SEQUENTIAL BIFURCATION AND DYNAMIC REARRANGEMENT OF COLUMNAR PATTERNS DURING CORTICAL DEVELOPMENT

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Abstract

We use a feature space model to show that timing and dynamic rearrangement due to Hebb–type self–organization can account for the different appearance of ocular dominance and orientation columns in cat and monkey visual cortex. Based on analytical results and biological evidence we propose 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. Our numerical simulations reveal that these predicted differences in timing of cortical pattern formation result in different spatial layouts, that are in excellent agreement with experimental observations.

Introduction

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 [1]. This is in sharp contrast to the

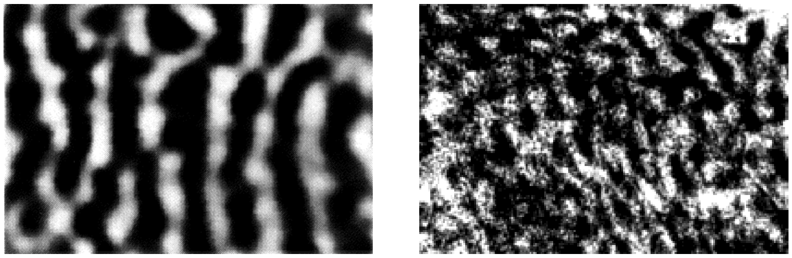

Figure 1: **Left:** OD–pattern from an adult macaque obtained by optical imaging of intrinsic signals (from [6]), **Right:** OD–pattern from an adult cat obtained by [^{3}H] proline autoradiography (from [7])

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 (see [2, 3], fig. 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[4]. 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 [5].
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.

METHODS AND RESULTS

We investigate the dynamics

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

where $\mathbf{R}(\mathbf{x})$ is the vector representation of the receptive field parameters: retinotopic position, orientation selectivity, preferred orientation and ocular dominance as a function of the cortical position $\mathbf{x}$. Dynamics (1) 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 (OP) columns (for a review see [8]).

Within this model, the parameter σ measures the size of a coactivated domain, evoced by an individual stimulus. We have shown [9], that the dynamics (1) depends critically on σ. For both, the OD– and OP–patterns exists an individual critical size of the coactivated domain σ_i^*. Only for σ smaller than σ_i^* the corresponding cortical pattern emerges spontaneously from a homogenous state. The wavelength Λ_i of the respective pattern is determined by the size of the coactivated domain: $\Lambda_i \propto \sigma$. We use the latter fact to chose the parameters of the dynamics (1) such that a columnar pattern exhibiting a given set of wavelengths emerges (see [9]).

A Sequential Bifurcation Scenario

In the biologcal system, the size of the coactivated domain cannot be considered to be constant during development. Instead, the size of a typical localized activation in the visual cortex is presumably determined by two time–dependent 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: [10],[11],[12]).

Concerning the critical sizes σ_i^*, there are generically two cases: (i) $\sigma_{\mathrm{OP}}^* < \sigma_{\mathrm{OD}}^*$ and (ii) $\sigma_{\mathrm{OP}}^* > \sigma_{\mathrm{OD}}^*$. 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. At any σ^*, this will trigger the emergence of a new columnar pattern starting with the system exhibiting the larger wavelength followed by the system characterized by the smaller length scale. Consequently, this behaviour translates the length scales of columnar patterns into a temporal sequence of instabilities, the sequential bifurcation scenario. Thus (i) leads to $\Lambda_{\mathrm{OP}} > \Lambda_{\mathrm{OD}}$ and (ii) leads to $\Lambda_{\mathrm{OP}} < \Lambda_{\mathrm{OD}}$ as observed in cat and monkey respectively.

The sequential bifurcation scenario provides a particularly simple and elegant solution for the problem of different length scales. It is therefore important to note that this scenario depends only on three very general properties of the dynamics (1):

(a) The size of a coactivated domain determines the length scale of the columnar pattern emerging at a given time.

(b) This size decreases during development.

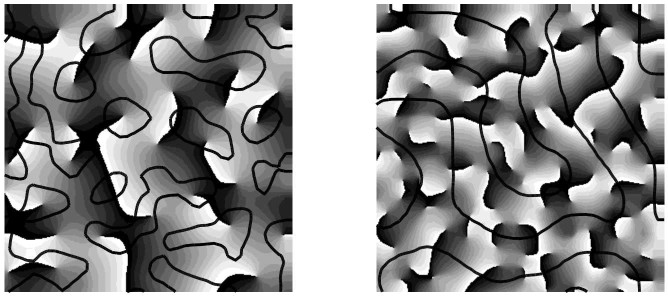

Figure 2: Predicted functional layouts of ocular dominance and iso–orientation domains in visual cortex of cat (left) and monkey (right). Iso–orientation domains are shown in greyscale, contours represent borders of ocular dominance columns.

(c) The existence of a critical size of coactivated domains 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 [13], 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 [14], while ocular dominance columns are known to emerge between postnatal weeks 3 and 7 (see [15]).

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.
To investigate whether the proposed scenario also reproduces the observed spatial layouts, we performed extensive numerical simulations of the dynamics (1). Typical results are shown in fig.2. One of the key factors that determines

the final layout in both cases is the interaction of iso–orientation domains and ocular dominance borders. Most importantly, this interaction prevents their rearrangement into a system of parallel ocular dominance stripes if the OP–map develops first.

In fig. 3 (left) this hypothesis is tested by comparing the development of an initial OD–map in absence and presence of the OP–map. The pattern that does not interact with the pattern of iso–orientation domains rearranges from a initially beaded appearence into a pattern of paralell stripes. This kind of rearrangement is prevented if the OP–map is present. Under these circumstances, both patterns rearrange, so that iso–orientation domains intersect OD–borders at right angels (fig. 3, right)

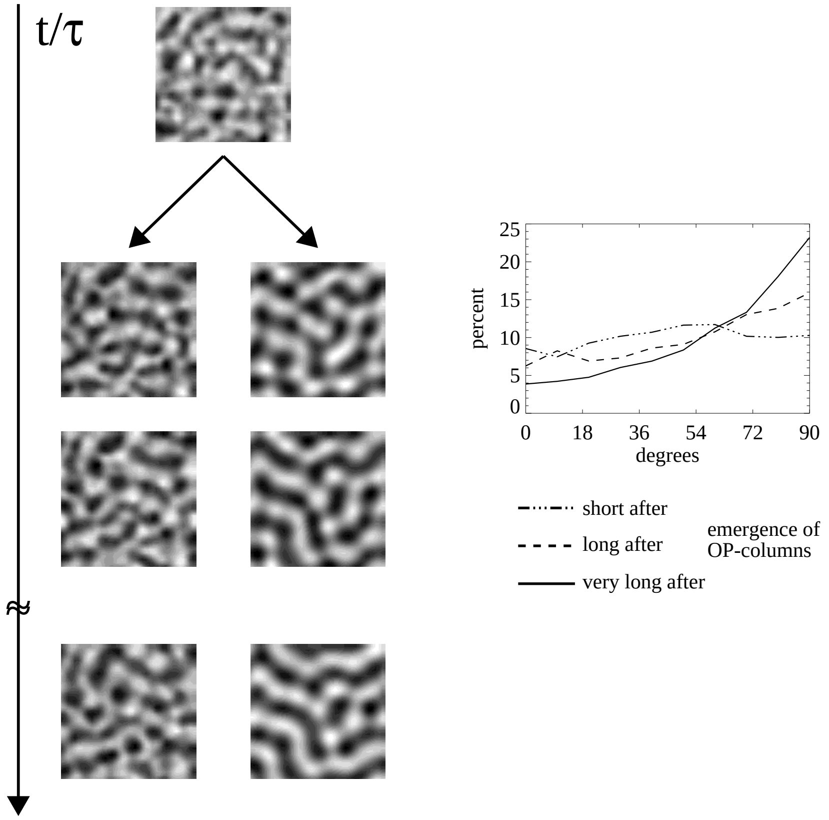

Figure 3: **Left:** Simulated development of an initial OD–map in presence (left panel) and absence (right panel) of the OP–pattern. **Right:** Development of the distribution of the intersection–angles between iso–orientation domains (not shown) and OD–borders (pattern in left panel).

Summary and 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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