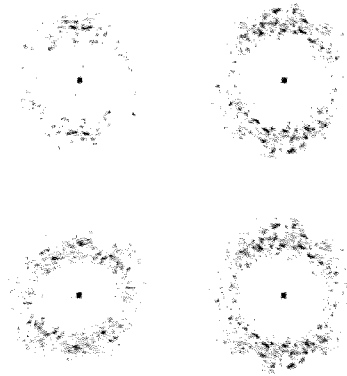
Fig. 4. Typical power spectra P(k) calculated from four different 2-DG patterns. In each power spectrum, the origin of k-space is represented by a dot in the center of the annulus. Grey values code the magnitude of P(k). Dark patches represent high magnitude.
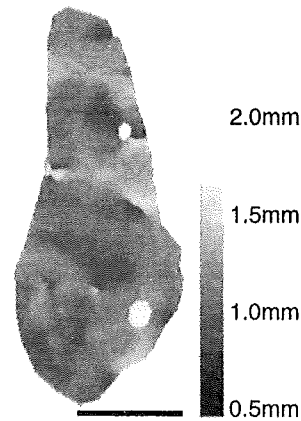

Fig. 5. The pattern of local wavelengths $\Lambda(x)$ of the 2-DG pattern displayed in Fig. 1. Local wavelengths are coded in gray scale. Light regions exhibit larger than average wavelengths. Dark regions exhibit smaller than average wavelengths. Scale bar, 1 cm.

Typical power spectra P(k) are displayed in Fig. 4. The major contributions to the power spectra are confined to an annulus in wave-vector space. Within this annulus the power P(k) depends on the direction of the wave-vector. Typically, the largest values were observed for wave-vectors parallel to the cortical representation of the vertical meridian. The smallest values were observed for wave-vectors parallel to the cortical representation of the horizontal meridian. Therefore, the anisotropy of P(k) reflects the preferred orientation of the bands.
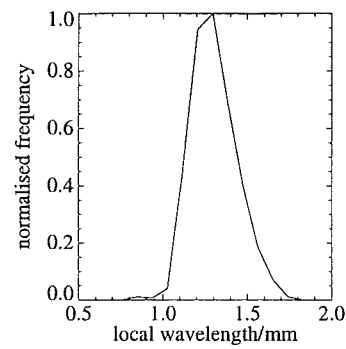
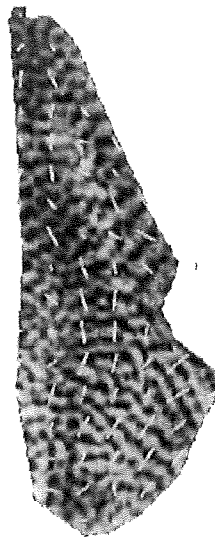Fig. 6. Histogram of the local wavelengths for the 2-DG pattern displayed in Fig. 1.

Fig. 7. Local anisotropy parameter $s(x)$ superimposed on the 2-DG pattern. Scale bar, 1 cm.

3.2. Local properties of orientation domains

The orientation of the band-like 2-DG pattern is not constant across area 17. The spatial structure of this inhomogeneity was quantified by the local anisotropy parameter $s(x)$ defined above. The local wavelength $\Lambda(x)$ was used to demonstrate that the dominant spatial scale of the pattern is rather constant throughout area 17. Fig. 5 shows the pattern of local wavelengths for the 2-DG pattern illustrated in Fig. 1. Bright regions correspond to larger values, dark regions to lower values. $\Lambda(x)$ change smoothly over the area thus exhibiting large regions with similar scales. In the pattern of wavelengths, no overall gradient seemed to be present. The corresponding
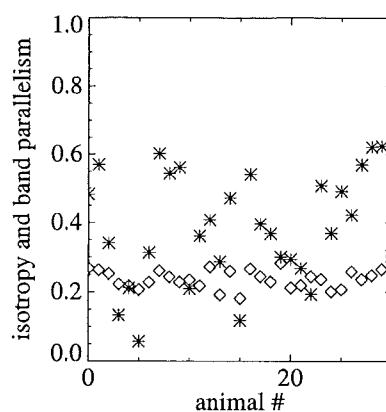
Fig. 8. α and ν for the 31 analyzed patterns. The values of α are represented by the diamonds. ν is represented by the stars. Note that the band parallelism ν varies substantially among different patterns, whereas the mean anisotropy α is rather similar.

histogram showing the distribution of the wavelengths in the same pattern is illustrated in Fig. 6.

Fig. 7 shows the local anisotropy parameter $s(x)$ superimposed on the 2-DG labeled orientation domains. ϕ is indicated by the orientation of the bright bars. The lengths of the bars are proportional to $|s|$. Within large regions of area 17 the bars have similar size and are oriented parallel to each other indicating the band-like structure of orientation domains in these regions. Fig. 8 shows the values of α and ν for all patterns. The anisotropy values were distributed between 0.2 and 0.3. The band parallelism varied strongly taking values between 0.0 and 0.6.

4. Discussion and conclusions

We extracted parameters describing quantitatively the layout of patterns of orientation domains in cat visual cortex. The correlation length λ and the band-parallelism ν varied strongly among the patterns and are therefore likely candidates for sensitive quantitative indicators of similarity and dissimilarity of the patterns. The wavelength Λ and the mean anisotropy α may also be useful in comparing the patterns. All four parameters appear to be statistically *independent*. Furthermore, our results show that the local wavelengths are rather constant across area 17. In contradistinction, the local orientation (with respect to cortical coordinates) of band-like orientation domains varies within area 17, thus defining subregions in which bands exhibit similar orientations. The spatial organization of these subregions may provide a more detailed characterization of the overall layout of the patterns of orientation domains.

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Matthias Kaschube is currently finishing his diploma at the Max-Planck-Institut für Strömungsforschung in Göttingen and at the Leibniz-Institut für Neurobiologie in Magdeburg. He studied physics and philosophy at the Johann–Wolfgang–Goethe University, Frankfurt am Main and at the Georg–August University in Göttingen, Germany. He is interested in nonlinear dynamics of neural systems, the development and plasticity of cortical maps, and the formation of patterns in spatially extended dynamical systems.

Fred Wolf is a postdoc in the Department of Nonlinear Dynamics of the Max-Planck-Institut für Strömungsforschung in Göttingen, Germany. He studied Physics and Neuroscience at the Johann–Wolfgang–Goethe University in Frankfurt am Main, Germany, where he received his Ph.D. in Theoretical Physics. His interests cover the nonlinear dynamics of complex systems and the development and function of visual cortical circuitry. He recently received the Altdorf–Leibniz-Award 1999 for his pioneering work in the theory of visual cortical development.

Theo Geisel is professor of theoretical physics at the University of Göttingen and director of the Max-Planck-Institut für Strömungsforschung. His present research in nonlinear dynamics and neuroscience focuses on chaos and quantum chaos in semiconductor nanostructures and on dynamical aspects of information processing in the brain. He studied physics at the universities of Frankfurt and Regensburg and was a post-doc at the Max-Planck-Institut für Festkörperforschung Stuttgart and the Xerox Palo Alto Research Center. He was Heisenberg fellow (1983–1987) and professor of theoretical physics at the universities of Würzburg (1988–1989) and Frankfurt (1989–1996), where he also was chairman of the Sonderforschungsbereich (SFB) on nonlinear dynamics. He is a recipient of the Leibniz award.

Siegrid Löwel is a research scientist at the Leibniz-Institut für Neurobiologie in Magdeburg, Germany. She is the leader of the independent Research Group "Visual Development and Plasticity" and is teaching at the Faculties for Neurosciences and Medicine at the Otto-von-Guericke-University in Magdeburg. PD Dr. Siegrid Löwel received both her diploma as a biologist and her Ph.D. (Dr.) from the Johann–Wolfgang–Goethe University, Frankfurt am Main, and did postdoctoral work at the Max-Planck-Institut für Hirnforschung in Frankfurt am Main, Germany. In 1995, she received the venia legendi (PD) for zoology. Her main research subject is to study the functional and anatomical consequences of early experience on the brain, in particular the development and plasticity of cortical maps and processing architectures in the visual cortex.