Sequential bifurcation of orientation– and ocular dominance maps

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Abstract: *In the visual cortex of mammals, information is processed by an array of columnar modules. The layout of these columns constitutes a complex spatial pattern, which is supposed to arise due to Hebb–type self–organization during early life. The layout of columnar patterns differs strongly among species. Here we show that timing and dynamic rearrangement due to Hebb–type self–organization explains the different appearance of ocular dominance and orientation columns in cat and monkey striate cortex. In particular, we demonstrate that the refinement of intracortical and afferent connections during development triggers a series of bifurcations, in which different columnar systems emerge in a sequence proceeding from larger to smaller spatial length scales. Numerical simulations show that these predicted differences in timing of cortical pattern formation result in different spatial layouts, that are in excellent agreement with experimental observations.*

1 Introduction

In this contribution, we use a feature space model for the development of cortical maps to investigate mechanisms and processes underlying the different appearance of ocular dominance and orientation maps in primary visual cortex of cats and monkeys.

Cortical maps obtained from monkey striate cortex reveal a highly regular pattern of ocular dominance (OD) columns. OD–columns form parallel bands of regular spacing with relatively few branching points. These bands are mainly oriented perpendicular to area boundaries [8]. This is in sharp contrast to the spatial organization of ocular dominance domains in cat visual cortex. Here, the OD–columns form an array of beaded bands exhibiting only a small tendency of elongation orthogonal to area boundaries [11, 1]. A second interspecies difference concerns the wavelength of the different columnar systems. In macaque monkeys, the average wavelength of iso–orientation domains is smaller than that of ocular dominance columns. This relation is reversed in cats, where the average wavelength of iso–orientation domains is larger than that of ocular dominance columns. Most interestingly in cat area 17, the pattern of orientation columns is rather regular and possesses a globally detectable orientation bias [10].

These differences are explained in a simple model for the development of cortical maps: We determine the conditions for the spontaneous formation of columnar patterns and calculate their expected wavelength. Based on biological evidence on the development of intracortical and afferent connectivity we propose a sequential bifurcation scenario that predicts the primary emergence of the columnar system exhibiting the larger wavelength followed by the one characterized by the smaller wavelength. We show that the predicted differences in timing give an explanation for the different spatial layout of the ocular dominance pattern in cat compared to monkey visual cortex.

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2 The Model

We investigate the dynamics

$$\frac{\partial}{\partial t}\mathbf{R}(\mathbf{x}) = \int_{\mathcal{S}} d^5S\ \rho(\mathbf{S})\ [\mathbf{S}-\mathbf{R}(\mathbf{x})]\ \frac{\exp\left(-[\mathbf{S}-\mathbf{R}(\mathbf{x})]^2/2\sigma^2\right)}{\int_{\mathcal{C}} d^2y\ \exp\left(-[\mathbf{S}-\mathbf{R}(\mathbf{y})]^2/2\sigma^2\right)}\ +\ \eta\Delta\mathbf{R}(\mathbf{x}) \tag{1}$$

where $\mathbf{R}(\mathbf{x}) = \left[R_x(\mathbf{x}),\, R_y(\mathbf{x}),\, r\cos(2\phi(\mathbf{x})),\, r\sin(2\phi(\mathbf{x})),\, o(\mathbf{x})\right]$ denotes the vector representation of the receptive field parameters: retinotopic position (R_x, R_y), orientation selectivity (r), preferred orientation (ϕ) and ocular dominance (o) as a function of the cortical position $\mathbf{x}$, Δ is a the 2d laplacian and $\mathcal{S}$ is a domain in R^5. This is a continuous description of the elastic net algorithm that has previously been used to model the spatial layout of ocular dominance and orientation preference columns ([5], for a critical review see [6]).
Within this model the parameter σ measures the size of a cortical excitation patch evoced by an individual stimulus.

2.1 Instabilities Leading to the Emergence of Columnar Patterns

The space–time continuous description (1) enables the analysis of the mechanisms of cortical pattern formation implicit in the above model and fascilitates the interpretation and use of the model as a dynamics of columnar patterns. Equation (1) exhibits a particular simple stationary state $\mathbf{R}_0(\mathbf{x}) = (x_1,\, x_2,\, 0,\, 0,\, 0)$ in which no columnar organization is present. All units are binocular and exhibit no orientation tuning. Whether a columnar pattern forms spontaneously from this state depends on the stability of this state with respect to spatially periodic deviations $\boldsymbol{\delta}(\mathbf{x}) = \mathbf{R}(\mathbf{x}) - \mathbf{R}_0(\mathbf{x})$. Functional taylor expansion of the right hand side of (1) — after dropping all nonlinear terms — leads to

$$\frac{\partial}{\partial t}\delta_i(\mathbf{x}) = -\delta_i(\mathbf{x}) + \frac{\langle S_i^2\rangle}{\sigma^2}\delta_i(\mathbf{x}) - \frac{\langle S_i^2\rangle}{2\pi\sigma^2}\int_{\mathbb{R}^2} d^2y\ e^{-\frac{(\mathbf{x}-\mathbf{y})^2}{4\sigma^2}}\,\delta_i(\mathbf{y})\ +\ \eta\Delta\delta_i(\mathbf{x}) \tag{2}$$

for the ocular dominance and orientation preference components.
It should be noted that only the variances of the stimulus density $\langle S_i^2\rangle$ enter the stability problem. The convolution operators on the right hand side are diagonal in Fourier representation. We consider only the columnar dimensions $(i = 3, 4, 5)$, and obtain

$$\frac{\partial}{\partial t}\tilde{\delta}_i(\mathbf{k}) = \left(-1 + \frac{\langle S_i^2\rangle}{\sigma^2} - \frac{\langle S_i^2\rangle}{\sigma^2}\,e^{-k^2\sigma^2} - \eta k^2\right)\tilde{\delta}_i(\mathbf{k}) = \lambda_i(k)\ \tilde{\delta}_i(\mathbf{k}) \tag{3}$$

The eigenvalues $\lambda_i(k)$ determine the stability of a deviation with wave number $k = |\mathbf{k}|$ and wavelength $\Lambda = 2\pi/k$. If $\lambda_i(k)$ is negative, the homogeneous state is stable with respect to deviations of wave number k. If $\lambda_i(k)$ is positive a deviation from the homogeneous state will grow exponentially leading to the spontaneous emergence of a columnar pattern. As $\lambda_i(k)$ has a single maximum at $k_{max} = \frac{1}{\sigma}\sqrt{\ln(\langle S_i^2\rangle/\eta)}$ (Fig.1a), the wavelength of the emerging structure is proportional to the range of cooperation σ. The maximum is positive for any $\sigma < \sigma^*$ where $\sigma^* = \sqrt{\langle S_i^2\rangle - \eta - \eta\ln(\langle S_i^2\rangle/\eta)}$
Fig.1b) shows the phase diagram of the system. For any smoothness parameter $\eta < \langle S_i^2\rangle$ exists a critical cooperation range σ^* at which the system undergoes a transition from the homogeneous state to a columnar pattern. The wave number of the structure that emerges at this transition for given η is a function of the variance $\langle S_i^2\rangle$.

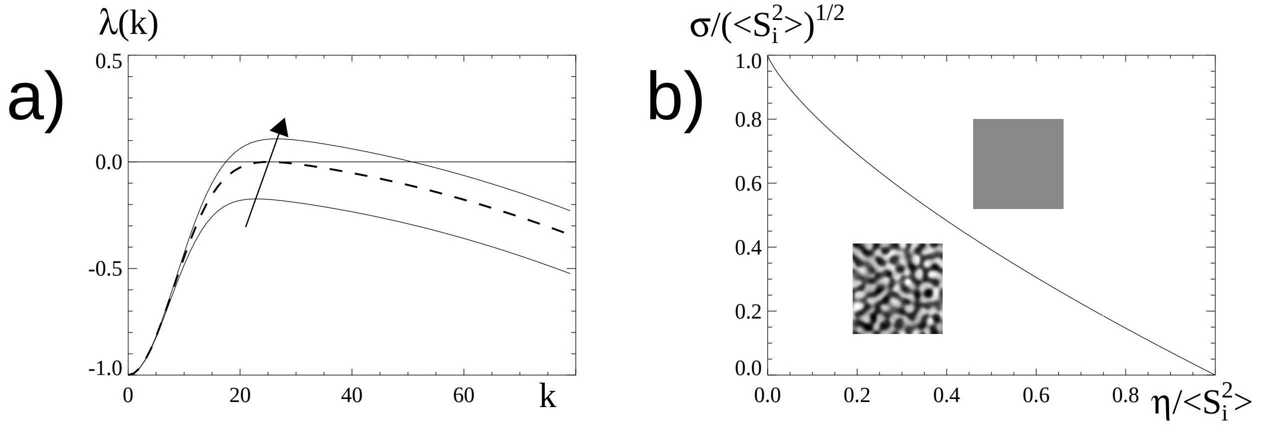

Figure 1: **a)** Eigenvalue–spectrum $\lambda(k)$ of the dynamics (1) for different values of σ. (Arrow marks the direction of decreasing σ.) Dashed line is drawn for $\sigma = \sigma^*$ **b)** Phasediagram of the model: The line indicates the transition from the homogenous to the inhomogenuous solution of the model. To obtain columnar patterns, the parameters σ and η have to be chosen in the region below the curve.

$$k^* = \sqrt{\frac{\ln(\langle S_i^2\rangle /\eta)}{\langle S_i^2\rangle - \eta - \eta \ln(\langle S_i^2\rangle /\eta)}} \tag{4}$$

We use the latter fact to chose the parameters $\langle S_i^2\rangle$ of the dynamics (1) such that a columnar pattern exhibiting a given set of wavelengths emerges. However, this property rests on rather general and biologically plausible assumptions about the time course of the control parameter σ.

3 A Sequential Bifurcation Scenario

The above analysis shows that columns form only if the range of cooperation σ is smaller than the critical values defined by the variances of the stimulus density in the respective feature space dimensions. As the length scale of the emerging columnar pattern is proportional to the range of cooperation σ, the size of a column is determined by the size of a localized excitation patch in the system. In the biologcal system, this size, namely the range of cortical cooperation, cannot be considered to be constant during development. Instead the size of a typical localized excitation in the visual cortex is presumably determined by two factors: the range of lateral intracortical connections and the size of the axonal arbors of afferent LGN neurons. Evidence from different lines of investigation suggests that both these quantities and consequently the range of cortical cooperation decrease during the maturation of cortical circuitry (see among others: [7],[3],[4]).

Given the above analysis we predict the consequences of assuming a continuously shrinking range of cortical cooperation in the model (1): as σ decreases it sequentially passes the different critical values associated with the different columnar patterns (see Fig.2). At any σ^*, this will trigger the emergence of a new columnar pattern starting with the system exhibiting the largest wavelength and followed by the system characterized by the smaller length scale. Consequently, this behaviour translates the length scales of columnar patterns (4) into a temporal sequence of instabilities, the sequential bifurcation scenario. The sequential bifurcation scenario provides a particularly simple and elegant solution for the problem of different length scales. Thus it is important to note that this scenario depends only on three very general properties of the dynamics (1):

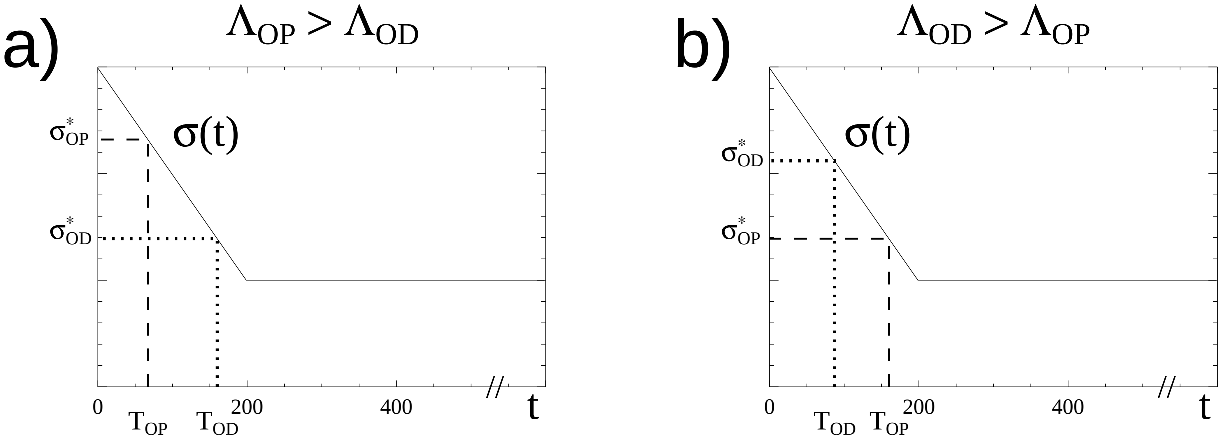

Figure 2: Sketches of the time-development of the model parameter σ used during simulations of **a)** cat–comparable maps (the orientation pattern emerges first and therefore has the larger spaceconstant) **b)** monkey–comparable maps (the ocular dominance pattern emerges first and therefore has the larger spaceconstant)

(a) The range of cortical cooperation determines the length scale of the columnar pattern emerging at a given time.

(b) The range of cortical cooperation decreases during development.

(c) The existence of a critical range of cortical cooperation above which the homogeneous state is stable and columnar patterns do not form.

Any dynamics that satisfies (a)–(c) will exhibit a sequential bifurcation of columnar pattern characterized by different length scales. Equation (1) should be considered as just one example within this much wider class of models.

The sequential bifurcation scenario implies that in cat striate cortex, the pattern of orientation preference should emerge first followed by the pattern of ocular dominance. In macaque monkey striate cortex, ocular dominance is predicted to develop before the pattern of orientation preference emerges. In monkeys, both systems seem to be present at birth [2], so that little can be said about the temporal ordering of their emergence. However in cat visual cortex orientation selective neurons have indeed been reported to be present very early in development [13], while ocular dominance columns are known to emerge between postnatal weeks 3 and 7 (see [9]).

3.1 Dynamic Rearrangement of Columnar Patterns

We now show that the above proposed sequential bifurcation scenario does not only explain the different length scales, but also explains the different layouts of visual cortical maps in cat and monkey. The most prominent difference between cat and monkey striate cortex is the different spatial organization of ocular dominance columns in the two species. The OD–pattern in cat visual cortex has a beaded appearance, while the same pattern in monkey striate cortex exhibits a high degree of paralellness. Here, the pattern also shows a globally predominant orientation, that is nearly absent in the pattern of the cat.

For principle reasons it is not possible for any patternforming instability of a local dynamics to instantaneously produce the degree of spatial coherence exhibited by the OD–columns in monkeys from a homogeneuos state [12]. Therefore we investigated the conditions under which the pattern of OD–columns reorganizes according to the dynamics (1) into a system of

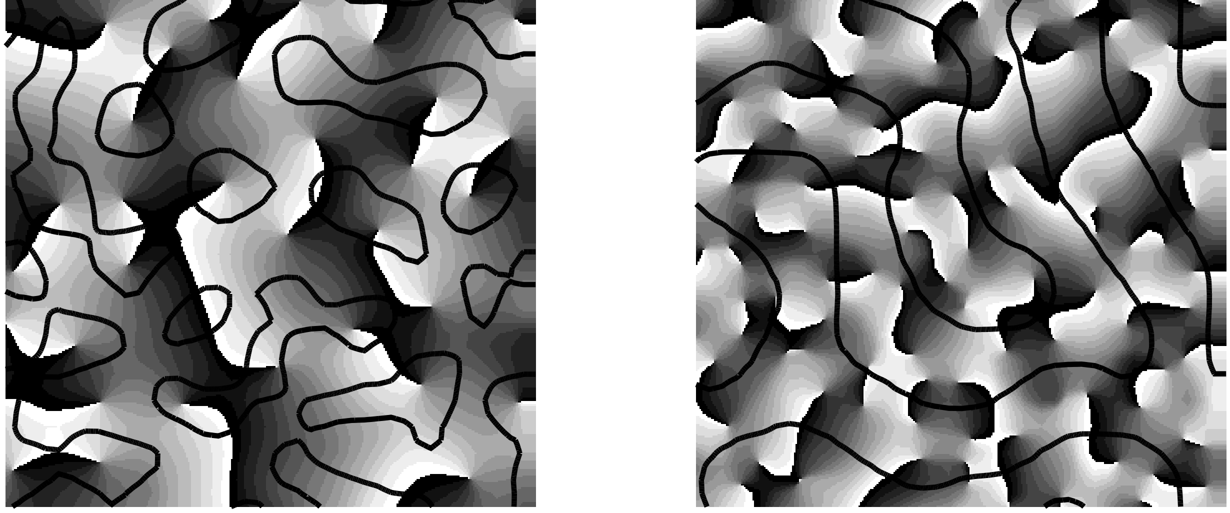

Figure 3: Predicted functional layouts of ocular dominance and iso–orientation domains in visual cortex of cat (left, corresponds to the scenario shown in Fig.2a) and monkey (right, corresponds to the scenario shown in Fig.2b). Iso–orientation domains are shown in greyscale, contours represent borders of ocular dominance columns.

parallel stripes. Two conditions are essential: i) The presence of areal borders that enforce a globally predominant axis of orientation on ocular dominance stripes and ii) the absence of iso–orientation domains during the rearrangement of the ocular dominance pattern.

Under these conditions, the pattern which starts as an array of beaded bands reorganizes to form parallel stripes (contours in Fig.3., right side). In the presence of a primarily established orientation preference pattern, the emerging ocular dominance columns rearrange to match the condition that iso–orientation domains should intersect ocular dominance borders at right angles [14]. Most importantly, this process prevents their rearrangement into a system of parallel ocular dominance stripes (contours in Fig.3, left side).

4 Conclusions

We conclude that dynamic rearrangement and interaction of iso–orientation and ocular dominance domains provide a new explanation for the different appearance of cortical maps in cats and monkeys. Due to these interactions *timing* becomes a key factor in determining the resulting layout of cortical maps. Whereas the highly coherent pattern of OD–columns in mokeys can be explained through dynamic rearrangement in absence of the orientation map, the 'beaded' appearence of OD–columns in cat area 17 can be explained if ocular dominance columns are 'bound' to the already established system of iso-orientation domains, and as a consequence cannot rearrange into a globally ordered pattern.

Based on the above results we summarize that the idea of dynamic rearrangement and interaction of columnar patterns during development provides powerful insights into the principles shaping cortical maps in different animals. Chronic optical imaging in individual animals during development will enable one to probe these mechanisms in the living brain.

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