

Phase Transitions, Hysteresis and Overshoot in Developing Neural Networks

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Abstract

We show that the presence of only two basic neuronal properties - a firing threshold and activity dependent outgrowth - is sufficient to generate overshoot phenomena in developing neural networks.

1 Introduction and Summary

During the development of the nervous system, neurons and connections are initially overproduced. These so-called overshoot or overgrowth phenomena constitute a general feature of neural network development, and occur everywhere in the central nervous system [1]. Selective elimination of neurons and synapses as well as outgrowth of neurons have been shown to be controlled by bioelectric activity [2].

In most neural network models, the dynamics of the system is studied given a particular collection of cells and network structure. In developing neural networks, however, connections between neurons are established and neurons may die while simultaneously the network acts as a dynamical system. Since network formation and system dynamics are mutually dependent upon each other, they must also be considered simultaneously.

We study these processes in a model where initially disconnected neurons develop into a synaptically connected network. The model is not meant to mimic a particular nervous system, but is used as a tool to understand the implications of activity dependent processes for network formation. In particular, we study the consequences of activity dependent outgrowth of neurons. The cells organize themselves into a network by growing out and establishing connections, under the influence of endogenous activity. First, we show that a developing network exhibits a phase transition from quiescent to activated state when connectivity passes through a certain critical value. Furthermore, when connectivity is subsequently decreased, the transition back to the quiescent state takes place at a lower connectivity value: hysteresis. Hysteresis is shown to hinge upon the firing-rate function being sigmoidal (i.e., a firing threshold). We next show that hysteresis in combination with activity dependent outgrowth of neurons is sufficient to generate overshoot in connectivity. Finally, the robustness of the results and the similarities with developing tissue cultures of dissociated cells are discussed.

2 The Model

We use a distributed, excitatory network, with neuron dynamics governed by [3]:

$$\frac{dX_i}{dt} = -\gamma \cdot X_i + (A - X_i) \cdot \sum_j W_{ij} \cdot F(X_j) \quad (1)$$

where X_i is the membrane potential, A is the saturation potential, γ determines the rate of decay, and W_{ij} is the connection strength between cell i and j . The firing-rate, $F(X_j)$, is given by:

$$F(X) = \frac{1}{1 + e^{(\theta - X)/\alpha}} \quad (2)$$

where α determines the non-linearity, and θ is the firing threshold. The small firing-rate when $X < \theta$ can be thought of as arising from spontaneous activity. In the simulations we took $A=1$, $\gamma=0.4$, $\alpha=0.11$ and $\theta=0.5$. The results, however, do not depend on the exact choices of the parameters. Growing cells are modelled as growing circular fields, which might be conceived of as dendritic fields. When two such fields overlap, the corresponding neurons become connected with a strength proportional to the area of overlap. Although in this way a symmetric network is built, the results do not depend on symmetry. The outgrowth of each individual cell depends upon its own level of electrical activity:

$$\frac{dR_i}{dt} = \rho \cdot \left[1 - \frac{2}{1 + e^{(\epsilon - F(X_i))/\beta}} \right] \quad (3)$$

where R_i is the radius of the field of cell i , ϵ is the firing-rate at which $\frac{dR_i}{dt} = 0$, and β determines the non-linearity. Eq(3) is just a phenomenological description of Kater's hypothesis [2] that the electrical activity level of a neuron affects (via Ca^{2+} influx) its rate of outgrowth. Any other function for which $\frac{dR_i}{dt} > 0$ at low values of $F(X_i)$ and < 0 at high values will yield similar results. ρ is taken very small relative to the relaxation time of the network. The network consists of 25 cells. Differential equations are solved numerically, using the variable time step Runge-Kutta integrator.

3 Results

To understand what is happening when outgrowth is activity dependent, we first consider the activity independent case.

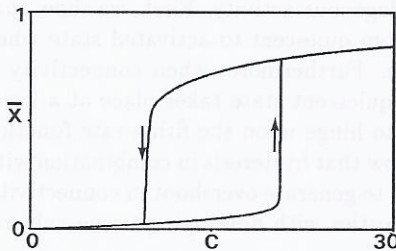


Fig. 1. Hysteresis. Average membrane potential of the network against connectivity.

When connectivity (defined as the total area of overlap) is increased by slowly increasing the size of the circular fields, starting with zero connectivity and low activity, a phase transition occurs between the quiescent and activated state when connectivity passes through a certain critical value (Fig. 1). When connectivity is subsequently decreased by slowly decreasing the cells' fields, starting with high connectivity and activity, the transition back to the quiescent state takes place at a different connectivity value: hysteresis. In other words, a higher connectivity is needed to induce activity in a silent network than to maintain it once the network has been activated.

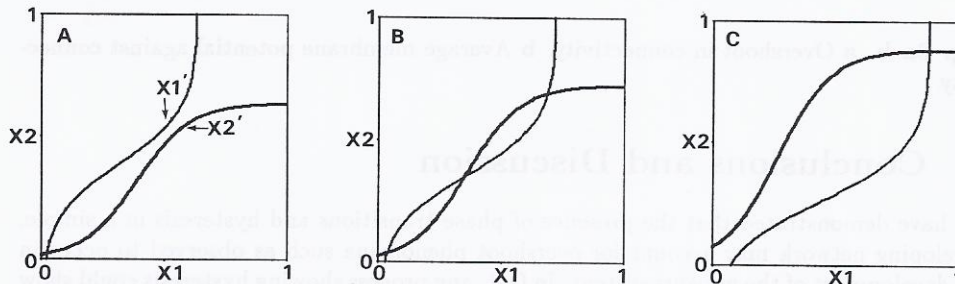


Fig. 2. Null-isoclines of the two-neuron model, for a low (a), an intermediate (b) and a high (c) value of W .

Phase transitions and hysteresis are retained in a two-neuron model:

$$\frac{dX_1}{dt} = -\gamma \cdot X_1 + (A - X_1) \cdot W_{21} \cdot F(X_2). \quad (4)$$

$$\frac{dX_2}{dt} = -\gamma \cdot X_2 + (A - X_2) \cdot W_{12} \cdot F(X_1). \quad (5)$$

For simplicity we take $W_{21} = W_{12} = W$. The phase portraits (Fig. 2) show the 0-isoclines $\frac{dX_1}{dt} = 0$ and $\frac{dX_2}{dt} = 0$. Because of the firing-rate function being sigmoidal, there exist two stable equilibrium points (quiescent state: X_1 and X_2 low, and activated state: X_1 and X_2 high) for intermediate values of W . With W initially being low, the system will settle in the single equilibrium point (quiescent state). When W becomes higher a second stable equilibrium point (activated state) appears, but the system will only move to that point, exhibiting a phase transition, when the first equilibrium point disappears as W becomes still higher. When, on the other hand, the system is initially in the activated state, the transition back to the quiescent state when W is decreased takes place only when the equilibrium point of the activated state disappears, i.e., the path through the state space is different for increasing or decreasing W : hysteresis.

We return to the larger network, but now outgrowth is governed by Eq.(3), with $\epsilon = 0.75$. There is a clear overshoot of connectivity (Fig. 3). Connectivity increases until the network is activated. At that point it starts decreasing, as the corresponding network activity is so high that on average $\frac{dR_i}{dt} < 0$. It remains decreasing until a level is attained at which $\frac{dR_i}{dt} = 0$. To reach this equilibrium value, however, the network has to pass through a phase of high connectivity (overshoot), thereby following the hysteresis path as shown in Fig.1.

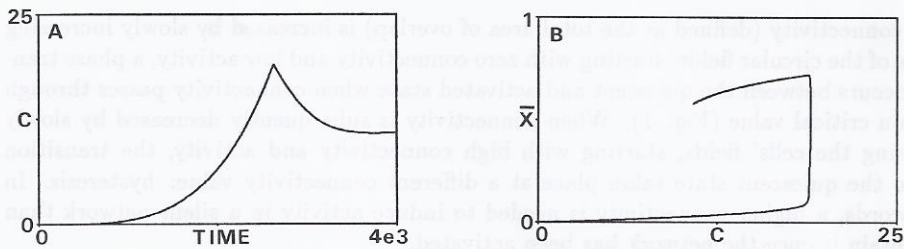


Fig. 3a-b. a Overshoot in connectivity. b Average membrane potential against connectivity.

4 Conclusions and Discussion

We have demonstrated that the presence of phase transitions and hysteresis in a simple, developing network may account for overshoot phenomena such as observed to occur in the development of the nervous system. In fact, any process showing hysteresis could show overshoot during development. The results are robust under: different firing-rate functions provided they possess a firing threshold, variance among the neurons in all parameters and initial conditions, different growth rate functions, symmetric or asymmetric connectivity matrix, different neuron models and network size. Our model results are similar to those found in developing tissue cultures with respect to numerical density of synapses [4] and the presence of a transition period with increasing electrical activity and associated retraction of neurites [5]. Moreover, the model responds in a similar way to suppression or intensification of bioelectric activity [4]. The present study might also have implications for the research of epilepsy. If, for whatever reason, activity is blocked during development, the reduction in connectivity does not take place, which may eventually lead to a network prone to epileptic-like activity.

5 References

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