

Hysteresis in a Two Neuron-Network: Basic Characteristics and Physiological Implications

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1 Introduction

Physiological evidences show that electrical activity affects a neuron's neurite outgrowth by modulating the concentration of intra-cellular calcium (Kater *et al.*, 1990). The change of connectivity thus produced modifies in turn the electrical activity. Based upon such evidences, van Ooyen and van Pelt devised a model for activity dependant neurite growth in neural networks (van Ooyen and van Pelt, 1992; 1993). Their study shows that when the neuron model has a sigmoidal transfer function with a spontaneous activity, the network connectivity goes through an overshoot followed by elimination before stabilizing. This behavior was explained by the activity being a hysteresis function of connectivity. In this paper we further investigate the basic characteristics required for the network activity to display such a behavior.

2 The model

Van Ooyen and van Pelt show that a two neuron-network connected with identical excitatory connections captures the main features of phase transition and hysteresis in activity dependant neurite outgrowth. The model network is governed by the following equations.

$$\begin{aligned}\frac{dX}{dt} &= -\gamma X + (A - X) W F(Y) \\ \frac{dY}{dt} &= -\gamma Y + (A - Y) W F(X) \\ \frac{dW}{dt} &= R(X, Y)\end{aligned}\tag{1}$$

Where X (resp. Y) is the membrane potential of neuron 1 (resp. 2), A is the saturation potential, γ determines the rate of decay, and W is the connection strength between cell 1 and 2 as well as between cell 2 and 1. Throughout this study the connection is excitatory and therefore W is a positive number. The firing rate of a neuron having a membrane potential X is determined by the function F , which is referred to as the neuron's transfer function. The basic assumptions on F are that it be a sigmoid function such that:

$$\begin{cases} F(0) = a, a > 0 \\ F'(x) > 0, \forall x \end{cases} \quad (2)$$

During growth the connection weight changes and this evolution takes place according to the third part of equation (1). The function R satisfies the following constraints:

$$\begin{cases} R \text{ is symmetrical in } X \text{ and } Y \text{ that is } R(X, Y) = R(Y, X). \\ \text{There exists } X_0 > 0 \text{ such that: } \begin{cases} \forall X < X_0 & R(X, X) > 0 \\ R(X_0, X_0) = 0 \\ \forall X > X_0 & R(X, X) < 0 \end{cases} \end{cases} \quad (3)$$

This study is concerned with the asymptotic evolution of the equations (1).

3 Results

The dynamics of weight modification are on a much slower time scale than the electrophysiological activity of the neurons. This makes it possible to separate the system into slow and fast dynamics. Such methods were first applied by Zeeman in the modelling of neural behavior (Zeeman, 1972).

3.1 The slow manifold

The slow manifold corresponds to the set of equilibria of the fast dynamics with the weight considered as a fixed parameter. It represents therefore the bifurcation scheme of the fast dynamics for values of the parameter W . The slow manifold is determined by the two following equations.

$$\begin{cases} -\gamma X + (A - X) W F(Y) = 0 \\ -\gamma Y + (A - Y) W F(X) = 0 \end{cases} \quad (4)$$

Taking into account the second constraint on F , it can be shown that system (4) is equivalent to the following system.

$$\begin{cases} X = Y \\ -\gamma X + (A - X) W F(X) = 0 \end{cases} \quad (5)$$

The dynamics of equations (1) display a hysteresis when the slow manifold is S-shaped or equivalently the bifurcation diagram of the fast dynamics has exactly two turning points where $\frac{dW}{dX} = 0$. The following result can then be deduced:

When the transfer function F satisfies constraints (2), system (1) displays a hysteresis if and only if the function v defined below has exactly two zeros on the interval $]0, A[$, and changes sign at these zeros.

$$v(X) = F'(X) - \frac{AF(X)}{X(A - X)} \quad (6)$$

From this point on we suppose v satisfies the condition described above and let X_1 and X_2 be the two zeros.

3.2 The isoclines

For $\frac{\gamma X_1}{(A-X_1)F(X_1)} < W < \frac{\gamma X_2}{(A-X_2)F(X_2)}$ the two isoclines (each isocline is defined by one of the equations in (4)) intersect in three points. Moreover the study of the slow manifold shows that these points are necessarily on the plane defined by $x = y$. Therefore for a weight given in this range each isocline crosses three times the line $x = y$.

3.3 Asymptotic behavior

As the slow manifold lies in the $x = y$ plane, equilibria of the system (1) must satisfy the same constraint. In fact an equilibrium point of the system is a point (X, X) on the slow manifold for which $R(X, X) = 0$. According to (3), there is only one point $\mathcal{P} = (X_0, X_0, \frac{\gamma X_0}{(A-X_0)F(X_0)})$ for which this condition holds. The analysis of the stability of this equilibrium point leads to the following result.

There are two values $X'_1 \equiv X_1$ and $X'_2 \equiv X_2$ such that: for $X_0 < X'_1$ or $X_0 > X'_2$ the system globally asymptotically converges to the equilibrium point \mathcal{P} . At X'_1 (resp. X'_2) the system goes through a Hopf bifurcation, thus for $X'_1 < X_0 < X'_2$ the system has a hyperbolic equilibrium point \mathcal{P} , and an attracting limit cycle lying in the plane $x = y$.

3.4 Application

In the case discussed by van Ooyen and van Pelt F is defined by:

$$F(X) = \frac{1}{1 + e^{(\theta-X)/\alpha}} \quad (7)$$

Applying equation (6) to this function shows that the system displays hysteresis for $\alpha < \alpha_0$, with α_0 satisfying:

$$A + (4\alpha_0 - A)e^{(\theta-2\alpha_0)/\alpha_0} = 0 \quad (8)$$

4 Discussion

In this paper the results obtained by van Ooyen and van Pelt were complemented. Here it was shown analytically that any neuron model defined by similar equations would present the same hysteresis phenomenon as long as its transfer function satisfies the constraints (2 and (6)). Moreover the geometrical interpretation of this constraint as the number of times the isocline (4) crosses the line $x = y$ for a given weight enables further generalization of this result to any neuron model. In fact the isocline curve represents the stationary potential X reached by a neuron when excited by another neuron at a fixed potential Y , through a synapse with strength W , and can therefore be evaluated for any neuron model. Let us note this function as $X = G(Y, W)$. Necessary and sufficient conditions for a neuron model to display hysteresis are then: 1) Spontaneous sporadic activity 2) Acceleration.

Spontaneous activity implies that $G(0, W) = a > 0$. This is a common living neuron property and is taken into account in many biologically plausible models. Acceleration refers to the fact that the isocline crosses the line $x = y$ for a range of weights, and that therefore for these values the post-synaptic neuron has a higher potential than the pre-synaptic neuron. In other words, under special circumstances, a neuron receiving a spike train with a rate f fires with $f' > f$. This kind of behavior is observed in living neurons. The accelerating power of a neuron depends on 1) post-synaptic potential characteristics such as its duration and amplitude 2) refractory period characteristics. The former depends on the neurotransmitter and the ionic channels involved as well as the nature of the connection (axo-somatic etc), and a detailed study of this is beyond the scope of this paper. The latter is mainly characterized by the post-spike potassium currents that depolarize the neuron. It should be noted that the duration of the refractory period is modulated by two such currents, referred to as I_C and I_{ahp} . I_C is a calcium-dependant, voltage-dependant potassium current, activated by μM concentrations of intra-cellular calcium at -50 mV , and it speeds up the post-spike depolarization thus shortening the refractory period and increasing the firing rate. I_{ahp} , on the other hand, is calcium-dependant voltage-independant potassium current, activated by mM concentrations of intra-cellular calcium. It slows down the post-spike depolarization thus increasing the refractory period and decreasing the firing rate. These currents illustrate well the fact that the intra-cellular calcium concentration which affects the neurite outgrowth may also be responsible for the changes in the firing rate observed in neurons.

5 Conclusion

Starting from a model developed by van Ooyen and van Pelt which accounted for phenomenon observed in neurite growth, methods for the analysis of dynamical systems were used to determine the geometrical characteristics required to reproduce the behavior. These features were then interpreted in terms of physiologically relevant observables. Further investigations in this direction are under way to improve the plausibility of the growth model.

6 References

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