Dynamics of Cortical Columns – Self-Organization of Receptive Fields

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Abstract. We present a system of differential equations which abstractly models neural dynamics and synaptic plasticity of a cortical macrocolumn. The equations assume inhibitory coupling between minicolumn activities and Hebbian type synaptic plasticity of afferents to the minicolumns. If input in the form of activity patterns is presented, self-organization of receptive fields (RFs) of the minicolumns is induced. Self-organization is shown to appropriately classify input patterns or to extract basic constituents form input patterns consisting of superpositions of subpatterns. The latter is demonstrated using the bars benchmark test. The dynamics was motivated by the more explicit model suggested in [1] but represents a much compacter, continuous, and easier to analyze dynamic description.

Keywords: cerebral cortex, cortical columns, non-linear dynamics, self-organization, receptive fields

1 Introduction

The minicolumn is believed to be the smallest neural module consisting of roughly a hundred neurons which are stacked orthogonal to the cortical surface. Axons and dendrites of pyramidal cells in the same minicolumn bundle together and are assumed to be strongly interconnected [2,3]. Connectivity of inhibitory cells suggests inhibition between the minicolumns. Minicolumns combine together to what is called a macrocolumn or segregate [4]. Minicolumns of a macrocolumn receive input from the same source, e.g. a patch of the body surface, but in the adult brain they react differently to different types of stimuli, i.e., the minicolumns possess different RFs. At birth afferents to cortical columns are found to be relatively unspecific (see, e.g., [5]). The subsequent specialization is believed to be mainly driven by synaptic plasticity and to crucially depend on sensory input.

In this paper a dynamical system is presented which models the neural dynamics of minicolumn activities in a macrocolumn and the specialization of minicolumnar RFs on the basis of Hebbian plasticity.

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2 Activity of Minicolumns

Instead of explicitly modeling the neural connectivity within a macro- and minicolumn [1] we consider an abstract dynamics of the activity p_{α} of minicolumn α in a macrocolumn of k minicolumns³:

$$\frac{d}{dt} p_{\alpha} = a p_{\alpha} \left(p_{\alpha} - h(\mathbf{p}) - p_{\alpha}^{2} \right) + \kappa I_{\alpha} + \sigma \eta_{t}, \qquad (1)$$

where a is a time constant, κ the coupling strength to external input I_{α} , and where σ^2 is the variance of zero-mean Gaussian white noise⁴ η_t . h is a function of the activities of all k minicolumns of the macrocolumn $\mathbf{p}=(p_1,\ldots,p_k)$. Dynamics (1) is a simple choice for modeling mini- and macrocolumn properties. An abstract derivation of (1) and a non-linear analysis of its dynamical properties can be found in [6]. The different summands on the right-hand-side (rhs) of (1) can be considered as modeling different neuro-dynamical aspects:

- $a\left(p_{\alpha}\right)^{2}$ models self-excitation by excitatory interconnectivity within a minicolumn.
- $-a(p_{\alpha})^3$ models negative feed-back due to neural refraction times which naturally limit the minicolumn activity.
- $-a\,p_{\alpha}\,h(\boldsymbol{p})$ models inhibition by the minicolumns of the macrocolumn. The function $h(\boldsymbol{p})$ is greater than zero. Note that because of the multiplication with p_{α} this term cannot drive the activity to non-biological negative values.

If we choose as inhibition function $h(\boldsymbol{p}) = \nu \max_{\beta=1,\dots,k} \{p_\beta\}$, it can be shown that for zero input and zero noise the system possesses exponentially many stationary points [6]. $\nu \in (0,1)$ plays the role of a bifurcation parameter. For $\nu \in (0,\frac{1}{2})$ there are (3^k-2^k+1) and for $\nu \in (\frac{1}{2},1)$ there are 2^k stationary points. In the point of structural instability, $\frac{1}{2} = \nu_c$, $2^k - k - 1$ non-trivial stable stationary points loose their stability in subcritical bifurcations. Analytical expressions for all stationary points and for their stabilities can be derived [6]. The system qualitatively reproduces the bifurcations observed in the explicit model defined in [1]: if ν is increased from a value $\nu < \frac{1}{2}$ to $\nu > \frac{1}{2}$ and if the macrocolumn has been in its symmetric stable state (all minicolumns are equally active) the minicolumns are deactivated via a process of symmetry breakings⁵ (compare [1]). For non-zero input the symmetry is broken on the basis of small differences between the inputs I_α to the minicolumns. The smallest value of ν for which the deactivation of a minicolumn occurs is a measure for the input strength relative to the other inputs.

³ $p_{\alpha}(t)$ can be thought of as the fraction of neurons in minicolumn α that have spiked during a short fixed time-interval around t.

 $^{^4}$ which is taken to be different for each α

 $^{^5}$ Note that for symmetry breakings infinitesimal perturbations are required, e.g., using a non-zero noise term with very small standard deviation.

3 Self-Organization of Receptive Fields

We operate the system with oscillating inhibitory gain factor ν . An oscillation or ν -cycle starts with a $\nu=0$ interval during which the system stabilizes the symmetric stable stationary state under the influence of noise ($\sigma>0$). Subsequently, ν is increased from a value ν_{\min} to a maximal value ν_{\max} (see Fig. 1).

The input to the minicolumns originates from a set of input units p_1^E to p_N^E ($p_j^E \in [0,1]$) and is mediated by afferent connections $R_{\alpha j}$: $I_{\alpha} = \sum_{j=1}^{N} R_{\alpha j} p_j^E$. The afferent fibers we take to be subject to synaptic plasticity of the form:

$$\frac{d}{dt}R_{\alpha j} = \left(\mathcal{E}\,p_{\alpha}\,p_{j}^{E} - \left(\sum_{l=1}^{N}\mathcal{E}p_{\alpha}\,p_{l}^{E}\right)R_{\alpha j}\right)\,\mathcal{H}(\chi - A(t))\,,\tag{2}$$

where $\mathcal{H}(x)=0$ for $x\leq 0$ and $\mathcal{H}(x)=1$ for x>0 is a step function and where \mathcal{E} is a synaptic growth factor. The positive term on the rhs of (2) models Hebbian type synaptic plasticity. It is only greater than zero if minicolumn α and input unit j are simultaneously active. The negative term insures that $\sum_j R_{\alpha j}$ converges to one for all α . The RFs, $\mathbf{R}_{\alpha}=(R_{\alpha 1},\ldots,R_{\alpha N})$, are only modified if the over-all activity $A(t)=\sum_{\alpha=1}^k p_{\alpha}$ falls below a threshold χ which ensures that learning takes place only after a number of minicolumns have been deactivated.

The system is sketched in Fig. 1 and the complete dynamics now reads:

$$\nu(t) = \begin{cases} 0 & \text{if } \tilde{t} < T_{\text{init}} \\ (\nu_{\text{max}} - \nu_{\text{min}}) \frac{\tilde{t} - T_{\text{init}}}{T - T_{\text{init}}} + \nu_{\text{min}} & \text{if } \tilde{t} \ge T_{\text{init}} \end{cases}, \tag{3}$$

$$\frac{d}{dt}p_{\alpha} = a p_{\alpha} \left(p_{\alpha} - \nu(t) \max_{\beta=1,\dots,k} \{p_{\beta}\} - p_{\alpha}^2 \right) + \kappa \sum_{i=1}^{N} R_{\alpha j} p_j^E + \sigma \eta_t, \quad (4)$$

$$\frac{d}{dt} R_{\alpha j} = \left(\mathcal{E} \, p_{\alpha} \, p_{j}^{E} \, - \, \left(\sum_{l=1}^{N} \mathcal{E} p_{\alpha} \, p_{l}^{E} \right) R_{\alpha j} \right) \, \mathcal{H}(\chi - A(t)) \,, \quad \mathcal{E} \, = \, \frac{\epsilon}{N} \,, \tag{5}$$

where $\tilde{t} = \text{mod}(t, T)$, i.e., $\tilde{t} = t - nT$ where n is the greatest integer satisfying $t - nT \geq 0$. ϵ is the relative synaptic growth factor. Equations (4) and (5) are a system of non-linear differential equations coupled to an oscillation given by (3). In simulations the oscillation is chosen to be slow compared to the dynamics of p_{α} . We study the system behavior by exposing it to different kinds of input. From a given database with different input patterns $P \in [0, 1]^N$ we present a randomly chosen pattern P^o during each ν -cycle, i.e., P^o defines the values of the input units for the duration of a ν -cycle, $p^E = P^o$. An input pattern P is, for visualization purposes, displayed as two-dimensional grey-level image.

Before we can start simulating the dynamics we have to choose a suitable set of parameters. To choose a consider an isolated minicolumn without self-excitation $(\frac{d}{dt}p = -a\,p^3)$. In this case we expect that, e.g., an activity p=1.00 rapidly decays to a value close to zero, e.g. p=0.05, in about 1ms (the order of magnitude of action potentials and refraction times). For the activity levels

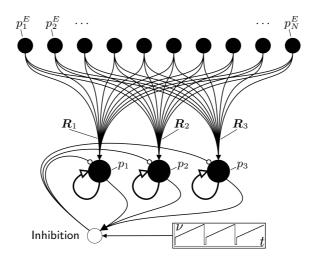


Fig. 1. Sketch of a macrocolumn with k=3 minicolumns. Interactions are indicated using arrows. The inhibition between minicolumns is visualized using a symbolic inhibitory neuron.

 $p(0\mathrm{ms})=1.00$ and $p(1\mathrm{ms})=0.05$ we get $a\approx 200\mathrm{ms}^{-1}$. Note that this is a very coarse estimate due to the arbitrariness in choosing the activities but one obtains the order of magnitude of a. The value of the coupling κ is taken to be only a small fraction of the value for $a, \kappa=1.0\mathrm{ms}^{-1}$, and standard deviation σ of the Gaussian white noise is taken to be only a fraction of κ , $\sigma=0.12\mathrm{ms}^{-1}$. For the oscillation of ν (3) we choose a period length of $T=25\mathrm{ms}$ and a time of $T_{\mathrm{init}}=2\mathrm{ms}$ with $\nu=0$ and additional noise to reset the dynamics. After initialization ν is increased from $\nu_{\mathrm{min}}=0.3$ to a value $\nu_{\mathrm{max}}=0.55$ which is slightly greater than the critical value $\nu_c=0.5$. For the dynamics of Hebbian plasticity (5) we choose $\epsilon=0.2$ and a threshold of $\chi=0.55$.

4 Simulations

Equations (3) to (5) can now be numerically simulated (e.g., using the Euler method for stochastic differential equations). In the first experiment we use the set of 42 input patterns displayed in Fig. 2A (compare [1]). By simulating dynamics (3) to (5) with k=6 and parameters as given above we get RF self-organization as can be observed in Fig. 2B. After random initialization the RFs specialize to different classes of input patterns. If we have fewer minicolumns than major classes exist, we get coarser RFs (see Fig. 2C) and if we have more minicolumns we get RFs with higher specialization degrees (see Fig. 2D).

In the second experiment we use the bars test [7] in order to demonstrate the system's ability of learning a distributed code for input consisting of subpattern superpositions. We operate the system using the same parameters as in

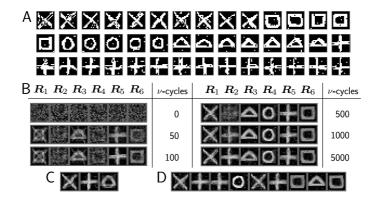


Fig. 2. In A the set of input patterns is displayed ($N=16\times16$). During each ν -cycle one randomly chosen pattern of this set is presented. In **B** the modification of the RFs of a macrocolumn with k=6 minicolumns is displayed. After 1000 ν -cycles six different pattern classes are represented. The RFs' degree of specialization further increases thereafter to a final degree. **C** RF specialization (after 250 ν -cycles) if an abstract macrocolumn with k=3 minicolumns is used with the same input. **D** RF specialization (after 10000 ν -cycles) if a macrocolumn with k=9 is used.

the previous experiment and we use a bars test with b=8 bars. Each bar occurs in an image with probability $\frac{1}{4}$ (see Fig. 3A). As can be seen in Fig. 3B, RF self-organization results in a representation of all bars. In 200 considered simulations with k=10 minicolumns a bars test with above parameters required less than 600 ν -cycles in 50% of the cases to represent all bars (less than 410 in 20% and less than 950 ν -cycles in 80% of the simulations). The system found a correct representation for all bars in all simulations and is robust against various perturbations to the bars test. Note that the results for the bars test show an improvement compared to the explicit system presented in [1] which requires more ν -cycles for the same bars test. Thus dynamics (3) to (5) represent not only an abstraction but, at least in the here discussed bars test, also an improvement of the explicit dynamics in [1] (also compare [8]). Note that already the system presented in [1] has on the basis of extensive measurements shown to be highly competitive to all other systems suggested to solve the bars test.

5 Conclusion

On the basis of recurrent activity in cortical minicolumns, oscillatory inhibitory coupling between the minicolumns, and phase coupled Hebbian synaptic plasticity of afferents we derived a system of coupled differential equations which models self-organization of RFs of cortical minicolumns. Self-organization allows a macrocolumn to represent input using distributed activity of its minicolumns relative to an oscillation. The model combines most often independently dis-

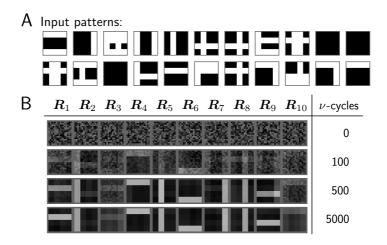


Fig. 3. A A selection of 22 typical input patterns ($N=16\times16$) of a bars test with 8 different four pixel wide bars. B Typical example of the self-organization of the RFs of a macrocolumn with k=10 minicolumns. During each ν -cycle a randomly generated input pattern of the upper type is presented.

cussed aspects of neural information processing and is functionally competitive in a standard benchmark test for feature extraction.

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