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

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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
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 \( \lambda \) 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 \( \lambda \). The correlation-length \( \lambda \) measures the average regularity of the pattern: \( \lambda \) 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 \( \Lambda \):

\[ \Lambda = 2\pi \left( \frac{1}{k_0^2} \int_0^{2\pi} dk \int_0^{\pi} d\theta P(k, \theta) \right)^{-1}. \]

The wavelength \( \Lambda \) 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

\[ \tilde{T}(l, x, \theta) = \int_{\mathbb{R}^2} I(x') \psi_{l,\theta}^*(x') \, d^2x', \]

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

\[ \psi_{l,\theta}(x') = \frac{1}{l} \psi \left( \Omega^{-1}(\theta) \frac{x' - x}{l} \right) \]

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

\[ \psi(x) = e^{ikx} \cdot e^{-|x|^2/2}, \]
where $k_t$ determines the number of oscillations within the Gaussian envelope. From the coefficients $\tilde{I}(l, x, \theta)$ we calculated a local scale parameter $l_m(x)$ defined as the mean value of $l$ over the energy distribution:

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

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

$$K_t(x) = l_m(x),$$

where $l_m(x)$ denotes the mean wavelength of the mother wavelet $\psi$.

Based on the dominant scale we further calculated the anisotropy parameter

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

where the dependence of the dominant scale is being suppressed. The factor 2 in the exponent is due to the $180^\circ$ 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 $A$.

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

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

and the band parallelism

$$v = \frac{\langle |s(x)| \rangle_x}{z}.$$

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 $\lambda$ and wavelength $\Lambda$ 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 $\Delta(\alpha)$ 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 $1\Lambda$, $2\Lambda$ and $3\Lambda$ 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.
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.
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 shows the values of $\alpha$ and $\nu$ 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 $\lambda$ and the band-parallelism $\nu$ varied strongly among the patterns and are therefore likely candidates for sensitive quantitative indicators of similarity and dissimilarity of the patterns. The wavelength $\lambda$ and the mean anisotropy $\alpha$ 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.
References


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