Dynamics of Cortical Columns – Sensitive Decision Making

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Abstract. Based on elementary assumptions on the interconnectivity within a cortical macrocolumn we derive a differential equation system which models the mean neural activities of its minicolumns. A stability analysis shows a rich diversity of stationary points and sensitive behavior with respect to a parameter of inhibition. If this parameter is continuously changed, the system shows the same types of bifurcations as the macrocolumn model presented in [1] which is based on explicitly defined interconnectivity and spiking neurons. Due to this behavior the macrocolumn is able to make very sensitive decisions with respect to external input. The decision making process can be used to induce selforganization of receptive fields as is shown in [2].

Keywords: cerebral cortex, cortical columns, non-linear dynamics, stability analysis, bifurcations

1 Introduction

In [1] a model of a cortical neural module called macrocolumn or *segregate* [3] was defined which is based on spiking neurons and columnar interconnectivity. The model showed neuroscientifically desirable properties and far reaching functional capabilities such as high sensitivity to external input and fast reaction times. In this paper we show how a continuous neural dynamics with qualitatively the same properties can be derived from few elementary assumptions about macrocolumnar connectivity.

2 Dynamics of Minicolumn Activities

Motivated by neuroanatomical findings (see, e.g., [4,5] or [6,7] for an overview) we assume a macrocolumn to consist of equal minicolumns and we take each minicolumn to be equally and inhibitorily coupled to the mean activities p_{α} of all minicolumns in the macrocolumn, i.e., we assume the dynamics to be invariant under permutations of minicolumns. An equation system which models such a macrocolumn is given by³:

$$\frac{d}{dt}p_{\alpha} = f(p_{\alpha}, h(\boldsymbol{p})), \quad \alpha = 1, \dots, k, \qquad (1)$$

 $^{^{3}}$ Note that we neglect external input to the minicolumns for the moment.

with functions $f : \mathbb{R} \times \mathbb{R} \to \mathbb{R}$ and $h : \mathbb{R}^k \to \mathbb{R}$. p_α is the mean activity of minicolumn α and h is invariant under all permutations of its arguments $(I = \{1, \ldots, k\})$:

$$\forall \boldsymbol{x} \in \mathbb{R}^k \ \forall \sigma : I \to I \text{ permutations}: \ h(x_1, \dots, x_k) = h(x_{\sigma(1)}, \dots, x_{\sigma(k)}).$$
(2)

The function h models the inhibitory input to a minicolumn, i.e, it models the effect of inhibitory postsynaptic potentials (IPSPs) on currently active neurons of a minicolumn. As explicit inhibitory coupling between the minicolumns we choose motivated by the inhibition function in [1]:

$$h(\boldsymbol{p}) = \nu \max_{\beta=1,\dots,k} \{p_{\beta}\}.$$
(3)

 $\nu \in \mathbb{R}$ is an inhibitory gain factor which will play the role of a bifurcation parameter. Note that (3) satisfies the assumption in $(2)^4$.

Stationary points and stability.

To analyze the dynamic behavior of (1) with (3) we first look for stationary points of the system. Consider the set Q of phase space points for fixed $\nu \in \mathbb{R}$ defined as follows:

$$\begin{array}{l}
\mathcal{P}_{1}^{0} := \max\{q \in \mathbb{R} \mid 0 = f(q, \nu q)\}, \\
\mathcal{P}_{i}^{0} := \max\{q \in \mathbb{R} \mid 0 = f(q, \nu q) \land \forall j < i : q \neq \mathcal{P}_{j}^{0}\}, \\
\mathcal{P}_{i}^{j} := \max\{q \in \mathbb{R} \mid 0 = f(q, \nu \mathcal{P}_{i}^{0}) \land q < \mathcal{P}_{i}^{0} \land (\forall r < j : q \neq \mathcal{P}_{i}^{r})\}, \\
Q_{i} := \{q \in \mathbb{R}^{k} \mid \max_{r \in I}\{q_{r}\} = \mathcal{P}_{i}^{0} \land (\forall r \in I \exists j \in \mathbb{N}_{o} : q_{r} = \mathcal{P}_{i}^{j})\}, \\
Q_{i} := \bigcup_{i} Q_{i},
\end{array}$$

$$(4)$$

where $I = \{1, \ldots, k\}$, $\mathbb{N}_o = \mathbb{N} \cup \{0\}$, $i \in \mathbb{N}$, $j \in \mathbb{N}_o$, and $r \in I$. Note that \mathcal{P}_i^j does not necessarily exist for all j. It can be shown that, for a large class⁵ of functions f, the set Q contains all the stationary points of (1) with (3). An element of Q, e.g. $q \in Q_i$, is of the form:

$$\boldsymbol{q} = \left(\underbrace{\mathcal{P}_{i}^{0}, \dots, \mathcal{P}_{i}^{0}}_{l(\boldsymbol{q})}, \underbrace{\mathcal{P}_{i}^{1}, \dots, \mathcal{P}_{i}^{1}}_{m_{1}(\boldsymbol{q})}, \dots, \underbrace{\mathcal{P}_{i}^{J}, \dots, \mathcal{P}_{i}^{J}}_{m_{J}(\boldsymbol{q})}\right), \quad l(\boldsymbol{q}) + \sum_{j=1}^{J} m_{j}(\boldsymbol{q}) = k, \quad (5)$$

or any permutation. For a given $q \in Q$ a stability analysis results because of the symmetries in (1) with (3) in the following eigenvalues of the Jacobian:

$$\lambda_{1} = \left(\frac{\partial}{\partial x_{1}}f\right)_{\left(\mathcal{P}_{i}^{0},\nu\mathcal{P}_{i}^{0}\right)} + \nu\left(\frac{\partial}{\partial x_{2}}f\right)_{\left(\mathcal{P}_{i}^{0},\nu\mathcal{P}_{i}^{0}\right)} \quad \text{multiplicity } 1 \\ \lambda_{2} = \left(\frac{\partial}{\partial x_{1}}f\right)_{\left(\mathcal{P}_{i}^{0},\nu\mathcal{P}_{i}^{0}\right)} \quad \text{multiplicity } (l(\boldsymbol{q})-1) \\ \lambda_{2+j} = \left(\frac{\partial}{\partial x_{1}}f\right)_{\left(\mathcal{P}_{j}^{j},\nu\mathcal{P}_{i}^{0}\right)} \quad \text{multiplicity } m_{j}(\boldsymbol{q})$$

$$\left. \left. \right\}$$

$$(6)$$

⁴ Note that using suitable coordinate transformation a similar analysis is also possible with a larger class of functions satisfying (2).

 $^{^{5}}$ Essentially f has to be continuous, continuously differentiable, and has to possess a finite number of zero points but weaker assumptions are also possible.

An explicit minicolumn activation function.

We now choose a specific function $f : \mathbb{R} \times \mathbb{R} \to \mathbb{R}$ for dynamics (1). For k = 1we expect (1) to model the activity dynamics of an isolated minicolumn. Selfexcitation due to excitatory connectivity within a minicolumn (see [7] for a review) and bounded activity due to self-inhibition and neural refraction times suggest an activation function $\hat{f}(p) = f(p, \nu p)$ as displayed in Fig. 1. Given very



Fig. 1. Activation function $\hat{f}(p) = f(p, \nu p)$ of an isolated minicolumn.

low activity in a minicolumn without input we expect the activity to decay to zero because of finite neural thresholds. For neural activity above a certain level we expect the activity to increase until neural refractoriness and self-inhibition compensate for self-excitation.

A simple choice for f which is consistent with these expectations and Fig. 1 is given by:

$$f(p_{\alpha}, h(\boldsymbol{p})) = a \, p_{\alpha} \left(p_{\alpha} - h(\boldsymbol{p}) - \Theta - b \, p_{\alpha}^2 \right), \tag{7}$$

where $a, b > 0, \Theta \ge 0$. Note that for k = 1 the function $f(p, \nu p)$ is a polynomial of order 3. A special case is to choose b = 1 and $\Theta = 0$ such that we get the dynamics:

$$\frac{d}{dt}p_{\alpha} = a p_{\alpha} (p_{\alpha} - \nu \max_{\beta=1,\dots,k} \{p_{\beta}\} - p_{\alpha}^2), \text{ where } a > 0, \text{ and } \nu \in [0,1].$$
(8)

Note that the inhibition by other minicolumns cannot drive the activities to non-biological negative values. Other functions $f : \mathbb{R} \times \mathbb{R} \to \mathbb{R}$ are also possible but (7) is especially well analyzable.

For $\nu > \frac{1}{2}$ we get using definitions (4) $\mathcal{P}_1^0 = 1 - \nu$, $\mathcal{P}_2^0 = 0$, $\mathcal{P}_1^1 = 0$. If $\nu < \frac{1}{2}$ we compute $\mathcal{P}_1^1 = \nu$ (instead of zero) and additionally $\mathcal{P}_1^2 = 0$. Thus, for $\nu < \frac{1}{2}$, the stationary points of the system are given by

$$Q_{1} = \{ (\underbrace{\mathcal{P}_{1}^{0}, \dots, \mathcal{P}_{1}^{0}}_{l}, \underbrace{\mathcal{P}_{1}^{1}, \dots, \mathcal{P}_{1}^{1}}_{m_{1}}, \underbrace{0, \dots, 0}_{m_{2}}) \text{ and permutations } | l \ge 1, m_{1,2} \ge 0 \},$$
(9)
$$Q_{2} = \{ (0, \dots, 0) \},$$

and for $\nu > \frac{1}{2}$ by

$$Q_{1} = \{ (\underbrace{\mathcal{P}_{1}^{0}, \dots, \mathcal{P}_{1}^{0}}_{l}, \underbrace{0, \dots, 0}_{m}) \text{ and permutations } | l \ge 1, m \ge 0 \},$$

$$Q_{2} = \{ (0, \dots, 0) \}.$$
(10)

Note that, by applying elementary combinatorics to (9) and (10), we get a number of $(3^k - 2^k + 1)$ stationary points for $\nu < \frac{1}{2}$ and 2^k stationary points for $\nu > \frac{1}{2}$. Using (6) the stabilities of the points in Q_1 and Q_2 are for $\nu < \frac{1}{2}$ given by the eigenvalues (together with their multiplicities):

$$\lambda_{1} = a \left(2(1-\nu)\mathcal{P}_{1}^{0} - 3(\mathcal{P}_{1}^{0})^{2} \right) = -a \left(1-\nu \right)^{2} \quad \text{mult. 1} \\ \lambda_{2} = a \left((2-\nu)\mathcal{P}_{1}^{0} - 3(\mathcal{P}_{1}^{0})^{2} \right) = a \left(1-\nu \right) \left(2\nu - 1 \right) \quad \text{mult. } (l-1) \\ \lambda_{3} = a \left(2\mathcal{P}_{1}^{1} - \nu\mathcal{P}_{1}^{0} - 3(\mathcal{P}_{1}^{1})^{2} \right) = a \nu \left(1-2\nu \right) \quad \text{mult. } m_{1} \\ \lambda_{4} = -a \nu\mathcal{P}_{1}^{0} \qquad = -a \nu \left(1-\nu \right) \quad \text{mult. } m_{2}$$

$$(11)$$

For $\nu > \frac{1}{2}$ we get the same eigenvalues except for λ_3 which does not exist. The stationary point (0, ..., 0) of Q_2 has as only eigenvalue $\lambda = 0$ and it turns out to be unstable with polynomial behavior in the vicinity of (0, ..., 0). Because of (11) we know that, e.g. for k = 2, the set of points $Q^{++} := \{(\mathcal{P}_1^0, 0), (0, \mathcal{P}_1^0)\}$ exists and is stable for all $\nu \in (0, 1)$ and that the stable stationary point $Q^+ := \{(\mathcal{P}_1^0, \mathcal{P}_1^0)\}$ exists for all $\nu \in (0, 1)$ but is only stable for $\nu < \frac{1}{2}$. The set of points in $Q^- := \{(\mathcal{P}_1^0, \mathcal{P}_1^1), (\mathcal{P}_1^1, \mathcal{P}_1^0)\}$ only exists for $\nu < \frac{1}{2}$ and the points are unstable. The stationary points in Q^- define the subcritical branches with respect to Q^+ .

In Fig. 2 we plotted the phase velocity of (8) for k = 2 and two different values of ν . For $\nu < \frac{1}{2}$ we get as non-zero stationary points the three stable points of Q^{++} and Q^+ and the two unstable points of Q^- . If ν is increased to a value greater than $\frac{1}{2}$, the unstable points in Q^- merge with the stable point in Q^+ in the point of structural instability $\nu_c = \frac{1}{2}$ and we get an unstable symmetric stationary point $(\mathcal{P}^0_1, \mathcal{P}^0_1)$ for $\nu > \nu_c$. This dynamic behavior exactly matches the behavior of the macrocolumn model with k = 2 minicolumns as it is described in [1]. For higher dimensions we know because of the multiplicities in (11) that all stationary points in a generalized Q^+ (points in Q^+ have $l(q) \ge 2$) loose their stability for the same value ν_c ($\nu_c = \frac{1}{2}$ in this case). The dynamics, therefore, generalizes to higher dimensions as the macrocolumn dynamics in [1]. Using (9), (10) and (11) it can further be shown that $(2^k - k - 1)$ non-trivial stable stationary points loose their stability in ν_c .

3 Conclusion

We derived a neural dynamics motivated by cortical connectivity. In contrast to [1], in which an explicit connectivity and a time-discrete neuron model was used, we here derived a dynamics from a small set of more abstract assumptions on macrocolumn connectivity. The resulting system of differential equations (8) represents a continuous time version of the difference equation system discussed



Fig. 2. Phase velocities F(p), $F_{\alpha}(p) = f(p_{\alpha}, h(p))$, of dynamics (8). A Phase velocity for $\nu = 0.4 < \nu_c$. Black points mark stationary points as given in (9). B Phase velocity for $\nu = 0.6 > \nu_c$. Black points mark stationary points as given in (10).

in [1]. Dynamics (8) has proven to capture the essential dynamical features of the model in [1], i.e., it spontaneously breaks the symmetry of minicolumn activities if the proportionality factor of inhibition ν is increased. If input to the minicolumns is considered as perturbation of the dynamics, the system breaks the symmetry on the basis of small input differences. Thus, the system is theoretically infinitely sensitive to external input. Using an oscillating ν the dynamics can make sensitive decisions during each oscillation (compare [1]). This behavior is further exploited in [2] where the dynamics is used to enable self-organization of RFs of minicolumns with far reaching computational capabilities.

Compared to the system [1] the dynamics presented in this paper is continuous, more compact and easier to handle than its predecessor. At the same time, it was derived from few assumptions on interconnectivity and is, in a sense, more independent of the concept of minicolumns and macrocolumn, i.e., any neural entities and connectivities giving rise to such an equation system possess equivalent information processing capabilities.

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