

## On the Phase-Space Dynamics of Systems of Spiking Neurons. II: Formal Analysis

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We begin with a brief review of the abstract dynamical system that models systems of biological neurons, introduced in the original article. We then analyze the dynamics of the system. Formal analysis of local properties of flows reveals contraction, expansion, and folding in different sections of the phase-space. The criterion for the system, set up to model a typical neocortical column, to be sensitive to initial conditions is identified. Based on physiological parameters, we then deduce that periodic orbits in the region of the phase-space corresponding to normal operational conditions in the neocortex are almost surely (with probability 1) unstable, those in the region corresponding to seizure-like conditions are almost surely stable, and trajectories in the region corresponding to normal operational conditions are almost surely sensitive to initial conditions. Next, we present a procedure that isolates all basic sets, complex sets, and attractors incrementally. Based on the two sets of results, we conclude that chaotic attractors that are potentially anisotropic play a central role in the dynamics of such systems. Finally, we examine the impact of this result on the computational nature of neocortical neuronal systems.

### 1 Introduction

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As mentioned in the original article, also appearing in this issue, the goal of our research is to determine whether there are coherent spatiotemporal structures in the dynamics of neuronal systems. Our approach to this problem has been to formulate an abstract dynamical system that models systems of biological neurons and subsequently conduct a comprehensive analysis of the dynamics of the system.

In the original article we presented a detailed exposition of an abstract dynamical system that models systems of biological neurons. We also presented results from simulations of the system set up to model a typical column in the neocortex. The agreement between the qualitative aspects of the simulation results and that of real data attested to the viability of the model. In this article, we conduct a formal analysis of the dynamics of the abstract system.

In section 2, we briefly review the abstract dynamical system introduced in the original article. In section 3, we augment the system with an additional structure, a Riemannian metric, and perform a perturbation analysis on the dynamics of the augmented system.

In section 4, we conduct a measure analysis on the system. The analysis reveals contraction, expansion, and folding in different sections of the phase-space. In section 5, we conduct a local cross-section analysis of the dynamics of the system. The criterion for the system, set up to model a typical neocortical column, to be sensitive to initial conditions is identified. The salient qualitative characteristics of the system are then deduced based on physiological parameters. The results not only explain the simulation results presented in the original article but also make predictions that are borne out by further experimentation.

In section 6, we present a procedure that isolates all basic sets, complex sets, and attractors incrementally. Based on these results we conclude that the coherent spatiotemporal structures in the dynamics of the system operating under conditions considered routine in the neocortex are almost surely chaotic attractors that are potentially anisotropic. Finally, in section 7 we examine the impact of this result on the computational nature of neocortical neuronal systems.

## 2 Abstract Dynamical System ---

We present a brief review of the abstract dynamical system that models systems of biological neurons, introduced in the original article. Readers who desire a comprehensive exposition of the system should consult the original article.

The dynamical system is constructed in two stages. A deterministic model of a neuron is first formulated based on a set of basic assumptions about the biological neuron. A designated number of instances of the model are then linked together appropriately to construct the dynamical system.

**2.1 Model of the Neuron.** A biological neuron, at the highest level of abstraction, is a device that transforms multiple series of action potentials (also known as spikes) arriving at its various afferent (incoming) synapses into a series of action potentials on its axon. At the heart of this transformation lies the quantity  $P$ , the membrane potential at the soma of the neuron. Effects of the afferent spikes that have arrived at the various synapses of the neuron, as well as those of the efferent (outgoing) spikes that have departed since being generated at its soma, interact nonlinearly to generate this potential. The efferent spikes generated by the neuron coincide with the times at which this potential reaches the threshold of the neuron.

It was demonstrated in the original article, based on the observations that (1) the biological neuron is a finite precision machine, (2) the individual effects of afferent as well as efferent spikes on the membrane potential at

the soma of a biological neuron decay after a while at an exponential rate, and (3) the interval between successive spikes generated by a biological neuron is bounded from below by its absolute refractory period, that in a deterministic model it can reasonably be assumed that the individual effects of afferent as well as efferent spikes on the membrane potential at the soma decay to 0 within a bounded period of time. It then follows that at any given moment in time, there are at most a bounded number of most recent spikes (afferent as well as efferent) that are effective on the membrane potential at the soma of the neuron.

This is modeled formally as follows. Let  $i = 1, \dots, m$  denote the afferent synapses on a given neuron. Let  $r_0$  denote its absolute refractory period, and  $r_i$  for  $i = 1, \dots, m$  the absolute refractory period of the neuron presynaptic to it at synapse  $i$ . Let  $\tau_i$  for  $i = 0, \dots, m$  denote the bound on the period of effectiveness of spikes. To elaborate, any spike that arrived at synapse  $i = 1, \dots, m$  before time  $\tau_i$  as well as any spike that was generated at its soma before time  $\tau_0$  can be disregarded in the computation of the current membrane potential at the soma of the neuron. It follows that for each  $i = 0, \dots, m$ , there are at most  $n_i = \lceil \tau_i / r_i \rceil$  most recent spikes that need to be considered in the computation of the current membrane potential at the soma of the neuron.

The neuron is assigned a  $C^\infty$  function  $P(x_1^1, \dots, x_1^{n_1}, \dots, x_m^1, \dots, x_m^{n_m}; x_0^1, \dots, x_0^{n_0})$  that models the current membrane potential at its soma. Subscripts  $i = 1, \dots, m$  represent the afferent synapses on the neuron. Each  $x_i^j$  for  $i = 1, \dots, m$  represents the time since the arrival of a distinct member of the  $n_i$  most recent spikes that have reached synapse  $i$ , and for  $i = 0$  the time since the departure of a distinct member of the  $n_0$  most recent spikes that were generated at the soma of the neuron. The domain of  $P(\cdot)$  is restricted to  $0 \leq x_i^j \leq \tau_i$  for all  $i, j$ . Since  $n_i$  is merely an upper bound on the number of spikes ( $x_i^j$ ) that satisfy  $0 \leq x_i^j \leq \tau_i$ , it is conceivable that fewer than  $n_i$  spikes satisfy the criterion, in which case the remaining variables are set at  $\tau_i$ . Following are an additional set of constraints imposed on  $P(\cdot)$  at boundaries 0 and  $\tau_i$  to maintain consistency in the model:

1.  $\forall i = 0, \dots, m$  and  $\forall j = 1, \dots, n_i \exists \delta > 0$  such that  $\forall t \in [\tau_i - \delta, \tau_i]$ ,  $\frac{\partial P}{\partial x_i^j} \Big|_{x_i^j=t} = 0$  irrespective of the values assigned to the other variables.
2.  $\forall i = 0, \dots, m$  and  $\forall j = 1, \dots, n_i \exists \delta > 0$  such that  $\forall t \in [0, \delta]$ ,  $\frac{\partial P}{\partial x_i^j} \Big|_{x_i^j=t} = 0$  irrespective of the values assigned to the other variables.
3.  $\forall i = 0, \dots, m$  and  $\forall j = 1, \dots, n_i P(\cdot) \Big|_{x_i^j=0} = P(\cdot) \Big|_{x_i^j=\tau_i}$  all other variables held constant at any values.
4. If  $\forall i = 0, \dots, m$  and  $\forall j = 1, \dots, n_i x_i^j = 0$  or  $\tau_i$ , then  $P(\cdot) = 0$ .

Finally, a spike is generated by the neuron whenever  $P(\cdot) = \mathcal{T}$  (the membrane potential at the soma reaches the threshold of the neuron), and  $dP/dt \geq 0$  (during its rising phase).

**2.2 The Dynamical System.** We first consider systems of neurons that do not receive external input. Let  $i = 1, \dots, \mathcal{S}$  denote the set of all neurons in any such system. Given any neuron  $i$ , an upper bound  $\Upsilon_i$  on the time period until which any spike, since its inception, can be effective on the membrane potential at the soma of neuron  $i$  can be computed by extending each  $\tau_j$ , for  $j = 1, \dots, m$ , by the time it takes a spike to reach synapse  $j$  from its inception at the soma of the corresponding presynaptic neuron, and choosing the maximum over all  $j = 0, \dots, m$ . It then follows that  $\Upsilon = \max_{i=1}^{\mathcal{S}}(\Upsilon_i)$  yields an upper bound on the time period until which any spike, since its inception, can be effective on any neuron in the system.

We now redefine  $x_i^j$  to denote the time since the inception of the spike at the soma of neuron  $i$  and reassign  $n_i$  to  $\lceil \Upsilon/r_i \rceil$ , where  $r_i$  is the absolute refractory period of neuron  $i$ .  $P_i(\cdot)$ 's (the subscript referring to neuron  $i$ ) are modified accordingly; each function is translated along certain axes to account for the change in the origin of the  $x_i^j$ 's, the functions are then appropriately redefined on higher-dimensional spaces to reflect the changes in the  $n_i$ 's, their domains are modified to  $\forall i, j \ 0 \leq x_i^j \leq \Upsilon$ , and references to synapses in the variables are switched to references to appropriate neurons. We note that the constraints (1 through 4) set forth in the previous section hold on these modified functions at the new boundaries 0 and  $\Upsilon$ .

The state of the system of neurons can now be specified completely by enumerating, for all neurons  $i = 1, \dots, \mathcal{S}$ , the positions of the  $n_i$  (or fewer) most recent spikes generated by neuron  $i$  within  $\Upsilon$  time from the present. Such a record specifies the exact location of all spikes that are still situated on the axons of respective neurons and, combined with the potential functions, it specifies the current state of the soma of all neurons. Note that all information regarding the topology of the network, the strength and location of the afferent synapses on the various neurons, their modulation of one another's effects at respective somas, the anatomical characteristics of the various axonal arborizations, and so forth is implicitly contained within the set of functions  $P_i(\cdot)$  for  $i = 1, \dots, \mathcal{S}$ .

We can now generalize the system to receive external input by introducing additional neurons whose state descriptions are identical to that of the external input.

While the set of  $n_i$ -tuples  $(x_i^1, x_i^2, \dots, x_i^{n_i}) \in [0, \Upsilon]^{n_i}$  for  $i = 1, \dots, \mathcal{S}$  does specify the state of the system as argued above, this representation is fraught with redundancy. First,  $n_i$  being merely an upper bound on the number of spikes generated by neuron  $i$  that satisfy  $0 \leq x_i^j \leq \Upsilon$ , fewer spikes might satisfy the criterion, in which case the remaining components of the  $n_i$ -tuple are set at  $\Upsilon$ . These components correspond to spikes whose effectiveness on

all neurons in the system has expired. The finite description of the state of a neuron requires that a variable be reused to represent a new spike (set at 0) when the effectiveness of the old spike it represented terminates (when it is set at  $\Upsilon$ ). One of the two positions, 0 and  $\Upsilon$ , is therefore redundant. Second, if  $\langle x_i^1, x_i^2, \dots, x_i^{n_i} \rangle$  and  $\langle y_i^1, y_i^2, \dots, y_i^{n_i} \rangle$  are two  $n_i$ -tuples that are a nontrivial permutation of one another, they represent the same state of the neuron. Hence, all but one member of each such permutation group is redundant.

The transformation  $\langle x^1, x^2, \dots, x^n \rangle \rightarrow \langle a_{n-1}, a_{n-2}, \dots, a_0 \rangle$  where each  $z_j = e^{\frac{2\pi i}{\Upsilon} x^j}$  for  $j = 1, \dots, n$  is a root of the complex polynomial  $f(z) = z^n + a_{n-1}z^{n-1} + \dots + a_0$ , eliminates these redundancies. It was shown in the original article that  $|a_0| = 1$  and  $a_i = \bar{a}_{n-i}a_0$  for  $i = 1, \dots, n-1$  constitute a necessary set of constraints for  $f(z)$  to have all roots on  $|z| = 1$ . Consequently, for odd  $n$ ,  $\langle a_{n-1}, \dots, a_{\lceil n/2 \rceil}; a_0 \rangle \in \mathbb{C}^{\lceil n/2 \rceil} \times S^1$  completely specifies  $f(z)$ , and for even  $n$ ,  $\langle a_{n-1}, \dots, a_{\lceil n/2 \rceil+1}; a_{\lceil n/2 \rceil}, a_0 \rangle \in \mathbb{C}^{\lceil n/2 \rceil-1} \times \mathbb{M}^2$  does the same, where  $\mathbb{C}$ ,  $S^1$ , and  $\mathbb{M}^2$  represent the complex plane, the unit circle, and the two-dimensional Möbius band, respectively. A sufficient set of constraints was also derived in the original article, and it was shown that when both sets of constraints are imposed, the resultant space is a compact subset of  $\mathbb{C}^{\lceil n/2 \rceil} \times S^1$  (for odd  $n$ ) or  $\mathbb{C}^{\lceil n/2 \rceil-1} \times \mathbb{M}^2$  (for even  $n$ ). We denote the resultant space by  $\overline{\mathbb{L}}_n$ .  $\overline{\mathbb{L}}_n$  is the closure of the open set  $\mathbb{L}_n$  that corresponds to all points  $\langle x^1, x^2, \dots, x^n \rangle$  that are composed of distinct components ( $j_1 \neq j_2 \Rightarrow e^{\frac{2\pi i}{\Upsilon} x^{j_1}} \neq e^{\frac{2\pi i}{\Upsilon} x^{j_2}}$ ).  $\overline{\mathbb{L}}_n \setminus \mathbb{L}_n$  is a multidimensional boundary set that corresponds to all points  $\langle x^1, x^2, \dots, x^n \rangle$  that have one or more identical components ( $e^{\frac{2\pi i}{\Upsilon} x^{j_1}} = e^{\frac{2\pi i}{\Upsilon} x^{j_2}}$  for some  $j_1 \neq j_2$ ). Finally, the boundary set can be partitioned, based on the multiplicity of the components, into subsets that are diffeomorphic to  $\mathbb{L}_{n-1}$ ,  $\mathbb{L}_{n-2}$ ,  $\dots$ , or  $\mathbb{L}_0$ . We assume hereafter that all variables  $x_i^j$  are normalized, that is, scaled from  $[0, \Upsilon]$  to  $[0, 2\pi]$ . Each  $P_i(\cdot)$  is likewise assumed to be modified to reflect the scaling of its domain.

We denote by  ${}^i\overline{\mathbb{L}}_{n_i}$  the resultant space for neuron  $i$ . The phase-space for the system of neurons is then given by  $\prod_{i=1}^S {}^i\overline{\mathbb{L}}_{n_i}$ . It was demonstrated in the original article that the transformation described above,  $F_{n_i}: T^{n_i} \rightarrow {}^i\overline{\mathbb{L}}_{n_i}$  (points in  $T^{n_i}$ , the  $n_i$ -torus, represented as  $\langle e^{ix_i^1}, e^{ix_i^2}, \dots, e^{ix_i^{n_i}} \rangle$ ), is a local diffeomorphism at all points satisfying  $e^{ix_i^1} \neq e^{ix_i^2} \neq \dots \neq e^{ix_i^{n_i}}$ , and that corresponding to each  $P_i(\cdot)$  there exists a  $C^\infty$  function  $\tilde{P}_i: \prod_{j=1}^S {}^j\overline{\mathbb{L}}_{n_j} \rightarrow \mathbb{R}$ .

We observed earlier that at certain times, neuron  $i$  might possess fewer than  $n_i$  effective spikes. It follows from the deliberations above that under such circumstances, the remaining variables are set at  $e^{ix_i^j} = 1$ . For each neuron  $i$  we denote the number of such variables by  $\sigma_i$ . The corresponding spikes we label as dead since their effectiveness on all neurons in the system has expired. All other spikes we label as live. We now present an informal description of the dynamics of the system. If the state of the system at a given instant is such that neither any live spike is on the verge of death nor

is any neuron on the verge of spiking, then all live spikes continue to age uniformly (the corresponding variables  $x_i^j$  grow at a constant rate). If a spike is on the verge of death, it expires, that is, stops aging. This occurs when the corresponding variable reaches  $e^{ix_i^j} = 1$ . If a neuron is on the verge of spiking, exactly one dead spike corresponding to that neuron is turned live.

This dichotomy between dead and live spikes induces a certain structure on  ${}^i\overline{\mathbb{L}}_{n_i}$ . We denote by  ${}^i\overline{\mathbb{L}}_{n_i}^j$  the subspace of  ${}^i\overline{\mathbb{L}}_{n_i}$  that satisfies  $\sigma_i \geq j$ . We note immediately that there exists a natural mapping from  ${}^i\overline{\mathbb{L}}_{(n_i-\sigma_i)}^0$ , a space corresponding to  $(n_i - \sigma_i)$  live or dead spikes, to  ${}^i\overline{\mathbb{L}}_{n_i}^{\sigma_i}$ , the subspace corresponding to  $(n_i - \sigma_i)$  live or dead spikes in a space corresponding to  $n_i$  spikes. It was demonstrated in the original article that the canonical mapping  $\mathcal{F}_{(n_i-\sigma_i)}^{n_i}: {}^i\overline{\mathbb{L}}_{(n_i-\sigma_i)}^0 \rightarrow {}^i\overline{\mathbb{L}}_{n_i}^{\sigma_i}$  is not only an imbedding for all  $\sigma_i \leq n_i$ , but also maps flows identically, a fact manifest in the informal description of the dynamics of the system. To elaborate, since all dead spikes remain stationary at  $e^{ix_i^j} = 1$ , they register as a constant factor in the dynamics of the system. While the total number of spikes assigned to a neuron dictates the dimensionality of its entire space, flows corresponding to a given number of live spikes lie on a fixed dimensional submanifold and are  $C^\infty$ -conjugate to one another.

The submanifolds  ${}^i\overline{\mathbb{L}}_{n_i}^j$  ( $j = 1, \dots, n_i$ ) are not revealed in the topology of  ${}^i\overline{\mathbb{L}}_{n_i}$  regarded (as the case may be) as a subspace of  $\mathbb{C}^{\lfloor n_i/2 \rfloor} \times S^1$  or of  $\mathbb{C}^{\lfloor n_i/2 \rfloor - 1} \times \mathbb{M}^2$  (topologized by respective standard differentiable structures). We therefore assign  ${}^i\overline{\mathbb{L}}_{n_i}$  the topology generated by the family of all relatively open subsets of  ${}^i\overline{\mathbb{L}}_{n_i}^j, \forall j \geq 0$ .

We denote by  $P_i^S$  the subspace of  $\prod_{i=1}^S {}^i\overline{\mathbb{L}}_{n_i}$  satisfying  $\tilde{P}_i(\cdot) = \mathcal{T}$ , and by  $P_i^I$  the subspace wherein  $d\tilde{P}_i(\cdot)/dt \geq 0$  is additionally true. It was demonstrated in the original article that  $P_i^S$  is a  $C^\infty$  regular submanifold of codimension 1 and that  $P_i^I$  is a closed subset of  $P_i^S$ .

The velocity field  $\mathcal{V}: \prod_{i=1}^S {}^i\overline{\mathbb{L}}_{n_i} \rightarrow \prod_{i=1}^S T({}^i\overline{\mathbb{L}}_{n_i})$  is stipulated by way of two fields:  $\mathcal{V}^1$  for the case wherein  $p \in \prod_{i=1}^S {}^i\overline{\mathbb{L}}_{n_i}$  satisfies  $\forall i = 1, \dots, S$   $p \notin P_i^I$ , and  $\mathcal{V}^2$  for the case wherein  $\exists i$   $p \in P_i^I$ .<sup>1</sup> We note from the informal description of the dynamics of the system that the component fields,  $\mathcal{V}_i^1$  and  $\mathcal{V}_i^2$ , for each neuron  $i = 1, \dots, S$  can be specified based solely on  $p_i \in {}^i\overline{\mathbb{L}}_{n_i}$ . Moreover, it follows that  $\mathcal{V}_i^1$  can be defined on  $({}^i\overline{\mathbb{L}}_{(n_i-\alpha)}^0 \setminus {}^i\overline{\mathbb{L}}_{(n_i-\alpha)}^1)$ , the corresponding field on  $({}^i\overline{\mathbb{L}}_{n_i}^{\alpha} \setminus {}^i\overline{\mathbb{L}}_{n_i}^{\alpha+1})$  then defined as  $\mathcal{F}_{(n_i-\alpha)_*}^{n_i}(\mathcal{V}_i^1)$ .<sup>2</sup>

<sup>1</sup>  $T(\cdot)$  denotes the tangent bundle (appropriated from  $\mathbb{C}^{\lfloor n_i/2 \rfloor} \times S^1$  or  $\mathbb{C}^{\lfloor n_i/2 \rfloor - 1} \times \mathbb{M}^2$ , as the case may be).

<sup>2</sup> We use the notation,  $F_*(X_p)f = X_p(f \circ F)$  where  $F$  is a  $C^\infty$  map of manifolds,  $X_p$  is a tangent vector at  $p$ , and  $f$  is an arbitrary function that belongs to  $C^\infty(F(p))$ .

Since  $\mathcal{V}_i^1$  for  $p_i \in ({}^i\overline{\mathbb{L}}_{(n_i-\sigma_i)}^0 \setminus {}^i\overline{\mathbb{L}}_{(n_i-\sigma_i)}^1)$  corresponds to all  $(n_i - \sigma_i)$  roots rotating at constant speed, it is defined as  $\frac{da_{n_i-\sigma_i-k}}{dt} = \frac{2\pi}{T} k \hat{\theta}$  for  $k = 1, \dots, \lfloor \frac{n_i - \sigma_i}{2} \rfloor$ ,  $(n_i - \sigma_i)$ , and when  $(n_i - \sigma_i)$  is even,  $\frac{d|a_{(n_i-\sigma_i)/2}|}{dt} = 0$ .  $\hat{\theta}$  is the basis vector  $\partial/\partial\theta$  on  $\mathbb{C}, \mathbb{M}^2$ , and  $S^1$  with elements represented respectively as  $re^{i\theta}$ ,  $(\pm r, \theta)$ , and  $\theta$ . Finally,  $\mathcal{V}_i^2$  for  $p_i \in ({}^i\overline{\mathbb{L}}_{n_i}^{\sigma_i} \setminus {}^i\overline{\mathbb{L}}_{n_i}^{\sigma_i+1})$  is equivalent to  $\mathcal{V}_i^1$  on  ${}^i\overline{\mathbb{L}}_{n_i}^{\sigma_i-1}$  ignoring the fact that  $p_i$  lies additionally on  ${}^i\overline{\mathbb{L}}_{n_i}^{\sigma_i} \subset {}^i\overline{\mathbb{L}}_{n_i}^{\sigma_i-1}$ .

### 3 The Augmented System and Its Basic Features

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Our first objective is to identify the local properties of the dynamics of the system. We pursue this goal through a measure analysis in section 4 and a cross-section analysis in section 5. These analyses require the phase-space to be endowed with a Riemannian metric. We begin with its specification.

**3.1 Riemannian Metric.** We choose the metric such that all flows corresponding to  $\mathcal{V}^1$  on  $\prod_{i=1}^S ({}^i\overline{\mathbb{L}}_{n_i}^{\sigma_i} \setminus {}^i\overline{\mathbb{L}}_{n_i}^{\sigma_i+1})$  (for all values of  $\sigma_i$ 's) are not only measure preserving but also shape preserving.

Since for every  $\sigma_i > 1$ ,  ${}^i\overline{\mathbb{L}}_{n_i}^{\sigma_i}$  corresponds to states of neuron  $i$  that feature multiple components set at  $e^{ix_i^j} = 1$ , it lies on the boundary of  ${}^i\overline{\mathbb{L}}_{n_i}^0$ . It follows from the description of  ${}^i\overline{\mathbb{L}}_{n_i}$  in the previous section that the boundary set in the neighborhood of  $p_i \in ({}^i\overline{\mathbb{L}}_{n_i}^{\sigma_i} \setminus {}^i\overline{\mathbb{L}}_{n_i}^{\sigma_i+1})$  is locally diffeomorphic to an open subset of  ${}^i\overline{\mathbb{L}}_{n_i}^{\sigma_i-1}$ . Finally, the nature of  $\mathcal{V}_i^1$  and  $\mathcal{V}_i^2$  reveals that for all  $p_i \in ({}^i\overline{\mathbb{L}}_{n_i}^{\sigma_i} \setminus {}^i\overline{\mathbb{L}}_{n_i}^{\sigma_i+1})$ ,  $\mathcal{V}_i \in T({}^i\overline{\mathbb{L}}_{n_i}^{\sigma_i-1})$ . It is therefore sufficient as well as appropriate that the Riemannian metric be defined over  $T(\prod_{i=1}^S {}^i\overline{\mathbb{L}}_{n_i}^{\sigma_i-1})$ , that is, as  $\Phi: T(\prod_{i=1}^S {}^i\overline{\mathbb{L}}_{n_i}^{\sigma_i-1}) \times T(\prod_{i=1}^S {}^i\overline{\mathbb{L}}_{n_i}^{\sigma_i-1}) \rightarrow \mathbb{R}$ .

Let  $p_i \in ({}^i\overline{\mathbb{L}}_{n_i}^{\sigma_i} \setminus {}^i\overline{\mathbb{L}}_{n_i}^{\sigma_i+1})$  denote the state of neuron  $i$ . We consider  $({}^i\overline{\mathbb{L}}_{n_i}^{\sigma_i} \setminus {}^i\overline{\mathbb{L}}_{n_i}^{\sigma_i+1})$  as a subspace of  ${}^i\overline{\mathbb{L}}_{n_i}^{\sigma_i-1}$ . The imbedding  $\mathcal{F}_{n_i-(\sigma_i-1)}^{n_i}$  maps  ${}^i\overline{\mathbb{L}}_{n_i-(\sigma_i-1)}^0$  onto  ${}^i\overline{\mathbb{L}}_{n_i}^{\sigma_i-1}$  such that  $({}^i\overline{\mathbb{L}}_{n_i-(\sigma_i-1)}^1 \setminus {}^i\overline{\mathbb{L}}_{n_i-(\sigma_i-1)}^2) \subset {}^i\overline{\mathbb{L}}_{n_i-(\sigma_i-1)}^0$  is mapped onto  $({}^i\overline{\mathbb{L}}_{n_i}^{\sigma_i} \setminus {}^i\overline{\mathbb{L}}_{n_i}^{\sigma_i+1}) \subset {}^i\overline{\mathbb{L}}_{n_i}^{\sigma_i-1}$ . The mapping  $F_{n_i-(\sigma_i-1)}: T^{n_i-(\sigma_i-1)} \rightarrow {}^i\overline{\mathbb{L}}_{n_i-(\sigma_i-1)}^0$  is a local diffeomorphism at all points satisfying  $e^{ix_i^1} \neq e^{ix_i^2} \neq \dots \neq e^{ix_i^{n_i-(\sigma_i-1)}}$ . Hence,  $(\mathcal{F}_{n_i-(\sigma_i-1)}^{n_i} \circ F_{n_i-(\sigma_i-1)})$  is a local diffeomorphism at all such points. Finally, whereas the section of  ${}^i\overline{\mathbb{L}}_{n_i}$  that is actually explored by the state dynamics of neuron  $i$ , that is, the feasible space, does contain states composed of identical components, such components are necessarily set at  $e^{ix_i^j} = 1$ . Consequently, if  $\mathbb{W} \subset T^{n_i-(\sigma_i-1)}$  denotes the pre-image of the feasible section of  $({}^i\overline{\mathbb{L}}_{n_i}^{\sigma_i-1} \setminus {}^i\overline{\mathbb{L}}_{n_i}^{\sigma_i+1})$ , then the constraint  $e^{ix_i^1} \neq e^{ix_i^2} \neq \dots \neq e^{ix_i^{n_i-(\sigma_i-1)}}$  is satisfied throughout  $\mathbb{W}$ .

We can now define a  $C^\infty$ -compatible basis for  $T(\prod_{i=1}^S \overline{\mathbb{L}}_{n_i})$  in the feasible section of  $\prod_{i=1}^S (\overline{\mathbb{L}}_{n_i}^{\sigma_i} \setminus \overline{\mathbb{L}}_{n_i}^{\sigma_i+1})$  as the set of vectors  $({}^i \mathcal{F}_{n_i - (\sigma_i - 1)}^{\sigma_i} \circ {}^i F_{n_i - (\sigma_i - 1)})_* (\partial/\partial x_i^j)$  for  $i = 1, \dots, S$  and  $j = 1, \dots, n_i - (\sigma_i - 1)$ . We shall, for the sake of brevity, henceforth refer to  $({}^i \mathcal{F}_{n_i - (\sigma_i - 1)}^{\sigma_i} \circ {}^i F_{n_i - (\sigma_i - 1)})_* (\partial/\partial x_i^j)$  as  $E_i^j$ . We set the Riemannian metric as  $\Phi(E_a^b, E_c^d) = 1$  if  $a = c$  and  $b = d$ , and  $\Phi(E_a^b, E_c^d) = 0$  otherwise.

The component labels in  $\mathbb{W}$  can be chosen in a manner such that  $E_i^1 \in T(\overline{\mathbb{L}}_{n_i}^{\sigma_i - 1})$  lies in  $T^\perp(\overline{\mathbb{L}}_{n_i}^{\sigma_i} \setminus \overline{\mathbb{L}}_{n_i}^{\sigma_i+1})$ .<sup>3</sup> The feasible section of  $\prod_{i=1}^S (\overline{\mathbb{L}}_{n_i}^{\sigma_i} \setminus \overline{\mathbb{L}}_{n_i}^{\sigma_i+1})$ , for any values of  $\sigma_i$ 's, can now be considered a Riemannian manifold in its own right.  $T(\prod_{i=1}^S (\overline{\mathbb{L}}_{n_i}^{\sigma_i} \setminus \overline{\mathbb{L}}_{n_i}^{\sigma_i+1}))$  in the feasible section is spanned by  $\langle E_i^j \mid i = 1, \dots, S; j = 2, \dots, n_i - (\sigma_i - 1) \rangle$ , which forms an orthonormal basis. The feasible section of  $(\overline{\mathbb{L}}_{n_i}^{\sigma_i} \setminus \overline{\mathbb{L}}_{n_i}^{\sigma_i+1})$  is therefore also a regular submanifold of  $\overline{\mathbb{L}}_{n_i}^{\sigma_i - 1}$ . We now consider  $\prod_{i=1}^S \overline{\mathbb{L}}_{n_i}$  as the union of the sets  $\prod_{i=1}^S (\overline{\mathbb{L}}_{n_i}^{\sigma_i} \setminus \overline{\mathbb{L}}_{n_i}^{\sigma_i+1})$  for all  $i = 1, \dots, S$ ,  $\sigma_i = 0, \dots, n_i$ , and assign it the topology generated by the family of all open sets in each  $\prod_{i=1}^S (\overline{\mathbb{L}}_{n_i}^{\sigma_i} \setminus \overline{\mathbb{L}}_{n_i}^{\sigma_i+1})$  induced by the Riemannian metric. It is clear that in the feasible section of  $\prod_{i=1}^S \overline{\mathbb{L}}_{n_i}$ , this topology is identical to that presented in section 2.

$\mathcal{V}^1$  on  $\prod_{i=1}^S (\overline{\mathbb{L}}_{n_i}^{\sigma_i} \setminus \overline{\mathbb{L}}_{n_i}^{\sigma_i+1})$  is defined as  $\sum_{i=1, j=2}^{S, n_i - (\sigma_i - 1)} (2\pi/\Upsilon) E_i^j$  in the new frame. Since the field of coordinate frames  $E_i^j$  for  $i = 1, \dots, S$ ,  $j = 2, \dots, n_i - (\sigma_i - 1)$  satisfies  $\nabla_{E_a^b} E_c^d = 0$  ( $\nabla$  being the Riemannian connection) for all  $a, c \in \{1, \dots, S\}$  and  $b, d \in \{2, \dots, n_i - (\sigma_i - 1)\}$ , and the coefficients  $(2\pi/\Upsilon)$  are constants,  $\mathcal{V}^1$  is a constant vector field on  $\prod_{i=1}^S (\overline{\mathbb{L}}_{n_i}^{\sigma_i} \setminus \overline{\mathbb{L}}_{n_i}^{\sigma_i+1})$ .  $\mathcal{V}^1$  is therefore not only measure preserving but also shape preserving on  $\prod_{i=1}^S (\overline{\mathbb{L}}_{n_i}^{\sigma_i} \setminus \overline{\mathbb{L}}_{n_i}^{\sigma_i+1})$ .

This leads to a substantial simplification in the analysis of the dynamics of the system. Since any trajectory  $\Psi_x(t)$  in the phase-space has associated with it a sequence of times  $\langle t_1, t_2, \dots, t_k, t_{k+1}, \dots \rangle$  such that for all  $j$  the segment  $\{\Psi_x(t) \mid t_j < t < t_{j+1}\}$  lies strictly on  $\prod_{i=1}^S (\overline{\mathbb{L}}_{n_i}^{\sigma_i} \setminus \overline{\mathbb{L}}_{n_i}^{\sigma_i+1})$  for fixed values of  $\sigma_i$ 's (segments that correspond to periods during which neither any live spike expires nor does any neuron fire), and since each such segment is both volume and shape preserving, the analysis of the local properties of  $\Psi_x(t)$  reduces to the analysis of a finite or countably infinite set of discrete events at times  $\langle t_1, t_2, \dots, t_k, t_{k+1}, \dots \rangle$ , each event denoting the birth and/or death of one or more spikes. Since any event involving the simultaneous birth and death of multiple spikes can be regarded as a series of mutually independent births and deaths of individual spikes,<sup>4</sup> the

<sup>3</sup> The orthogonal complement of  $T(\overline{\mathbb{L}}_{n_i}^{\sigma_i} \setminus \overline{\mathbb{L}}_{n_i}^{\sigma_i+1})$ .

<sup>4</sup> At the time of its birth or death, a spike has no impact on any membrane potential function.



analysis can be further restricted to the birth of a spike and the death of a spike.

### 3.2 Perturbation Analysis.

**3.2.1 Birth.** Let  $\{\Psi_x(t) \mid t_j < t < t_{j+1}\}$  lie strictly on  $\prod_{i=1}^S ({}^i\overline{\mathbb{I}}_{n_i}^\sigma \setminus {}^i\overline{\mathbb{I}}_{n_i}^{\sigma+1})$  for arbitrary but fixed values of  $\sigma_i$ 's. Let the event associated with  $\Psi_x(t_{j+1})$  be, without loss of generalization, the birth of a spike at neuron 1, that is,  $\Psi_x(t_{j+1}) \in P_1^l$  and no other  $P_i^l$ . Then  $\{\Psi_x(t) \mid t_{j+1} < t < t_{j+2}\}$  lies strictly on  $({}^1\overline{\mathbb{I}}_{n_1}^{\sigma-1} \setminus {}^1\overline{\mathbb{I}}_{n_1}^{\sigma}) \times \prod_{i=2}^S ({}^i\overline{\mathbb{I}}_{n_i}^\sigma \setminus {}^i\overline{\mathbb{I}}_{n_i}^{\sigma+1})$ . Consider  $p_1 = \Psi_x(t_{j+1} - t^*)$  on the segment  $\{\Psi_x(t) \mid t_j < t < t_{j+1}\}$  and  $p_2 = \Psi_x(t_{j+1} + t^*)$  on the segment  $\{\Psi_x(t) \mid t_{j+1} < t < t_{j+2}\}$  such that  $\Psi_x(t)$  for  $t_{j+1} - t^* \leq t \leq t_{j+1} + t^*$  lies within a single coordinate neighborhood<sup>5</sup> of  $\prod_{i=1}^S ({}^i\overline{\mathbb{I}}_{n_i}^{\sigma-1} \setminus {}^i\overline{\mathbb{I}}_{n_i}^{\sigma+1})$ . Let  $p_1$  be represented as  $\langle a_1^1, \dots, a_1^{n_1 - (\sigma_1 - 1)}, a_2^1, \dots, a_2^{n_2 - (\sigma_2 - 1)}, \dots, a_S^1, \dots, a_S^{n_S - (\sigma_S - 1)} \rangle$  where  $a_i^1 = 0$  for  $i = 1, \dots, S$ , and  $p_2$  as  $\langle b_1^1, \dots, b_1^{n_1 - (\sigma_1 - 1)}, b_2^1, \dots, b_2^{n_2 - (\sigma_2 - 1)}, \dots, b_S^1, \dots, b_S^{n_S - (\sigma_S - 1)} \rangle$ , in local coordinates. Then  $b_1^1 = (2\pi/\Upsilon)t^*$ ,  $b_i^1 = 0$  for  $i = 2, \dots, S$ , and  $b_i^j = a_i^j + (2\pi/\Upsilon)2t^*$  for the remaining  $i = 1, \dots, S$  and  $j = 2, \dots, n_i - (\sigma_i - 1)$ .

Let  $\tilde{p}_1$  on  $\prod_{i=1}^S ({}^i\overline{\mathbb{I}}_{n_i}^\sigma \setminus {}^i\overline{\mathbb{I}}_{n_i}^{\sigma+1})$  be sufficiently close to  $p_1$  such that  $\Psi_{\tilde{x}}(t)$ , the trajectory through  $\tilde{p}_1$ , has a corresponding segment on  $({}^1\overline{\mathbb{I}}_{n_1}^{\sigma-1} \setminus {}^1\overline{\mathbb{I}}_{n_1}^{\sigma}) \times \prod_{i=2}^S ({}^i\overline{\mathbb{I}}_{n_i}^\sigma \setminus {}^i\overline{\mathbb{I}}_{n_i}^{\sigma+1})$ . Let  $\tilde{p}_1$  be represented in local coordinates as  $\langle \tilde{a}_1^1, \dots, \tilde{a}_1^{n_1 - (\sigma_1 - 1)}, \tilde{a}_2^1, \dots, \tilde{a}_2^{n_2 - (\sigma_2 - 1)}, \dots, \tilde{a}_S^1, \dots, \tilde{a}_S^{n_S - (\sigma_S - 1)} \rangle$  where  $\tilde{a}_i^1 = a_i^1 = 0$  for  $i = 1, \dots, S$ , and  $\tilde{a}_i^j = a_i^j + \Delta x_i^j$  for  $i = 1, \dots, S$ ,  $j = 2, \dots, n_i - (\sigma_i - 1)$ . Let  $\Psi_{\tilde{x}}(t)$  be parameterized such that  $\tilde{p}_1 = \Psi_{\tilde{x}}(t_{j+1} - t^*)$ . Let  $\tilde{p}_2 = \Psi_{\tilde{x}}(t_{j+1} + t^*)$  be represented in local coordinates as  $\langle \tilde{b}_1^1, \dots, \tilde{b}_1^{n_1 - (\sigma_1 - 1)}, \tilde{b}_2^1, \dots, \tilde{b}_2^{n_2 - (\sigma_2 - 1)}, \dots, \tilde{b}_S^1, \dots, \tilde{b}_S^{n_S - (\sigma_S - 1)} \rangle$  where  $\tilde{b}_1^1 = b_1^1 + \Delta y_1^1$ ,  $\tilde{b}_i^1 = b_i^1 = 0$  for  $i = 2, \dots, S$ , and  $\tilde{b}_i^j = b_i^j + \Delta y_i^j$  for  $i = 1, \dots, S$ ,  $j = 2, \dots, n_i - (\sigma_i - 1)$ .

$\Delta y_i^j = \Delta x_i^j$  for  $i = 1, \dots, S$  and  $j = 2, \dots, n_i - (\sigma_i - 1)$  since  $\tilde{b}_i^j = \tilde{a}_i^j + (2\pi/\Upsilon)2t^*$  for all such values of  $i$  and  $j$ . Let  $\Delta t$  be such that  $\Psi_{\tilde{x}}(t_{j+1} + \Delta t)$  lies on  $P_1^l$ . Then  $\Delta y_1^1 = -(2\pi/\Upsilon)\Delta t$ . Since both  $\Psi_x(t_{j+1})$  and  $\Psi_{\tilde{x}}(t_{j+1} + \Delta t)$  lie on  $P_1^l$ ,

$$P_1 \left( a_1^1, a_1^2 + \frac{2\pi}{\Upsilon}t^*, \dots, a_1^{n_1 - (\sigma_1 - 1)} + \frac{2\pi}{\Upsilon}t^*, \dots, \right. \\ \left. a_S^1, a_S^2 + \frac{2\pi}{\Upsilon}t^*, \dots, a_S^{n_S - (\sigma_S - 1)} + \frac{2\pi}{\Upsilon}t^* \right) = \mathcal{T}, \quad \text{and} \quad (3.1)$$

<sup>5</sup> With the distinguished set of coordinate frames described in section 3.1.

$$\begin{aligned}
P_1 \left( a_1^1, a_1^2 + \Delta x_1^2 + \frac{2\pi}{\Upsilon}(t^* + \Delta t), \dots, a_1^{n_1 - (\sigma_1 - 1)} + \Delta x_1^{n_1 - (\sigma_1 - 1)} + \frac{2\pi}{\Upsilon}(t^* + \Delta t), \right. \\
\dots, a_S^1, a_S^2 + \Delta x_S^2 + \frac{2\pi}{\Upsilon}(t^* + \Delta t), \dots, a_S^{n_S - (\sigma_S - 1)} + \Delta x_S^{n_S - (\sigma_S - 1)} \\
\left. + \frac{2\pi}{\Upsilon}(t^* + \Delta t) \right) = \mathcal{T}. \tag{3.2}
\end{aligned}$$

$P_1(\cdot)$ , being  $C^\infty$ , can be expanded as a Taylor series around  $\Psi_x(t_{j+1})$ . Minor algebraic manipulations, and neglecting all higher-order terms, then yields

$$\Delta y_1^j = \sum_{i=1, j=2}^{S, n_i - (\sigma_i - 1)} \left( \frac{\partial P_1}{\partial x_i^j} \times \Delta x_i^j \right) / \sum_{i=1, j=2}^{S, n_i - (\sigma_i - 1)} \frac{\partial P_1}{\partial x_i^j}. \tag{3.3}$$

All  $\frac{\partial P_1}{\partial x_i^j}$ 's in equation 3.3 are evaluated at  $\Psi_x(t_{j+1})$ . We denote  $\frac{\partial P_k}{\partial x_i^j} / \sum_{i,j} \frac{\partial P_k}{\partial x_i^j}$  by  $k\alpha_i^j$ . Then  $\forall k = 1, \dots, S \sum_{i,j} k\alpha_i^j = 1$ , and  $\Delta y_1^j = \sum_{i,j} \alpha_i^j \Delta x_i^j$ .

**3.2.2 Death.** We assume that the event associated with  $\Psi_x(t_{j+1})$  is, without loss of generalization, the death of a spike at neuron 1. Then  $\{\Psi_x(t) \mid t_{j+1} < t < t_{j+2}\}$  lies strictly on  $({}^1\overline{\mathbb{I}}_{n_1}^{\sigma_1+1} \setminus {}^1\overline{\mathbb{I}}_{n_1}^{\sigma_1+2}) \times \prod_{i=2}^S ({}^i\overline{\mathbb{I}}_{n_i}^{\sigma_i} \setminus {}^i\overline{\mathbb{I}}_{n_i}^{\sigma_i+1})$ . We now consider points  $p_1 = \Psi_x(t_{j+1} - t^*)$  and  $p_2 = \Psi_x(t_{j+1} + t^*)$  such that  $\Psi_x(t)$  for  $t_{j+1} - t^* \leq t \leq t_{j+1} + t^*$  lies within a single coordinate neighborhood of  $\prod_{i=1}^S ({}^i\overline{\mathbb{I}}_{n_i}^{\sigma_i} \setminus {}^i\overline{\mathbb{I}}_{n_i}^{\sigma_i+2})$ . Let  $p_1$  be represented in local coordinates as  $\langle a_1^1, \dots, a_1^{n_1 - \sigma_1}, a_2^1, \dots, a_2^{n_2 - \sigma_2}, \dots, a_S^1, \dots, a_S^{n_S - \sigma_S} \rangle$ , and  $p_2$  be represented as  $\langle b_1^1, \dots, b_1^{n_1 - \sigma_1}, b_2^1, \dots, b_2^{n_2 - \sigma_2}, \dots, b_S^1, \dots, b_S^{n_S - \sigma_S} \rangle$ . Then  $b_1^j = 0$ , and  $b_i^j = a_i^j + (2\pi/\Upsilon)2t^*$  for all  $i = 1, \dots, S, j = 1, \dots, (n_i - \sigma_i)$  except  $i = j = 1$ .

Let  $\tilde{p}_1 = \Psi_{\tilde{x}}(t_{j+1} - t^*)$  and  $\tilde{p}_2 = \Psi_{\tilde{x}}(t_{j+1} + t^*)$  be points on a  $\Psi_{\tilde{x}}(t)$  sufficiently close to  $\Psi_x(t)$  so as to have corresponding segments on the noted submanifolds. Let  $\tilde{p}_1$  be represented in local coordinates as  $\langle \tilde{a}_1^1, \dots, \tilde{a}_1^{n_1 - \sigma_1}, \tilde{a}_2^1, \dots, \tilde{a}_2^{n_2 - \sigma_2}, \dots, \tilde{a}_S^1, \dots, \tilde{a}_S^{n_S - \sigma_S} \rangle$  where  $\tilde{a}_i^j = a_i^j + \Delta x_i^j$  for all  $i = 1, \dots, S, j = 1, \dots, (n_i - \sigma_i)$ , and  $\tilde{p}_2$  be represented as  $\langle \tilde{b}_1^1, \dots, \tilde{b}_1^{n_1 - \sigma_1}, \tilde{b}_2^1, \dots, \tilde{b}_2^{n_2 - \sigma_2}, \dots, \tilde{b}_S^1, \dots, \tilde{b}_S^{n_S - \sigma_S} \rangle$  where  $\tilde{b}_i^j = b_i^j + \Delta y_i^j$  for all  $i = 1, \dots, S, j = 1, \dots, (n_i - \sigma_i)$ . Then it follows from  $\tilde{b}_1^1 = b_1^1 = 0$  and  $\tilde{b}_i^j = \tilde{a}_i^j + (2\pi/\Upsilon)2t^*$  for all other  $i, j$  that  $\Delta y_1^1 = 0$  and  $\Delta y_i^j = \Delta x_i^j$  for all  $i = 1, \dots, S, j = 1, \dots, (n_i - \sigma_i)$  except  $i = j = 1$ .

## 4 Measure Analysis

**4.1 Expansion.** We demonstrate that a trajectory is expansive at the birth of a spike. We consider the adjacent segments of  $\Psi_x(t)$  described in section 3.2.1. Let  $\mathcal{C}$  denote an infinitesimal  $\sum_{i=1}^S (n_i - \sigma_i)$ -dimensional hypercube

spanned by vectors  $\epsilon E_i^j$  ( $\epsilon \rightarrow 0$ ) for  $i = 1, \dots, S, j = 2, \dots, n_i - (\sigma_i - 1)$  at any location on the segment of  $\Psi_x(t)$  on  $\prod_{i=1}^S ({}^i\mathbb{L}_{n_i}^\sigma \setminus {}^i\mathbb{L}_{n_i}^{\sigma+1})$ . When  $\mathcal{C}$  passes into  $({}^1\mathbb{L}_{n_1}^{\sigma-1} \setminus {}^1\mathbb{L}_{n_1}^\sigma) \times \prod_{i=2}^S ({}^i\mathbb{L}_{n_i}^\sigma \setminus {}^i\mathbb{L}_{n_i}^{\sigma+1})$  it is transformed into the  $\sum_{i=1}^S (n_i - \sigma_i)$ -dimensional parallelepiped  $\mathcal{C}'$  spanned by the vectors  $\epsilon(E_i^j + {}^1\alpha_i^j E_1^1)$  for  $i = 1, \dots, S, j = 2, \dots, n_i - (\sigma_i - 1)$ , where the  ${}^1\alpha_i^j$ 's are evaluated at the point  $\Psi_x(t) \cap P_1^I$ .

Vectors  $E_i^j$  for  $i = 1, \dots, S, j = 1, \dots, n_i - (\sigma_i - 1)$  are by assumption orthonormal. Let  $A$  and  $A'$  denote the matrices associated with the vectors spanning  $\mathcal{C}$  and  $\mathcal{C}'$  represented as row coordinate vectors with respect to the above basis.  $A$  and  $A'$  are then the  $(\sum_{i=1}^S n_i - \sigma) \times (\sum_{i=1}^S n_i - (\sigma_i - 1))$  matrices:

$$A = \begin{pmatrix} 0 & \epsilon & 0 & \dots & 0 \\ 0 & 0 & \epsilon & \dots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & \dots & \epsilon \end{pmatrix} \quad \text{and} \quad A' = \begin{pmatrix} {}^1\alpha_1^2 \epsilon & \epsilon & 0 & \dots & 0 \\ {}^1\alpha_1^3 \epsilon & 0 & \epsilon & \dots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ {}^1\alpha_S^{n_S - (\sigma_S - 1)} \epsilon & 0 & 0 & \dots & \epsilon \end{pmatrix}. \quad (4.1)$$

In  $A$ , columns corresponding to  $E_i^1$  for  $i = 1, \dots, S$  are 0 vectors. All other columns contain an  $\epsilon$  at an appropriate location.  $A'$  is identical to  $A$  except for the first column, which is replaced by the vector  $({}^1\alpha_1^2 \epsilon, \dots, {}^1\alpha_1^{n_1 - (\sigma_1 - 1)} \epsilon, \dots, {}^1\alpha_S^2 \epsilon, \dots, {}^1\alpha_S^{n_S - (\sigma_S - 1)} \epsilon)^T$ .

The  $\sum_{i=1}^S (n_i - \sigma_i)$ -dimensional measure of  $\mathcal{C}$  and  $\mathcal{C}'$  can then be computed as the square root of the Gram determinants<sup>6</sup> of the respective matrices,  $A$  and  $A'$ . They are

$$|A| = \epsilon^{\sum_{i=1}^S n_i - \sigma}$$

and

$$|A'| = \epsilon^{\sum_{i=1}^S n_i - \sigma} \times \sqrt{1 + \sum_{i=1, j=2}^{S, n_i - (\sigma_i - 1)} ({}^1\alpha_i^j)^2}.$$

It follows from  $\sum_{i,j} {}^1\alpha_i^j = 1$  that the volume of  $\mathcal{C}'$  is strictly greater than that of  $\mathcal{C}$ .

**4.2 Contraction.** We demonstrate that a trajectory is contractile at the death of a spike. We consider the adjacent segments of  $\Psi_x(t)$  described in section 3.2.2. Let  $\mathcal{C}$  denote an infinitesimal  $\sum_{i=1}^S (n_i - \sigma_i)$ -dimensional

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<sup>6</sup> The Gram determinant of matrix  $B$  is given by  $\det(B * B^T)$ . The square root of the Gram determinant is also known as the modulus of  $B$  and is represented as  $|B|$ .

hypercube spanned by vectors  $\in E_i^j$  ( $\epsilon \rightarrow 0$ ) for  $i = 1, \dots, S$ ,  $j = 1, \dots, (n_i - \sigma_i)$  at any location on the segment of  $\Psi_x(t)$  on  $\prod_{i=1}^S ({}^i\mathbb{L}_{n_i}^{\sigma_i} \setminus {}^i\mathbb{L}_{n_i}^{\sigma_i+1})$ . When  $\mathcal{C}$  passes into  $({}^1\mathbb{L}_{n_1}^{\sigma_1+1} \setminus {}^1\mathbb{L}_{n_1}^{\sigma_1+2}) \times \prod_{i=2}^S ({}^i\mathbb{L}_{n_i}^{\sigma_i} \setminus {}^i\mathbb{L}_{n_i}^{\sigma_i+1})$ , it is transformed into the  $(\sum_{i=1}^S n_i - \sigma_i)$ -1-dimensional hypercube  $\mathcal{C}'$  spanned by the vectors  $\in E_i^j$  for all  $i = 1, \dots, S$  and  $j = 1, \dots, (n_i - \sigma_i)$  except  $i = j = 1$ . In other words, the  $\sum_{i=1}^S (n_i - \sigma_i)$ -1-dimensional hypercube  $\mathcal{C}$  collapses along  $E_1^1$  to produce a  $(\sum_{i=1}^S n_i - \sigma_i)$ -1-dimensional hypercube  $\mathcal{C}'$ . Any lower-dimensional parallelepiped inside  $\mathcal{C}$  spanned by the vectors  $\in (E_i^j + \beta_i^j E_1^1)$  for  $i = 1, \dots, S$ ,  $j = 1, \dots, (n_i - \sigma_i)$  except  $i = j = 1$  such that  $\beta_i^j \neq 0$  for some  $i, j$  therefore experiences a contraction in volume as it passes from  $\prod_{i=1}^S ({}^i\mathbb{L}_{n_i}^{\sigma_i} \setminus {}^i\mathbb{L}_{n_i}^{\sigma_i+1})$  into  $({}^1\mathbb{L}_{n_1}^{\sigma_1+1} \setminus {}^1\mathbb{L}_{n_1}^{\sigma_1+2}) \times \prod_{i=2}^S ({}^i\mathbb{L}_{n_i}^{\sigma_i} \setminus {}^i\mathbb{L}_{n_i}^{\sigma_i+1})$ .

**4.3 Folding.** We demonstrate that folding can occur across a series of births and deaths of spikes. Let  $\tilde{\mathcal{C}}$  denote a  $\sum_{i=1}^S (n_i - \sigma_i)$ -dimensional hypercuboid of maximal measure in the feasible section of  $\prod_{i=1}^S ({}^i\mathbb{L}_{n_i}^{\sigma_i} \setminus {}^i\mathbb{L}_{n_i}^{\sigma_i+1})$  that is transformed after time  $\frac{\Upsilon t}{2\pi}$  into a  $\sum_{i=1}^S (n_i - \sigma_i)$ -dimensional hypersurface  $\tilde{\mathcal{C}}'$  in  $({}^1\mathbb{L}_{n_1}^{\sigma_1-1} \setminus {}^1\mathbb{L}_{n_1}^{\sigma_1}) \times \prod_{i=2}^S ({}^i\mathbb{L}_{n_i}^{\sigma_i} \setminus {}^i\mathbb{L}_{n_i}^{\sigma_i+1})$ , past the birth of a spike at neuron 1. Let  $\tilde{\mathcal{C}}$  be represented as  $\prod_{i=1, j=2}^{S, n_i - (\sigma_i - 1)} [a_i^j, a_i^j + \Delta_i]$ , and  $\tilde{\mathcal{C}}'$  as  $x_1^1 = h(x_1^2, \dots, x_1^{n_1 - (\sigma_1 - 1)}, x_2^2, \dots, x_2^{n_2 - (\sigma_2 - 1)}, \dots, x_S^2, \dots, x_S^{n_S - (\sigma_S - 1)})$  in local coordinates, where  $x_i^j \in [a_i^j + t, a_i^j + \Delta_i + t]$  for  $i = 1, \dots, S$ ,  $j = 2, \dots, n_i - (\sigma_i - 1)$ . Then  $P_1^l \cap \prod_{i=1, j=2}^{S, n_i - (\sigma_i - 1)} [a_i^j + (t - T), a_i^j + \Delta_i + (t - T)]$  (the hypersurface  $\tilde{\mathcal{C}}$  after time  $\frac{\Upsilon}{2\pi}(t - T)$  intersected with  $P_1^l$ ),<sup>7</sup> when translated by a distance  $T$  along all dimensions  $(\partial/\partial x_i^j)$  for  $i = 1, \dots, S$ ,  $j = 2, \dots, n_i - (\sigma_i - 1)$ ,  $i = j = 1$ , yields identically the hypersurface  $h(\cdot) = T$  in  $\tilde{\mathcal{C}}'$ . The shape of  $\tilde{\mathcal{C}}'$  and the result of a dimensional collapse along any  $E_i^j$  for  $i = 1, \dots, S$ ,  $j = 2, \dots, n_i - (\sigma_i - 1)$  on  $\tilde{\mathcal{C}}'$  is therefore completely specified by the position of  $\tilde{\mathcal{C}}$  in  $\prod_{i=1}^S ({}^i\mathbb{L}_{n_i}^{\sigma_i} \setminus {}^i\mathbb{L}_{n_i}^{\sigma_i+1})$  and the nature of  $P_1^l \cap \prod_{i=1}^S ({}^i\mathbb{L}_{n_i}^{\sigma_i} \setminus {}^i\mathbb{L}_{n_i}^{\sigma_i+1})$ .

We now assume that  $P_1(\cdot)$  is unimodal with respect to all variables that, at the given moment, correspond to effective spikes. Any coordinate curve of an effective variable can then have only point intersections (at most two) with  $P_1^l \cap \prod_{i=1}^S ({}^i\mathbb{L}_{n_i}^{\sigma_i} \setminus {}^i\mathbb{L}_{n_i}^{\sigma_i+1})$ . Finally, if a spike, over its finite lifetime, is effective in the generation of one or more spikes, then there exists, trivially, a last spike that it is effective on. We assume, without loss of generalization, that  $x_2^2$  is one such spike, and  $x_1^1$  is the final spike it is effective on.

<sup>7</sup> We use  $P_1^l$  and  $P_1^S$  to represent both the hypersurfaces in the phase-space and the corresponding hypersurfaces in local coordinates. The context will determine which hypersurface is being referred to.

In order for  $\tilde{\mathcal{C}}'$  to be curved in such a manner that at the subsequent death of  $x_2^2$  (irrespective of any number of intermediate births and/or deaths of spikes) it folds upon itself, there must exist a coordinate curve for  $x_2^2$  that intersects  $P_1^I \cap \tilde{\mathcal{C}}$  twice for at least one position of  $\tilde{\mathcal{C}}$ .<sup>8</sup> Since  $P_1(\cdot)$  is  $C^\infty$  and  $P_1(\cdot)|_{x_2^2=0} = P_1(\cdot)|_{x_2^2=2\pi}$  when all other variables are held constant, such coordinate curves exist for all points on  $P_1^S \cap \prod_{i=1, j=2}^{S, n_i - (\sigma - 1)}(0, 2\pi)$ . Furthermore, if  $|\partial P_1 / \partial x_2^2|$  at the intersection of any such coordinate curve with  $P_1^S$ , at the falling phase of  $P_1(\cdot)$ , is not so large as to make  $\sum_{i=1, j=2}^{S, n_i - (\sigma - 1)} \partial P_1 / \partial x_i^j < 0$ ,<sup>9</sup> then  $dP_1(\cdot)/dt \geq 0$  is satisfied by both intersections. Consequently, the coordinate curve intersects twice with the hypersurface  $P_1^I \cap \prod_{i=1, j=2}^{S, n_i - (\sigma - 1)}(0, 2\pi)$ .

The only question that remains unresolved is whether both intersections of such a coordinate curve lie on  $\prod_{i=1}^S ({}^i\overline{\mathbb{L}}_{n_i}^{\sigma} \setminus {}^i\overline{\mathbb{L}}_{n_i}^{\sigma+1})$ . While this question can be settled only when the specific instantiation of  $P_1(\cdot)$  is known, there are two aspects of the system that have a significant impact on the answer. First, the closer  $\mathcal{T}$  is to  $\max\{P_1(x) \mid x \in \prod_{i=1, j=2}^{S, n_i - (\sigma - 1)}(0, 2\pi)\}$  and the tighter the peak of  $P_1(\cdot)$  is, the greater the chances are that a coordinate curve exists in  $\prod_{i=1}^S ({}^i\overline{\mathbb{L}}_{n_i}^{\sigma} \setminus {}^i\overline{\mathbb{L}}_{n_i}^{\sigma+1})$  that intersects  $P_1^I$  twice. Second, the largest  $\Delta_i$  for which a  $\sum_{i=1}^S (n_i - \sigma_i)$ -dimensional hypercuboid can fit into the feasible section of  $\prod_{i=1}^S ({}^i\overline{\mathbb{L}}_{n_i}^{\sigma} \setminus {}^i\overline{\mathbb{L}}_{n_i}^{\sigma+1})$  is  $(\frac{2\pi}{(n_i - \sigma_i)} - \frac{(n_i - \sigma_i)r_i}{(n_i - \sigma_i)Y})$ . Clearly, folding of  $\tilde{\mathcal{C}}'$  is more likely when  $(n_i - \sigma_i)$  is small, that is, when the system is sparsely active.

## 5 Local Cross-Section Analysis

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Whereas we have just demonstrated that both expansion and contraction occur locally around any trajectory, the cumulative effect of such events remains obscure. We address this issue in this section with regard to the dynamics of the system set up to model a typical neocortical column. The solution is presented in stages. First, the problem is phrased in terms of a quantifiable property of a particular matrix. A deterministic process that constructs the matrix incrementally is described. Next, each step in the process is reformulated as a stochastic event. The event is analyzed, and conclusions are drawn regarding its effect on the matrix. Physiological parameters of a typical neocortical column are then used to identify the qualitative properties of trajectories in various sections of the phase-space.

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<sup>8</sup>  $x_2^2$  is by assumption not effective on any intermediate births of spikes. The two intersections of the coordinate curve with  $\tilde{\mathcal{C}}'$  therefore remain on a coordinate curve of  $x_2^2$  after such births. Any intermediate deaths of spikes have no impact on whether the intersections in question remain on a coordinate curve.

<sup>9</sup> This is generally the case for excitatory spikes in the cortex. The impact of such spikes on the potential function is given by a steep rising phase and a relatively gentle falling phase.

**5.1 The Deterministic Process.** We consider the class of trajectories that are not drawn into the trivial fixed point  $\prod_{i=1}^S \bar{\mathbb{L}}_{n_i}^{n_i}$  (state of quiescence). We demonstrated that if  $\langle \Delta x_1^2, \dots, \Delta x_1^{n_1 - (\sigma_1 - 1)}, \dots, \Delta x_S^2, \dots, \Delta x_S^{n_S - (\sigma_S - 1)} \rangle^T$  and  $\langle \Delta x_1^1, \dots, \Delta x_1^{n_1 - \sigma_1}, \dots, \Delta x_S^{n_S - \sigma_S} \rangle^T$  are, respectively, perturbations on a trajectory before the birth and the death of a spike at neuron 1, and the perturbations after the corresponding events are  $\langle \Delta y_1^1, \dots, \Delta y_1^{n_1 - (\sigma_1 - 1)}, \dots, \Delta y_S^2, \dots, \Delta y_S^{n_S - (\sigma_S - 1)} \rangle^T$  and  $\langle \Delta y_1^2, \dots, \Delta y_1^{n_1 - \sigma_1}, \dots, \Delta y_S^1, \dots, \Delta y_S^{n_S - \sigma_S} \rangle^T$ , then

$$\begin{pmatrix} \Delta y_1^1 \\ \Delta y_1^2 \\ \vdots \\ \Delta y_S^{n_S - (\sigma_S - 1)} \end{pmatrix} = \begin{pmatrix} \alpha_1^2 & \dots & \alpha_S^{n_S - (\sigma_S - 1)} \\ 1 & 0 & 0 \\ \vdots & \ddots & \vdots \\ 0 & 0 & 1 \end{pmatrix} \begin{pmatrix} \Delta x_1^2 \\ \vdots \\ \Delta x_S^{n_S - (\sigma_S - 1)} \end{pmatrix} \quad (5.1)$$

and

$$\begin{pmatrix} \Delta y_1^2 \\ \vdots \\ \Delta y_S^{n_S - \sigma_S} \end{pmatrix} = \begin{pmatrix} 0 & 1 & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & 1 \end{pmatrix} \begin{pmatrix} \Delta x_1^1 \\ \Delta x_1^2 \\ \vdots \\ \Delta x_S^{n_S - \sigma_S} \end{pmatrix}. \quad (5.2)$$

If we denote by  $A_k$  the matrix that corresponds to the event  $\Psi_x(t_k)$ , by the column vector  $\Delta \mathbf{x}_0$  a perturbation just prior to the event  $\Psi_x(t_1)$ , and by the column vector  $\Delta \mathbf{x}_k$  the corresponding perturbation just past the event  $\Psi_x(t_k)$ , then  $\Delta \mathbf{x}_k = A_k * A_{k-1} * \dots * A_1 * \Delta \mathbf{x}_0$ . Alternatively, if  $A_0^k$  denotes the product  $A_k * A_{k-1} * \dots * A_1$ , then  $\Delta \mathbf{x}_k = A_0^k * \Delta \mathbf{x}_0$ , where  $A_0^k$  is defined recursively as  $A_0^0 = I$  (the identity matrix) and  $\forall k \geq 0, A_0^{k+1} = A_{k+1} * A_0^k$ .

Given the nature of these matrices, we deduce that (1) if  $\Psi_x(t_{k+1})$  corresponds to the birth of a spike at neuron  $l$ , then  $A_0^{k+1}$  can be generated from  $A_0^k$  by identifying rows  $r_i^j$  in  $A_0^k$  that correspond to spikes that are effective in the birth of the given spike, and introducing a new row  $\sum_{i,j} \alpha_i^j r_i^j$  at an appropriate location into  $A_0^k$ , and (2) if  $\Psi_x(t_{k+1})$  corresponds to the death of a spike at neuron  $l$ , then  $A_0^{k+1}$  can be generated from  $A_0^k$  by identifying the row in  $A_0^k$  that corresponds to the given spike, and deleting it from  $A_0^k$ . Finally, since we shall be analyzing periodic orbits and trajectories, both the initial and the final perturbations must lie on local cross-sections of  $\Psi_x(t)$ . The velocity field being  $\sum_{i=1, j=2}^{S, n_i - (\sigma_i - 1)} (2\pi / \Upsilon) E_i^j$ , the initial perturbation must satisfy  $\sum_{i=1, j=2}^{S, n_i - (\sigma_i - 1)} \Delta x_i^j = 0$ , and the final perturbation must be adjusted along the orbit (each component must be adjusted by the same quantity) to satisfy the same equation. In terms of matrix operations, this translates

into  $B * A_0^k * C$ , where  $B$  and  $C$  (assuming  $A_0^k$  is an  $(m \times n)$  matrix) are the  $(m - 1 \times m)$  and  $(n \times n - 1)$  matrices:

$$B = \begin{pmatrix} 1 - \frac{1}{m} & -\frac{1}{m} & \dots & -\frac{1}{m} & -\frac{1}{m} \\ -\frac{1}{m} & 1 - \frac{1}{m} & \dots & -\frac{1}{m} & -\frac{1}{m} \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ -\frac{1}{m} & -\frac{1}{m} & \dots & 1 - \frac{1}{m} & -\frac{1}{m} \end{pmatrix}, \quad C = \begin{pmatrix} 1 & 0 & \dots & 0 \\ 0 & 1 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & 1 \\ -1 & -1 & \dots & -1 \end{pmatrix}. \quad (5.3)$$

If  $\Psi_x(t)$  is aperiodic,  $\Delta x'_k = B * A_0^k * C * \Delta x'_0$  for arbitrary value of  $k$  specifies the relation between an initial and a final perturbation, both of which lie on transverse sections of the trajectory. The sensitivity of the trajectory to initial conditions is then determined by  $\|B * A_0^k * C\|_2$ .<sup>10</sup> If  $\lim_{k \rightarrow \infty} \|B * A_0^k * C\|$  is unbounded (0), then the trajectory is sensitive (insensitive) to initial conditions. If, instead,  $\Psi_x(t)$  is periodic with  $\Psi_x(t_1) = \Psi_x(t_{k+1})$  (a closed orbit with period  $(t_{k+1} - t_1)$ ), then  $A_0^k$  is a square matrix and  $\Delta x'_k = B * A_0^k * C * \Delta x'_0$  is a Poincaré map. The stability of the periodic orbit is then determined by  $\rho(B * A_0^k * C)$ .<sup>11</sup> If  $\rho(B * A_0^k * C) > 1 (< 1)$ , that is,  $\lim_{r \rightarrow \infty} \|(B * A_0^k * C)^r\|$  is unbounded (0), then the periodic orbit is unstable (stable).

It should be noted that  $\lim_{k \rightarrow \infty} \|B * A_0^k * C\|$  and  $\lim_{r \rightarrow \infty} \|(B * A_0^k * C)^r\|$ , by virtue of the nature of their limiting values, yield identical results irrespective of the choice of the matrix norm. We use the Frobenius norm ( $\|A\|_F = \sqrt{\text{Trace}(A^T * A)}$ ) in the upcoming analysis.

*5.1.1 The Revised Process.* We present a revised process that constructs a matrix  $\tilde{A}_0^k$  that substantially simplifies the computation of the spectral properties of  $B * A_0^k * C$ . We begin with  $\tilde{A}_0^0 = I - \frac{1}{n}(\mathbf{1})$ , where  $(\mathbf{1})$  represents the matrix all of whose elements are 1, and  $n = \sum_{i=1}^S (n_i - \sigma_i)$  is the number of components in the initial perturbation. We then proceed with the rest of the process (generating  $\tilde{A}_0^{k+1}$  from  $\tilde{A}_0^k$ ) unaltered. The following lemma relates the properties of  $\tilde{A}_0^k$  to those of  $B * A_0^k * C$ .

**Lemma 1.** *If  $\tilde{A}_0^k$  is an  $(n \times n)$  square matrix, then if  $\lim_{r \rightarrow \infty} \|(I - \frac{1}{n}(\mathbf{1})) * (\tilde{A}_0^k)^r\| = \lim_{r \rightarrow \infty} \|\tilde{A}_0^0 * (\tilde{A}_0^k)^r\|$  is unbounded (0), then  $\lim_{r \rightarrow \infty} \|(B * A_0^k * C)^r\|$  is unbounded (0). If instead  $\tilde{A}_0^k$  is an  $(m \times n)$  matrix, then if  $\lim_{k \rightarrow \infty} \|(I - \frac{1}{m}(\mathbf{1})) * \tilde{A}_0^k\|$  is unbounded (0),  $\lim_{k \rightarrow \infty} \|B * A_0^k * C\|$  is unbounded (0).*

<sup>10</sup>  $\|A\|_2$  is the spectral norm of the matrix  $A$  (the natural matrix norm induced by the  $l_2$  norm), that is,  $\|A\|_2 = \sup_{x \neq 0} \frac{\|Ax\|_2}{\|x\|_2}$ .

<sup>11</sup>  $\rho(A)$  is the spectral radius of the matrix  $A$ , that is,  $\rho(A) = \max_{1 \leq i \leq n} |\lambda_i|$  where the  $\lambda_i$ 's are the eigenvalues of the matrix ( $Ax_i = \lambda_i x_i$ ).

**Proof.**  $\tilde{A}_0^k$  is an  $(n \times n)$  square matrix: The sum of the elements of any row in  $A_0^0 = I$  is 1. Since  $\forall l \sum_{i,j} \alpha_i^j = 1$ , it follows that  $\forall k \geq 0$  the sum of the elements of any row in  $A_0^k$  remains 1. The sum of the elements of any row in  $\tilde{A}_0^0$  being 0, the same argument proves that  $\forall k \geq 0$  the sum of the elements of any row in  $\tilde{A}_0^k$  is 0. Moreover, induction on  $k$  proves that  $\forall k \tilde{A}_0^k = A_0^k - \frac{1}{n}(\mathbf{1})$ .

We also note that  $C * B = I - \frac{1}{n}(\mathbf{1})$ ,  $\tilde{A}_0^k * \frac{1}{n}(\mathbf{1}) = (\mathbf{0})$ , and  $\frac{1}{n}(\mathbf{1}) * \frac{1}{n}(\mathbf{1}) = \frac{1}{n}(\mathbf{1})$ , and conclude via induction on  $r$  that  $(B * A_0^k * C)^r = B * (\tilde{A}_0^k)^r * C$ .  $B$  being  $\tilde{A}_0^0$  without the last row,  $B * (\tilde{A}_0^k)^r$  is  $\tilde{A}_0^0 * (\tilde{A}_0^k)^r$  without the last row. If  $\lim_{r \rightarrow \infty} \|\tilde{A}_0^0 * (\tilde{A}_0^k)^r\| = 0$ , then  $\lim_{r \rightarrow \infty} \tilde{A}_0^0 * (\tilde{A}_0^k)^r = (\mathbf{0})$ . Hence,  $\lim_{r \rightarrow \infty} B * (\tilde{A}_0^k)^r = (\mathbf{0})$ . If, on the other hand,  $\lim_{r \rightarrow \infty} \|\tilde{A}_0^0 * (\tilde{A}_0^k)^r\|$  is unbounded, then so is  $\lim_{r \rightarrow \infty} \|B * (\tilde{A}_0^k)^r\|$  since  $\tilde{A}_0^0 * (\tilde{A}_0^k)^r$  amounts to deleting the row mean from each row of  $(\tilde{A}_0^k)^r$ . Finally, the product with  $C$  does not have an impact on the unboundedness of the matrix because the sum of the elements of any row in  $B * (\tilde{A}_0^k)^r$  is 0.

$\tilde{A}_0^k$  is not constrained to be a square matrix:  $B$  is  $I - \frac{1}{m}(\mathbf{1})$  with the last row eliminated. Moreover, since  $\forall k \geq 0 \tilde{A}_0^k = A_0^k - \frac{1}{n}(\mathbf{1})$ , we have  $B * A_0^k = B * \tilde{A}_0^k$ . The remainder of the proof follows along the lines of the previous case.

**5.2 The Stochastic Process.** We present a stochastic counterpart for the above process. The process is begun with an  $(n \times n)$  matrix  $\mathbb{A}$ , each of whose  $n$  rows are drawn independently from a uniform distribution on  $[-0.5, 0.5]^n$ . Therefore, if  $v_1, v_2, \dots, v_n$  denote the  $n$  rows of the matrix, then  $E(v_i) = (0, 0, \dots, 0)$ , where  $E(\cdot)$  denotes the expected value. Next, the row mean  $\bar{v} = (1/n) \sum_{i=1}^n v_i$  is deducted from each row of  $\mathbb{A}$ . This yields  $\tilde{\mathbb{A}}_0 * \mathbb{A}$ , which we set to  $\mathbb{A}_0^0$ . It is clear that  $E(v_i)$  in  $\mathbb{A}_0^0$  remains  $(0, 0, \dots, 0)$ . Let  $\mathbb{A}_0^k$  for some  $k$  be an  $(m \times n)$  matrix where  $m$  is a large but finite integer.

For the birth of a spike,  $\mathbb{A}_0^{k+1}$  is generated from  $\mathbb{A}_0^k$  as follows:

1. Randomly sample the space of row vectors in  $\mathbb{A}_0^k$  and choose  $p$  rows,  $v_1, v_2, \dots, v_p$ , where  $p$  is a random number chosen from a predefined range  $[P_{low}, P_{high}]$ .  $m$  being large, it can safely be assumed that the rows are chosen with replacement even if they are not.
2. Choose  $p$  i.i.d. random variables  $X_1, X_2, \dots, X_p$  from a given independent distribution. Let  $x_1, x_2, \dots, x_p$  be the derived random variables  $x_i = X_i / \sum_{i=1}^p X_i$ .
3. Construct  $v_{new} = \sum_{i=1}^p x_i v_i$ , and insert the row at a random location into  $\mathbb{A}_0^k$  to generate  $\mathbb{A}_0^{k+1}$ .

For the death of a spike,  $\mathbb{A}_0^{k+1}$  is generated from  $\mathbb{A}_0^k$  as follows:

1. Randomly choose a row from the space of row vectors in  $\mathbb{A}_0^k$ .



2. Delete the row from  $\mathbb{A}_0^k$  to generate  $\mathbb{A}_0^{k+1}$ .

In the case of a system set up to model a typical neocortical column, the deterministic process described earlier can reasonably be viewed as the stochastic process described above. First, the connectivity between neurons within a column, while having evolved to achieve a specific function, has been experimentally ascertained to fit a uniform distribution (Schüz, 1992). Therefore, when neurons in the system are spiking at comparable rates, one can reasonably assume that each spike, during its finite lifetime, is equally likely to be effective in the birth of a new spike somewhere in the system. Second, whereas  $v_i$  specifies the sensitivity of the corresponding spike to the initial set of spikes,  $x_i$  specifies the sensitivity of the spike that just originated to the spike in question. Clearly the two are causally independent. Third, whereas spikes that are effective in the birth of a new spike are related spatially in the system, this does not translate into any necessary relation among the elements of the corresponding rows. Finally, the location of afferent synapses on the collaterals of neurons in a column has been shown to fit a statistical distribution (Braitenberg & Schüz, 1991). Since  $X_1, \dots, X_p$  (corresponding to the various  $\partial P / \partial x_i^j$ 's) depend on the positions of the corresponding spikes and the nature of  $P$ , they can reasonably be approximated by i.i.d. random variables.

If  $\mathbb{A}_0^k = \tilde{A}_0^k * \mathbb{A}$ , and  $\mathbb{A}_0^{k+1}$  is generated as above, then  $\mathbb{A}_0^{k+1} = \tilde{A}_0^{k+1} * \mathbb{A}$ . On the one hand, if a row is deleted from  $\mathbb{A}_0^k$  to generate  $\mathbb{A}_0^{k+1}$ , the act corresponds to the deletion of the corresponding row from  $\tilde{A}_0^k$  to generate  $\tilde{A}_0^{k+1}$ . On the other hand, if  $v_1, v_2, \dots, v_p$  are the rows chosen from  $\mathbb{A}_0^k$  to construct  $v_{new}$ , and  $u_1, u_2, \dots, u_p$  are the corresponding rows in  $\tilde{A}_0^k$ , since  $v_i = \langle u_i.c_1, u_i.c_2, \dots, u_i.c_n \rangle$  (where  $c_1, \dots, c_n$  are the columns of  $\mathbb{A}$ ),  $\sum_{i=1}^p x_i v_i = \langle (\sum x_i u_i).c_1, (\sum x_i u_i).c_2, \dots, (\sum x_i u_i).c_n \rangle$ . Therefore,  $\mathbb{A}_0^{k+1} = \tilde{A}_0^{k+1} * \mathbb{A}$ .

The following lemma describes the statistical properties of the rows of the matrix past the act of addition and/or deletion of a row.  $V(\cdot)$  denotes the variance of the rows, that is,  $V(v_i) = E((v_i - \mu).(v_i - \mu))$ , and  $C(\cdot)$  denotes the covariance between rows, that is,  $C(v_i, v_j) = E((v_i - \mu).(v_j - \mu))_{i \neq j}$ .

**Lemma 2.** *Let  $E_k(v_i) = \mu$ ,  $V_k(v_i) = \sigma^2$ , and  $C_k(v_i, v_j) = \xi^2$  after the  $k$ th step (the result being the  $(m \times n)$  matrix  $\mathbb{A}_0^k$ ).*

- i. *If the  $(k + 1)$ th step involves the deletion of a row ( $v_{del}$ ), then  $E_{k+1}(v_i) = \mu$ , and  $V_{k+1}(v_i) - C_{k+1}(v_i, v_j) = (\sigma^2 - \xi^2)$ .*
- ii. *If instead, the  $(k + 1)$ th step involves the addition of a row ( $v_{new}$ ), then  $E_{k+1}(v_i) = \mu$ . Moreover, if  $pE(x_i^2) = (1 + \Delta)$  for some  $\Delta \in \mathbb{R}$  ( $\Delta > -1$  necessarily), then  $V_{k+1}(v_i) - C_{k+1}(v_i, v_j) = (1 + \frac{\Delta(m-1)-2}{m(m+1)})(\sigma^2 - \xi^2)$ .*

**Proof.**

i. Since  $v_{del}$  is chosen randomly from the population of rows in the matrix, we have  $E(v_{del}) = E_k(v_i) = \mu$ ,  $V(v_{del}) = V_k(v_i) = \sigma^2$ , and  $C(v_{del}, v_i) = C_k(v_i, v_j) = \xi^2$ . Consequently,  $E_{k+1}(v_i) = \mu$  and  $V_{k+1}(v_i) - C_{k+1}(v_i, v_j) = (\sigma^2 - \xi^2)$ .

Before considering ii, we note that for the derived random variables  $x_1, x_2, \dots, x_p$ , (a)  $\forall i$ ,  $pE(x_i) = 1$ , and (b)  $\forall i, j$ ,  $i \neq j$ ,  $pE(x_i^2) + p(p-1)E(x_i x_j) = 1$ .

(a) follows from  $\sum_{i=1}^p E(X_i / \sum X_i) = 1$ , and  $\forall i, j$   $E(X_i / \sum X_i) = E(X_j / \sum X_j)$  because of the i.i.d. nature of the  $X_i$ 's.

(b) follows from  $\sum_{i=1}^p E(X_i^2 / (\sum X_i)^2) + \sum_{i=1, j=1, i \neq j}^{p, p} E((X_i X_j) / (\sum X_i)^2) = 1$ , and that, the  $X_i$ 's being i.i.d.,  $\forall i, j$   $E(X_i^2 / (\sum X_i)^2) = E(X_j^2 / (\sum X_j)^2)$  and  $\forall i, j$ ,  $i \neq j$   $E((X_i X_j) / (\sum X_i)^2)$  yields the same result irrespective of the values of  $i$  and  $j$ .

ii.  $E(v_{new}) = E_k(\sum_{i=1}^p x_i v_i) = \sum_{i=1}^p E_k(x_i v_i)$ . Since the  $x_i$ 's are chosen independent of the  $v_i$ 's,  $E(v_{new}) = \sum_{i=1}^p E(x_i) E_k(v_i) = \sum_{i=1}^p \frac{1}{p} E_k(v_i) = \mu$ . Moreover, since  $E(v_i) = \langle 0, 0, \dots, 0 \rangle$  for the initial population of row vectors, we can now conclude that  $\forall k$ ,  $E_k(v_i) = \langle 0, 0, \dots, 0 \rangle$ .

Since  $\mu = \langle 0, 0, \dots, 0 \rangle$ ,  $V(v_{new}) = E(v_{new} \cdot v_{new}) = E_k(\sum_{i=1}^p x_i v_i \cdot \sum_{i=1}^p x_i v_i) = E_k(\sum_{i=1}^p x_i^2 (v_i \cdot v_i) + E_k(\sum_{i=1, j=1, i \neq j}^{p, p} x_i x_j (v_i \cdot v_j)))$ . Since the  $x_i$ 's are chosen independent of the  $v_i$ 's,  $V(v_{new}) = E(x_i^2) E_k(\sum_{i=1}^p v_i \cdot v_i) + E(x_i x_j) E_k(\sum_{i=1, j=1, i \neq j}^{p, p} v_i \cdot v_j) = \frac{1+\Delta}{p} E_k(\sum_{i=1}^p v_i \cdot v_i) + \frac{-\Delta}{p(p-1)} E_k(\sum_{i=1, j=1, i \neq j}^{p, p} v_i \cdot v_j) = (1+\Delta)\sigma^2 - \Delta(\frac{1}{m}\sigma^2 + \frac{m-1}{m}\xi^2) = \sigma^2 + \Delta \frac{m-1}{m} (\sigma^2 - \xi^2)$ .

Likewise,  $C(v_{new}, v_i) = E(v_{new} \cdot v_i) = p(\frac{1}{m}(\frac{1}{p}\sigma^2) + \frac{m-1}{m}(\frac{1}{p}\xi^2)) = \xi^2 + \frac{1}{m}(\sigma^2 - \xi^2)$ . The two results give rise to the recurrence relations:  $V_{k+1} = V_k + \frac{\Delta(m-1)}{m(m+1)}(V_k - C_k)$  and  $C_{k+1} = C_k + \frac{2}{m(m+1)}(V_k - C_k)$ . Therefore,  $V_{k+1} - C_{k+1} = (1 + \frac{\Delta(m-1)-2}{m(m+1)})(V_k - C_k)$ .

Finally, in the base case let  $E(v_i \cdot v_i) = \sigma_0^2$  for  $\mathbb{A}$ .  $E(v_i \cdot v_j)_{i \neq j} = 0$  since  $v_i$  is chosen independent of  $v_j$ , and  $E(v_i) = \mu = \langle 0, 0, \dots, 0 \rangle$ . In the case of  $\mathbb{A}_0^0 = \tilde{\mathbb{A}}_0^0 * \mathbb{A}$ ,  $E(v_i \cdot v_i) = (1 - \frac{1}{n})^2 \sigma_0^2 + (\frac{n-1}{n^2}) \sigma_0^2 = (1 - \frac{1}{n}) \sigma_0^2$ .  $E(v_i \cdot v_j)_{i \neq j} = \frac{-2}{n} (1 - \frac{1}{n}) \sigma_0^2 + (\frac{n-2}{n^2}) \sigma_0^2 = -\frac{1}{n} \sigma_0^2$ . Therefore,  $V_0 - C_0 = \sigma_0^2$ .

Since we have assumed that the trajectory is not drawn into the trivial fixed point, if  $\mathbb{A}_0^k$  is an  $(m_k \times n)$  matrix, then  $m_k \in [M_{high}, M_{low}]$  where  $M_{low} \gg 0$ . Moreover,  $E(\|\mathbb{A}_0^k\|_F) = \sqrt{m_k V_k}$ . For the sake of brevity, we shall henceforth refer to  $V_k(v_i)$  and  $C_k(v_i, v_j)$  for rows in  $\mathbb{A}_0^k$  as  $V(\mathbb{A}_0^k)$  and  $C(\mathbb{A}_0^k)$ , respectively.

The following theorem identifies the local properties of trajectories based on the above lemma. In all cases, we assume that the trajectory is not drawn into the trivial fixed point  $\prod_{i=1}^S \prod_{m_i}^{i \in m_i}$ . It might be claimed that without external input sustaining the dynamics of the system, an aperiodic trajectory that is

not drawn into the fixed point is not realizable. We therefore consider two cases: one with and one without external input. For the case with external input, the connectivity of the neurons in the system, whether they are input neurons or interneurons, is assumed to be uniform. The number of spikes generated within the system for any given trajectory  $\Psi_x(t)$  since time  $t_1$  is denoted by  $I(t)$ , and the number of external spikes introduced into the system since time  $t_1$  is denoted by  $E(t)$ .

**Theorem 1** (Sensitivity). *Let  $\Psi_x(t)$  be a trajectory that is not drawn into the trivial fixed point.*

- i. *Given a system receiving no external input, if  $\Psi_x(t)$  is aperiodic, then if  $\Delta > \frac{2}{M_{low}}$  ( $\Delta < \frac{2}{M_{high}}$ ),  $\Psi_x(t)$  is, with probability 1, sensitive (insensitive) to initial conditions.*
- ii. *Given a system sustained by external input, if  $\Psi_x(t)$  is aperiodic, and constants  $\nu, c$  satisfy  $\forall t |E(t) - \nu I(t)| < c$ , then if  $\Delta > \frac{2}{M_{low}}(1 + \nu + \frac{c}{M_{low}})^2 + 2(\nu + \frac{c}{M_{low}})(1 + \nu + \frac{c}{M_{low}})$ ,  $\Psi_x(t)$  is, with probability 1, sensitive to initial conditions.*
- iii. *Given a system receiving no external input, if  $\Psi_x(t)$  is periodic such that  $\Psi_x(t_1) = \Psi_x(t_{k+1})$ , then if  $\Delta > \frac{2}{M_{low}}$  ( $\Delta < \frac{2}{M_{high}}$ ),  $\Psi_x(t)$  is, with probability 1, unstable (stable).*

**Proof.**

i. Of the  $k$  steps in the process if  $k_b$  involve birth of spikes and  $k_d$  involve death of spikes then  $k_b + k_d = k$ , and  $|k_b - k_d|$  is bounded. Therefore,  $k \rightarrow \infty$  implies  $k_b \rightarrow \infty$  and  $k_d \rightarrow \infty$ .

$$\text{If } \Delta > 0, \text{ then } (1 + \frac{\Delta M_{high} - 2}{M_{low}^2})^{k_b} \sigma_0^2 > V(\mathbb{A}_0^k) - C(\mathbb{A}_0^k) > (1 + \frac{\Delta M_{low} - 2}{M_{high}^2})^{k_b} \sigma_0^2.$$

Simple algebra shows that  $V((I - \frac{1}{m}(\mathbf{1})) * \mathbb{A}_0^k) = (1 - \frac{1}{m})(V(\mathbb{A}_0^k) - C(\mathbb{A}_0^k))$ . It therefore follows that if  $\Delta < \frac{2}{M_{high}}$ , then  $\lim_{k \rightarrow \infty} E(\|(I - \frac{1}{m}(\mathbf{1})) * \mathbb{A}_0^k\|_F) = 0$ , and since  $\|A\|_F \geq 0$  for any  $A$ ,  $Pr(\lim_{k \rightarrow \infty} \|(I - \frac{1}{m}(\mathbf{1})) * \mathbb{A}_0^k\|_F > 0) = 0$ . If, on the other hand,  $\Delta > \frac{2}{M_{low}}$ , then  $\lim_{k \rightarrow \infty} E(\|(I - \frac{1}{m}(\mathbf{1})) * \mathbb{A}_0^k\|_F)$  is unbounded. Moreover,  $Pr(\lim_{k \rightarrow \infty} \|(I - \frac{1}{m}(\mathbf{1})) * \mathbb{A}_0^k\|_F \text{ is bounded}) = 0$ .<sup>12</sup>

Since  $(I - \frac{1}{m}(\mathbf{1})) * \mathbb{A}_0^k = (I - \frac{1}{m}(\mathbf{1})) * \tilde{A}_0^k * \mathbb{A}$ , and  $\mathbb{A}$  is, with probability 1, a bounded rank  $n$  matrix,  $\lim_{k \rightarrow \infty} \|(I - \frac{1}{m}(\mathbf{1})) * \mathbb{A}_0^k\| = 0$  (unbounded)  $\stackrel{a.s.}{\iff} \lim_{k \rightarrow \infty} \|(I - \frac{1}{m}(\mathbf{1})) * \tilde{A}_0^k\| = 0$  (unbounded). The result then follows from lemma 1.

ii. Since  $\forall t |E(t) - \nu I(t)| < c$ , if there are  $m$  live internal spikes at any given time, the number of live external spikes at the same time lies in the range

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<sup>12</sup> For it to be bounded, an infinite subsequence of events, each of which occurs with probability  $< 1$ , must take place.

$[\nu m - c, \nu m + c]$ . If  $p$  live spikes are randomly chosen from the system and  $q$  of those are internal spikes, then  $E(q) \in [\frac{pm}{(1+\nu)m+c}, \frac{pm}{(1+\nu)m-c}]$ .

We now modify the stochastic process as follows. The process is begun with  $\mathbb{A}_0^0 = \mathbb{A}$ . If the  $k$ th step involves the introduction of an external spike into the system,  $\mathbb{A}_0^k$  is set to  $\mathbb{A}_0^{k-1}$ . If the  $k$ th step involves the birth of an internal spike,  $\mathbb{A}_0^k$  is generated from  $\mathbb{A}_0^{k-1}$  by randomly choosing  $q$  rows from  $\mathbb{A}_0^{k-1}$ , choosing random variables  $x_1, x_2, \dots, x_p$  as described earlier, constructing  $v_{new} = \sum_{i=1}^q x_i v_i$ , and inserting it at a random location into  $\mathbb{A}_0^{k-1}$ .

Clearly, as in case i,  $\forall k E_k(v_i) = (0, 0, \dots, 0)$ . Simple algebra also demonstrates that at the birth of a spike  $V_k = (\frac{m}{m+1} + \frac{(1+\Delta)q}{(m+1)p} - \frac{\Delta q(q-1)}{m(m+1)p(p-1)})V_{k-1} - \frac{\Delta(m-1)q(q-1)}{m(m+1)p(p-1)}C_{k-1}$ , and  $C_k = \frac{2q}{m(m+1)p}V_{k-1} + (\frac{m-1}{m+1} + \frac{2(m-1)q}{m(m+1)p})C_{k-1}$ . Noting that  $m \geq p \geq q$  and assuming that  $\Delta > 0$ , we arrive at  $V_k - C_k \geq (1 + \frac{\Delta(m-1)q(q-1) - 2(mp-mq+q)(p-1)}{m(m+1)p(p-1)})(V_{k-1} - C_{k-1})$ .

Therefore, if  $\Delta > \frac{2}{M_{low}}(1+\nu + \frac{c}{M_{low}})^2 + 2(\nu + \frac{c}{M_{low}})(1+\nu + \frac{c}{M_{low}})$  it follows that  $V_k - C_k > V_{k-1} - C_{k-1}$ . Finally, arguments identical to those in lemma 1 yield  $\lim_{k \rightarrow \infty} \|(I - \frac{1}{m}(\mathbf{1})) * A_0^k * \mathbb{A}\|$  is unbounded  $\xrightarrow{a.s.} \lim_{k \rightarrow \infty} \|B * A_0^k * C\|$  is unbounded.

iii. We modify the stochastic process so as to construct the new matrix  $(\tilde{A}_0^k)^r * \mathbb{A}$  for arbitrary  $r$ . As in case i, the process is begun with  $\mathbb{A}_0^0 = \tilde{A}_0^0 * \mathbb{A}$ . Each step in the process is then carried out in the exact same manner as in case i. However, after every  $k$  steps, the row mean of the matrix is deducted from each row, that is, the row mean is deducted from each row of  $\mathbb{A}_0^{kr}$ , for  $r = 1, 2, \dots$  before the next step is performed.

Deletion of the row mean at the end of the first passage around the periodic orbit amounts to the operation  $\tilde{A}_0^0 * \mathbb{A}_0^k = \tilde{A}_0^0 * \tilde{A}_0^k * \mathbb{A}$ . It follows from a previous discussion that every subsequent addition or deletion of rows can be considered as being performed on  $\tilde{A}_0^0$ . Therefore, just prior to the deletion of the row mean after the  $r$ th passage around the periodic orbit, we have  $(\tilde{A}_0^k)^r * \mathbb{A}$ .

Since  $V(\tilde{A}_0^0 * \tilde{A}_0^{kr} * \mathbb{A}) = (1 - \frac{1}{n})(V(\tilde{A}_0^{kr} * \mathbb{A}) - C(\tilde{A}_0^{kr} * \mathbb{A}))$  and  $C(\tilde{A}_0^0 * \tilde{A}_0^{kr} * \mathbb{A}) = -\frac{1}{n}(V(\tilde{A}_0^{kr} * \mathbb{A}) - C(\tilde{A}_0^{kr} * \mathbb{A}))$ , we have  $V(\tilde{A}_0^0 * \tilde{A}_0^{kr} * \mathbb{A}) - C(\tilde{A}_0^0 * \tilde{A}_0^{kr} * \mathbb{A}) = V(\tilde{A}_0^{kr} * \mathbb{A}) - C(\tilde{A}_0^{kr} * \mathbb{A})$ . The rest of the argument follows along the lines of case i.

Case iii is based on the assumption that the  $v_i$ 's remain independent of the  $x_i$ 's in spite of the  $x_i$ 's being identical each time a specific event is encountered on the periodic orbit as it is traversed repeatedly by the process. We demonstrate that the assumption is reasonable.

Figure 1 depicts a single traversal of a periodic orbit in a three-neuron system. The four spikes, A, B, C, and D, in region H1 constitute the initial set of spikes (therefore,  $n = 4$ ). Nodes in region N, also labeled A, B, C, and D, represent the deletion of the row mean at the end of each passage

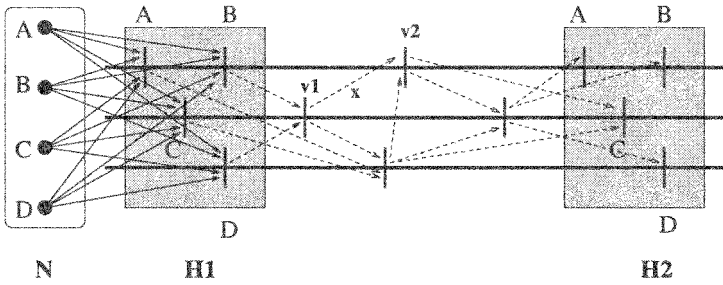


Figure 1: Graphical depiction of the construction of  $(\tilde{A}_0^k)^n$ .

around the periodic orbit. The periodic orbit is extended to the right (H2) to mark the repetition of the spikes A, B, C, and D. The dotted arrows relate which spikes are effective in the birth of any given spike. We now regard the diagram as a directed graph with the additional constraint that nodes in N be identified with corresponding spikes in H2, that is, they be regarded as one and the same. Edges from nodes in N/H2 to corresponding spikes in H1 are assigned weights  $(1 - \frac{1}{n})$ , and to other spikes in H1 are assigned weights  $-\frac{1}{n}$ . Each dotted edge is assigned weight  $x_i$ .

Let  $v_i$  correspond to any given spike  $i$  in the periodic orbit. The  $n$  ( $= 4$ ) elements of the row  $v_i$  (sensitivity to A, B, C, and D) after the  $r$ th passage around the periodic orbit can then be computed by identifying all paths from A in N/H2 (respectively, B, C, and D for the three remaining elements) to spike  $i$  such that each path crosses N/H2  $r$  times before terminating at spike  $i$ , and setting  $v_i = \sum_{\text{paths}} e_{1e_2 \dots e_q} w(e_1)w(e_2) \dots w(e_q)$ , where  $e_1 \dots e_q$  are the edges in a path and  $w(e_j)$ 's their weights.

Given any spike  $v_i$  in the periodic orbit, a spike  $v_j$  that it is effective on, and the corresponding effectiveness  $x_i$ , contributions to  $v_i$  from paths that do not pass through  $v_j$  are independent of  $x_i$ .<sup>13</sup> Assuming that there are approximately  $n$  live spikes at any time,<sup>14</sup> the proportion of such paths is approximately  $(1 - \frac{1}{n})^r$ . The remaining paths can be partitioned into sets based on the number of times  $l = 1, \dots, r$ , that each path passes through  $v_j$ . The assumption of independence is unbiased for each such set because the corresponding terms satisfy  $E(x_i) \sum_{j_1=1, \dots, j_l=1}^{p, \dots, p} E(x_{j_1} \dots x_{j_l}) = \sum_{j_1=1, \dots, j_l=1}^{p, \dots, p} E(x_i x_{j_1} \dots x_{j_l})$ .

**5.3 Qualitative Dynamics of Columns in the Neocortex.** The parameters of  $P_k(\cdot)$ , for any neuron  $k$ , can be partitioned into two sets: the set of

<sup>13</sup> For example, in Figure 1 contributions to  $v_1$  from paths that do not pass through  $v_2$  are independent of  $x$ .  
<sup>14</sup> Given that there are  $\approx 10^5$  neurons in a typical column, the spiking rate of a typical neuron is  $\approx 40/\text{sec}$ , and that the effects of a PSP lasts for  $\approx 150$  msec,  $n \approx 6 \times 10^5$ .

afferent spikes into neuron  $k$ , and the set of spikes generated by neuron  $k$ . Under normal conditions, the spiking rate of a typical neuron in the neocortex is approximately 40 per second. The interspike intervals being large,  $\partial P_k / \partial x_k^j |_{P_k(\cdot)=T}$  is negligible. Consequently, at the birth of a spike at neuron  $k$ ,  ${}^k\alpha_k^j$  is negligible for all  $j = 1, \dots, n_k$ .

Approximately 80% of all neurons in the neocortex are spiny (physiological experiments indicate that they are predominantly excitatory), and the rest are smooth (predominantly inhibitory) (Peters & Proskauer, 1980; Peters & Regidor, 1981; Braitenberg & Schüz, 1991; Shepherd, 1998). It therefore follows that the majority of the spikes in the system at any given time are excitatory. The impact of such spikes on  $P(\cdot)$  of a typical neuron is given by a steep rising phase followed by a relatively gentle and prolonged falling phase (Bernander, Douglas, & Koch, 1992). Consequently, the typical distribution of the  ${}^k\alpha_i^j$ 's at the birth of a spike at any neuron  $k$  comprises a few large positive elements and numerous small negative elements. We determined through numerical calculations based on mean spike rate, connectivity, and potential function data from the models presented in the original article that  $E(\sum_{i,j} ({}^k\alpha_i^j)^2) > 1$  under such conditions, and that  $E(\sum_{i,j} ({}^k\alpha_i^j)^2)$  rises as the number of small negative elements increase. The resultant values were in fact quite large and met all relevant conditions (from cases i, ii, and iii) in theorem 1.

A neuronal system is considered to be operating under seizure-like conditions when most of the neurons in the system spike at intervals approaching the relative refractory period. Under such conditions, the first spike in the second set progressively assumes a significant role in the determination of the time at which the neuron spikes next. Stated formally, if the most recent spike at neuron  $k$  is  $x_k^1$ , then at the subsequent birth of a spike at neuron  $k$ ,  ${}^k\alpha_k^1 = 1 - \epsilon$  and the remainder of the  ${}^k\alpha_i^j$ 's (that sum to  $\epsilon$ ) satisfy an appropriately scaled version of the distribution presented in the previous paragraph. As the system progressively approaches seizure-like conditions,  $\epsilon$  drops from 1 to 0. Simple algebra shows that when  $\epsilon$  is small,  $E(\sum_{i,j} ({}^k\alpha_i^j)^2) \approx 1 - 2\epsilon$ .

In summary, as one proceeds from the region of the phase-space associated with low neuronal activity ( $\epsilon \approx 1$ ) to the region associated with high neuronal activity ( $\epsilon \approx 0$ ), periodic orbits go from being almost surely unstable (trajectories almost surely sensitive to initial conditions), to almost surely neutral, to almost surely stable, and back to being almost surely neutral.

We also found that under conditions of sparse activity,  $E(\sum_{i,j} ({}^k\alpha_i^j)^2) < 1$  if the distribution of the  $\partial P_k / \partial x_i^j$ 's is inverted, a state that can be realized by setting the impact of an excitatory (inhibitory) spike to have a gentle and prolonged rising (falling) phase followed by a steep and short falling (rising) phase. Piecewise linear functions were used to fashion the potential

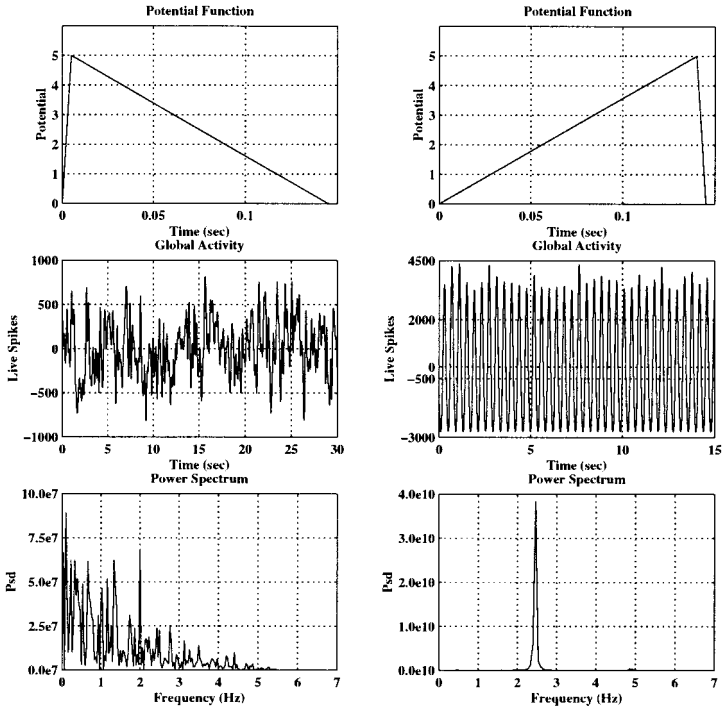


Figure 2: Dynamics of two systems of neurons that differ in terms of the impact of spikes on  $P_i(\cdot)$ .

functions in the models presented in the original article, and simulation experiments were conducted. The results were consistent with the assertions of theorem 1. Figure 2 presents the result of one such experiment. The columns represent two systems comprising 1000 neurons each, identical in all respects save the potential functions of the neurons. The first row depicts the effect of a typical excitatory spike on the potential function of a neuron, the second normalized time-series data pertaining to the total number of live spikes in each system, and the third results of a power spectrum analysis on each time series. While in the first case the dynamics is chaotic, in the second it is at best quasi-periodic.

## 6 Global Analysis

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In this section, we demonstrate how all basic sets, complex sets, attractors, and their realms of attraction can be isolated, given the exact instantiations of  $P_i^l$  for  $i = 1, \dots, S$ .

We begin by introducing an equivalence relation on  $\prod_{i=1}^S \overline{\mathbb{I}}_{n_i} \setminus \bigcup_{i=1}^S P_i^I$ . We define  $p \sim q$  if  $p, q \in \prod_{i=1}^S (\overline{\mathbb{I}}_{n_i}^{\sigma_i} \setminus \overline{\mathbb{I}}_{n_i}^{\sigma_i+1}) \setminus \bigcup_{i=1}^S P_i^I$  for arbitrary but fixed values of the  $\sigma_i$ 's, and  $\exists \Psi_x(t)$  such that  $p = \Psi_x(t_1)$ ,  $q = \Psi_x(t_2)$ , and  $\forall t \in [\min(t_1, t_2), \max(t_1, t_2)]$ ,  $\Psi_x(t) \in \prod_{i=1}^S (\overline{\mathbb{I}}_{n_i}^{\sigma_i} \setminus \overline{\mathbb{I}}_{n_i}^{\sigma_i+1})$ . We define the equivalence class  $[p] = \{q \mid q \sim p\}$ , and a mapping  $\Theta: (\prod_{i=1}^S \overline{\mathbb{I}}_{n_i} \setminus \bigcup_{i=1}^S P_i^I) / \sim \rightarrow (\prod_{i=1}^S \overline{\mathbb{I}}_{n_i} \setminus \bigcup_{i=1}^S P_i^I) / \sim$  as  $\Theta([p]) = [q]$  if there exists a  $\Psi_x(t)$  such that two of its successive segments (as defined in section 3) satisfy  $\{\Psi_x(t) \mid t_j < t < t_{j+1}\} \subseteq p$  and  $\{\Psi_x(t) \mid t_{j+1} < t < t_{j+2}\} \subseteq q$ . We operate hereafter on  $(\prod_{i=1}^S \overline{\mathbb{I}}_{n_i} \setminus \bigcup_{i=1}^S P_i^I) / \sim$ ,<sup>15</sup> and forsake  $\Psi(x, t)$  in favor of  $\Theta$ .

We note immediately that  $\Theta$  is only a piecewise continuous function. The analysis in the previous section was restricted to  $\Psi_x(t)$ 's that are locally continuous in  $x$  for the simple reason that all other  $\Psi_x(t)$ 's are, trivially, sensitive to initial conditions. The following definitions are to be regarded in the light of the fact that  $\Theta$  is discontinuous.

$[p]$  is labeled a wandering point if  $\exists U$  an open neighborhood of  $[p]$ , and  $\exists n_{\min} \geq 0$  such that  $\forall n > n_{\min}, \Theta^n(U) \cap U = \emptyset$ .  $[p]$  is labeled a nonwandering point if  $\forall U$  open neighborhood of  $[p]$ , and  $\forall n_{\min} \geq 0, \exists n > n_{\min}$  such that  $\Theta^n(U) \cap U \neq \emptyset$ .  $\Lambda \subset (\prod_{i=1}^S \overline{\mathbb{I}}_{n_i} \setminus \bigcup_{i=1}^S P_i^I) / \sim$  is labeled a basic set if  $\forall [p], [q] \in \Lambda, \forall U, V$  open neighborhoods of  $[p]$  and  $[q]$  respectively, and  $\forall n_{\min} \geq 0, \exists n_1, n_2, n_3, n_4 > n_{\min}$  such that  $\Theta^{n_1}(U) \cap U \neq \emptyset, \Theta^{n_2}(U) \cap V \neq \emptyset, \Theta^{n_3}(V) \cap V \neq \emptyset$ , and  $\Theta^{n_4}(V) \cap U \neq \emptyset$ , and furthermore,  $\Lambda$  is a maximal set with regard to this property.

It follows from the definition that the set of all nonwandering points,  $\Omega$ , is closed, and that any basic set  $\Lambda$  is a closed subset of  $\Omega$ . Membership in the same basic set, however, falls short of an equivalence relation. The relation is reflexive since  $\forall U, V$  open neighborhoods of  $[p], U \cap V$  is an open neighborhood of  $[p]$ , symmetric by definition, but not transitive since  $\Theta$  is not a homeomorphism. Each nonwandering point is therefore a member of one or more basic sets.

This feature significantly affects the characterization of an attractor. Two basic sets  $\Lambda$  and  $\Lambda'$  are considered coupled if either  $\Lambda \cap \Lambda' \neq \emptyset$  or there exists a finite or countably infinite sequence of basic sets  $\underline{\Lambda_1, \dots, \Lambda_k, \dots}$  such that  $\forall i \Lambda_i$  and  $\Lambda_{i+1}$  are coupled, and in addition,  $\Lambda \cap \bigcup_{i=1}^{k/\infty} \Lambda_i \neq \emptyset$  and  $\Lambda' \cap \bigcup_{i=1}^{k/\infty} \Lambda_i \neq \emptyset$ . We note immediately that this is an equivalence relation, and it therefore partitions the set of all basic sets into equivalence classes. More significant, however, is the fact that the relation partitions  $\Omega$  into disjoint sets. This follows from the observation that if, on the contrary,  $[p]$  belongs to two distinct classes, then there exist basic sets  $\Lambda$  and  $\Lambda'$ , members

<sup>15</sup> We regard  $\prod_{i=1}^S \overline{\mathbb{I}}_{n_i} \setminus \bigcup_{i=1}^S P_i^I$  with the topology defined in section 2, and assign  $(\prod_{i=1}^S \overline{\mathbb{I}}_{n_i} \setminus \bigcup_{i=1}^S P_i^I) / \sim$  the corresponding quotient topology.



of the respective classes, that are coupled. Each such disjoint subset of  $\Omega$  is labeled a complex set.

We demonstrate that any complex set,  $\Xi$ , is a closed subset of  $\Omega$ . If  $[p]$  is a limit point of  $\Xi$ , every open neighborhood of  $[p]$  contains a nonwandering point.  $[p]$  is therefore a nonwandering point. Moreover,  $\exists \Lambda_1, \dots, \Lambda_k, \dots \subset \Xi$  such that  $[p] \in \overline{\bigcup_{i=1}^{\infty} \Lambda_i}$ . Consequently, if  $[p] \in \Lambda$ , then  $\Lambda \subset \Xi$ , and therefore  $[p] \in \Xi$ .  $\Xi$  is therefore closed. Finally, a complex set  $\Xi$  is labeled an attractor if  $\exists U$  such that  $\Xi \subset \text{int}(U)$  the interior of  $U$ ,  $\forall \Xi' \neq \Xi \overline{U} \cap \Xi' = \emptyset$ , and  $U$  is a trapping region, that is,  $\Theta(U) \subset U$ . The discontinuity of  $\Theta$ , in essence, sanctions the existence of anisotropic<sup>16</sup> attractors.

A procedure to locate all nonwandering points, basic sets, complex sets, and attractors in  $(\prod_{i=1}^S \overline{\mathbb{I}}_{n_i} \setminus \bigcup_{i=1}^S P_i^j) / \sim$  is presented in Figure 3. It begins with the initial partition of the phase-space  $\{\prod_{i=1}^S (\overline{\mathbb{I}}_{n_i}^{\alpha} \setminus \overline{\mathbb{I}}_{n_i}^{\alpha+1}) \setminus \bigcup_{i=1}^S P_i^j / \sim \mid 0 \leq \alpha \leq n_i; i = 1, \dots, S\}$ , and generates a succession of refinements. The partition operation is well defined since any  $\mathcal{P}$  partitioned satisfies  $\Theta(\mathcal{P}) \cap \mathcal{P} = \emptyset$ .

We label node  $\mathcal{N}_a^j$  from stage  $j$  a descendant of node  $\mathcal{N}_b^k$  from stage  $k$  if  $j > k$  and the corresponding sets in the partition of the phase-space satisfy  $\mathcal{P}_a^j \subset \mathcal{P}_b^k$ . Let  $\mathcal{N}_1^j \mathcal{N}_2^j \dots \mathcal{N}_n^j$  be a path in the graph at stage  $j$ . We define  $iP$  recursively as:  ${}_1P = \mathcal{P}_n^j$  and  ${}_{i+1}P = \Theta^{-1}({}_iP) \cap \mathcal{P}_{n-i}^j$ . We label  $\mathcal{N}_1^j \mathcal{N}_2^j \dots \mathcal{N}_n^j$  a false path of primary length  $p$  if  $\forall i = 1, \dots, p \ {}_iP \neq \emptyset$  and  ${}_{p+1}P = \emptyset$ . We now make certain observations about the procedure.

If at stage  $j$  there is a trajectory in the phase-space that has consecutive segments in the sets  $\mathcal{P}_1^j, \mathcal{P}_2^j, \dots, \mathcal{P}_n^j$ , then the corresponding graph contains the path  $\mathcal{N}_1^j \mathcal{N}_2^j \dots \mathcal{N}_n^j$ . In other words, the trajectories in the phase-space are a subset of the paths in the graph at all stages.

If at stage  $j$  the graph does not contain the path  $\mathcal{N}_1^j \mathcal{N}_2^j \dots \mathcal{N}_n^j$ , then at stage  $(j + 1)$  the graph does not contain the path  $\mathcal{N}_{i_1}^{j+1} \mathcal{N}_{i_2}^{j+1} \dots \mathcal{N}_{i_n}^{j+1}$  for any descendant  $\mathcal{N}_{i_k}^{j+1}$  of  $\mathcal{N}_k^j$ ,  $k = 1, \dots, n$ .

If at stage  $j$ ,  $\mathcal{N}_1^j \mathcal{N}_2^j \dots \mathcal{N}_n^j$  is a false path of primary length  $p$ , then at stage  $(j + p - 1)$  no path  $\mathcal{N}_{i_1}^{j+p-1} \mathcal{N}_{i_2}^{j+p-1} \dots \mathcal{N}_{i_n}^{j+p-1}$  exists for any descendant  $\mathcal{N}_{i_k}^{j+p-1}$  of  $\mathcal{N}_k^j$ ,  $k = 1, \dots, n$ . This follows from the observations: (i) (base case) If at stage  $j$ ,  $\mathcal{N}_1^j \mathcal{N}_2^j \dots \mathcal{N}_n^j$  is a false path of primary length 2, then at stage  $(j + 1)$  no path  $\mathcal{N}_{i_1}^{j+1} \mathcal{N}_{i_2}^{j+1} \dots \mathcal{N}_{i_n}^{j+1}$  exists for any descendant  $\mathcal{N}_{i_k}^{j+1}$  of  $\mathcal{N}_k^j$ ,  $k = 1, \dots, n$ , and (ii) (inductive case) If at stage  $j$ ,  $\mathcal{N}_1^j \mathcal{N}_2^j \dots \mathcal{N}_n^j$  is a false path of primary length  $p$ , then at stage  $(j + 1)$  if a path

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<sup>16</sup> A trapped trajectory does not necessarily visit every basic set in the complex set. Moreover, the sequence of basic sets visited by any such trajectory depends on its point of entry.

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j := 0 /* Stage 0 */
Set Initial Partition of  $(\prod_{i=1}^S \bar{i} \bar{m}_i \setminus \cup_{i=1}^S P_i^l) / \sim$ 
to  $\{\prod_{i=1}^S (\bar{i} \bar{m}_i \setminus \bar{i} \bar{m}_i^{\sigma_i+1}) \setminus \cup_{i=1}^S P_i^l / \sim \mid 0 \leq \sigma_i \leq m_i; i = 1, \dots, S\}$ .
Generate initial Directed Graph:
(i) Queue  $Q_0 = \emptyset$ ,
(ii) Assign unique node to each set in the partition,
/* Henceforth referred to as  $\mathcal{N}$ 's and  $\mathcal{P}$ 's respectively. */
(iii)  $\forall a, b$  assign edge from  $\mathcal{N}_a$  to  $\mathcal{N}_b$  if  $\exists [p], [q]$  s.t  $[p] \in \mathcal{P}_a, [q] \in \mathcal{P}_b$ , and  $\Theta([p]) = [q]$ .
Push all nodes into Queue  $Q_0$ 
For (j=1 to  $\infty$ ) { /* Stages 1 through  $\infty$  */
Queue  $Q_j = \emptyset$ 
Repeat Until  $(Q_{j-1} = \emptyset)$  {
 $\mathcal{N}^{j-1} = \text{Pop}(Q_{j-1})$ 
/* Let  ${}^l \mathcal{N}_1^l, \dots, {}^l \mathcal{N}_m^l$  ( $l = j-1$  or  $j$ ) be the nodes that receive edges from  $\mathcal{N}^{j-1}$  */
/* Let  ${}^o \mathcal{N}_1^l, \dots, {}^o \mathcal{N}_n^l$  ( $l = j-1$  or  $j$ ) be the nodes that direct edges to  $\mathcal{N}^{j-1}$  */
/* Let  ${}^l \mathcal{P}_1^l, \dots, {}^l \mathcal{P}_m^l, {}^o \mathcal{P}_1^l, \dots, {}^o \mathcal{P}_n^l, \mathcal{P}^{j-1}$  be the sets in the current partition that
correspond to nodes  ${}^l \mathcal{N}_1^l, \dots, {}^l \mathcal{N}_m^l, {}^o \mathcal{N}_1^l, \dots, {}^o \mathcal{N}_n^l, \mathcal{N}^{j-1}$  */
Construct a finite partition of  $\mathcal{P}^{j-1}$  in the following manner.
Set tentative partition of  $\mathcal{P}^{j-1}$ 
to  $\{\Theta^{-1}({}^l \mathcal{P}_i^l) \cap \mathcal{P}^{j-1} \mid i = 1, \dots, m\} \cup \{\mathcal{P}^{j-1} \setminus \cup_{i=1}^m \Theta^{-1}({}^l \mathcal{P}_i^l)\}$ .
Now construct a finite refinement of this tentative partition,  $\{\mathcal{P}_1^j, \dots, \mathcal{P}_p^j\}$ ,
such that  $\forall i = 1, \dots, p$   $\mathcal{P}_i^j$  is connected, and  $\text{diam}(\mathcal{P}_i^j) \leq \frac{1}{2} \text{diam}(\mathcal{P}^{j-1})$ .
Delete  $\mathcal{N}^{j-1}$  and add  $\mathcal{N}_1^j, \dots, \mathcal{N}_p^j$  to Graph /* Corresponding to sets  $\mathcal{P}_1^j, \dots, \mathcal{P}_p^j$  */
Replace all previous edges from  $\mathcal{N}^{j-1}$  to  ${}^l \mathcal{N}_1^l, \dots, {}^l \mathcal{N}_m^l$  with new edges from
 $\mathcal{N}_1^j, \dots, \mathcal{N}_p^j$  to  ${}^l \mathcal{N}_1^l, \dots, {}^l \mathcal{N}_m^l$  according to rule (iii) in Stage 0.
Replace all previous edges from  ${}^o \mathcal{N}_1^l, \dots, {}^o \mathcal{N}_n^l$  to  $\mathcal{N}^{j-1}$  with new edges from
 ${}^o \mathcal{N}_1^l, \dots, {}^o \mathcal{N}_n^l$  to  $\mathcal{N}_1^j, \dots, \mathcal{N}_p^j$  according to rule (iii) in Stage 0.
Push nodes  $\mathcal{N}_1^j, \dots, \mathcal{N}_p^j$  into Queue  $Q_j$ 
}
}

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Figure 3: A procedure to locate all nonwandering points, basic sets, complex sets, and attractors in the phase-space.

$\mathcal{N}_{i_1}^{j+1} \mathcal{N}_{i_2}^{j+1} \dots \mathcal{N}_{i_n}^{j+1}$  exists for any descendant  $\mathcal{N}_{i_k}^{j+1}$  of  $\mathcal{N}_k^j$ ,  $k = 1, \dots, n$ , then the path  $\mathcal{N}_{i_1}^{j+1} \mathcal{N}_{i_2}^{j+1} \dots \mathcal{N}_{i_{n-1}}^{j+1}$  is a false path of primary length  $(p-1)$ .

These follow from the fact that at stage  $(j+1)$ ,  $\mathcal{P}_{n-1}^j$  is partitioned such that  $\exists \mathcal{P}_{i_{n-1}}^{j+1}, \dots, \mathcal{P}_{i_{n-1}}^{j+1}$  that satisfy  $\bigcup_{k=1}^q \mathcal{P}_{i_{n-1}}^{j+1} = \Theta^{-1}(\mathcal{P}_n^j) \cap \mathcal{P}_{n-1}^j$ .

Given any stage  $j$ , we refer to a set of nodes  $\langle \mathcal{N}_k^j \rangle = \{\mathcal{N}_{i_k}^j \mid l = 1, \dots, m_k^j\}$  as a cluster if  $\bigcap_{l=1}^{m_k^j} \overline{\mathcal{P}_{i_k}^j} \neq \emptyset$ . We define a relation  $Recurrent(\cdot, \cdot)$  between clusters

as  $\text{Recurrent}(\langle \mathcal{N}_a^j \rangle, \langle \mathcal{N}_b^j \rangle)$  if and only if  $\exists l_a, l'_a \in \{1, \dots, m_a^j\}$  and  $\exists l_b, l'_b \in \{1, \dots, m_b^j\}$  such that paths  $\mathcal{N}_{i_a}^j \mathcal{N}_{e_1}^j \dots \mathcal{N}_{e_p}^j \mathcal{N}_{i_b}^j$  and  $\mathcal{N}_{i_a}^j \mathcal{N}_{f_1}^j \dots \mathcal{N}_{f_q}^j \mathcal{N}_{i_a}^j$  exist in the graph where  $\mathcal{N}_h^j$  lies on a cycle for some  $h \in \{i_a^j, e_1, \dots, e_p, i_b^j\}$  and some  $h \in \{i_b^j, f_1, \dots, f_q, i_a^j\}$ . The following theorem identifies all nonwandering points in  $(\prod_{i=1}^S i\overline{\mathbb{T}}_{n_i} \setminus \bigcup_{i=1}^S P_i^l) / \sim$  with the exception of the trivial fixed point at  $\prod_{i=1}^S i\overline{\mathbb{T}}_{n_i}^{n_i}$ . We assign the node corresponding to  $\prod_{i=1}^S i\overline{\mathbb{T}}_{n_i}^{n_i}$  nonwandering status at the start of the process.

**Theorem 2.** *Let  $\{\langle \mathcal{N}_k^j \rangle \mid k = 1, \dots, n_j\}$  be the set of all clusters at stage  $j$  such that  $\forall k = 1, \dots, n_j$ ,  $\text{Recurrent}(\langle \mathcal{N}_k^j \rangle, \langle \mathcal{N}_k^j \rangle)$ . Then the set of all nonwandering points is given by  $\Omega = \bigcap_{j=0}^\infty (\bigcup_{k=1, l=1}^{n_j, m_k^j} \mathcal{P}_{i_k}^j)$ .*

**Proof.**  $[p]$  is a nonwandering point  $\Rightarrow [p] \in \bigcap_{j=0}^\infty (\bigcup_{k=1, l=1}^{n_j, m_k^j} \mathcal{P}_{i_k}^j)$ . Let  $[p] \in \prod_{i=1}^S (i\overline{\mathbb{T}}_{n_i}^{\sigma_i} \setminus i\overline{\mathbb{T}}_{n_i}^{\sigma_i+1}) \setminus \bigcup_{i=1}^S P_i^l / \sim$  for arbitrary but fixed values of the  $\sigma_i$ 's. We assume, without loss of generalization, that  $[p] \in \mathcal{P}_1^j$  at stage  $j$ . If  $[p]$  lies in the interior of  $\mathcal{P}_1^j$ , an open neighborhood  $U$  of  $[p]$  can be chosen such that  $U \subset \mathcal{P}_1^j$ . There is then a trajectory through  $\mathcal{P}_1^j$  that returns to it. The unitary cluster  $\{\mathcal{N}_1^j\}$  then satisfies the criterion. If, on the other hand,  $[p]$  lies on the boundary of  $\mathcal{P}_1^j$ , there are only finitely many sets  $\overline{\mathcal{P}}_1^j, \dots, \overline{\mathcal{P}}_r^j$  in  $\prod_{i=1}^S (i\overline{\mathbb{T}}_{n_i}^{\sigma_i} \setminus i\overline{\mathbb{T}}_{n_i}^{\sigma_i+1}) \setminus \bigcup_{i=1}^S P_i^l / \sim$  such that  $\forall l = 1, \dots, r$ ,  $[p] \in \overline{\mathcal{P}}_l^j$ .<sup>17</sup> We choose  $U$  such that  $U \subset \bigcup_{l=1}^r \overline{\mathcal{P}}_l^j$ . Then, since  $\Theta^n(U) \cap U \neq \emptyset$  for an infinite sequence of  $n$ 's,  $\exists l_1, l_2 \in \{1, \dots, r\}$ , not necessarily distinct, such that there are arbitrarily long trajectories from  $\mathcal{P}_{l_1}^j$  to  $\mathcal{P}_{l_2}^j$ . Since the graph has a finite number of nodes at any stage, there exists a path from  $\mathcal{N}_{l_1}^j$  to  $\mathcal{N}_{l_2}^j$  such that a node on the path lies on a cycle. The cluster  $\{\mathcal{N}_{l_1}^j, \dots, \mathcal{N}_{l_2}^j\}$  then satisfies the criterion.

$[p]$  is a wandering point  $\Rightarrow [p] \notin \bigcap_{j=0}^\infty (\bigcup_{k=1, l=1}^{n_j, m_k^j} \mathcal{P}_{i_k}^j)$ . As above, we assume  $[p] \in \mathcal{P}_1^j$  at stage  $j$ . Since at each stage the diameter<sup>18</sup> of each set in the partition drops by a factor of two, given any open neighborhood  $U$  of  $[p]$ , there exists a stage  $j$  where  $(\mathcal{P}_1^j \subset U) \wedge \forall l (\overline{\mathcal{P}}_1^j \cap \overline{\mathcal{P}}_l^j \neq \emptyset \Rightarrow \mathcal{P}_l^j \subset U)$ . Let

<sup>17</sup> Given the nature of the topology,  $[p] \notin \overline{\mathcal{P}}$  for any  $\mathcal{P}$  in the partition that does not lie in  $\prod_{i=1}^S (i\overline{\mathbb{T}}_{n_i}^{\sigma_i} \setminus i\overline{\mathbb{T}}_{n_i}^{\sigma_i+1}) \setminus \bigcup_{i=1}^S P_i^l / \sim$ .  
<sup>18</sup>  $\max_{\forall [p], [q]} (d([p], [q]))$  where  $d(\cdot, \cdot)$  is the distance between  $[p]$  and  $[q]$  based on the Riemannian metric.

$\overline{\mathcal{P}}_1^j \cap \overline{\mathcal{P}}_l^j \neq \emptyset$  for  $l = 1, \dots, r$ . Then any cluster that contains  $\mathcal{N}_1^j$  can, at best, contain  $\mathcal{N}_l^j$  for some  $l \in \{1, \dots, r\}$ . Given any such cluster, if  $\exists l_1, l_2$  such that there is a path from  $\mathcal{N}_{l_1}^j$  to  $\mathcal{N}_{l_2}^j$  through a cycle, then the path is a false path since  $\bigcup_{l=1}^r \mathcal{P}_l^j \subset U$ . There is then a stage  $(j + p)$  wherein all descendants of  $\mathcal{N}_{l_1}^j$  and  $\mathcal{N}_{l_2}^j$  do not lie on the path.

**Corollary 1.** Let  $\{\langle \mathcal{N}_k^j \mid k = 1, \dots, n_j \rangle$  for stages  $j = 1, 2, \dots$  be successive sets such that (i) each such set comprises of a maximal set of clusters satisfying  $\forall k_1, k_2 \in \{1, \dots, n_j\}$ ,  $\text{Recurrent}(\langle \mathcal{N}_{k_1}^j \rangle, \langle \mathcal{N}_{k_2}^j \rangle)$ , and (ii)  $\forall j \bigcup_{k=1, l=1}^{n_j, m_k^j} \mathcal{P}_{i_k}^j \subseteq \bigcup_{k=1, l=1}^{n_{j-1}, m_k^{j-1}} \mathcal{P}_{i_k}^{j-1}$ . Then  $\bigcap_{j=0}^\infty (\bigcup_{k=1, l=1}^{n_j, m_k^j} \mathcal{P}_{i_k}^j)$  is a basic set. Conversely, every basic set is representable as such.

**Proof.** If  $[p]_1, [p]_2 \in \bigcap_{j=0}^\infty (\bigcup_{k=1, l=1}^{n_j, m_k^j} \mathcal{P}_{i_k}^j)$  for any sequence of sets satisfying criteria i and ii, then based on arguments similar to those in the previous theorem, we conclude that there exists a basic set  $\Lambda$  such that  $[p]_1, [p]_2 \in \Lambda$ . Moreover,  $\Lambda$  being maximal,  $\bigcap_{j=0}^\infty (\bigcup_{k=1, l=1}^{n_j, m_k^j} \mathcal{P}_{i_k}^j) \subseteq \Lambda$ . Finally, if  $\exists [p] \in \Lambda$  such that  $[p] \notin \bigcap_{j=0}^\infty (\bigcup_{k=1, l=1}^{n_j, m_k^j} \mathcal{P}_{i_k}^j)$ , then  $\{\langle \mathcal{N}_k^{j_0} \mid k = 1, \dots, n_{j_0} \rangle$  is not maximal for some stage  $j_0$ .

Conversely, if  $\Lambda$  is a basic set, a sequence of sets satisfying criteria i and ii can be constructed such that  $\forall [p] \in \Lambda$ , and for every stage  $j$ ,  $[p] \in \langle \mathcal{N}_k^j \rangle$  for some  $\langle \mathcal{N}_k^j \rangle$  in the set. This is based on (a) if  $\{\langle \mathcal{N}_k^j \mid k = 1, \dots, n_j \rangle$  for some stage  $j$  satisfies criterion i, then the minimal set  $\{\langle \mathcal{N}_k^{j-1} \rangle \mid \forall \mathcal{N}_{i_k}^j \in \langle \mathcal{N}_k^j \rangle \exists \mathcal{N}_{i_k}^{j-1} \in \langle \mathcal{N}_k^{j-1} \rangle \mathcal{P}_{i_k}^j \subset \mathcal{P}_{i_k}^{j-1}\}$  is *Recurrent* for all pairs of member clusters, and can therefore be expanded to satisfy criteria i and ii, (b) if  $\{\langle \mathcal{N}_k^{j_0} \mid k = 1, \dots, n_{j_0} \rangle$  at some stage  $j_0$  is a set of clusters such that  $\forall [p] \in \Lambda \exists \langle \mathcal{N}_k^{j_0} \rangle$  where  $[p] \in \text{int}(\langle \mathcal{N}_k^{j_0} \rangle)$  and vice versa, then there are only finitely many ways it can be expanded to satisfy criterion i, and (c) there is then a stage  $(j_0 + p)$  wherein all points in these additional clusters do not lie in  $\bigcap_{j=0}^{j_0+p} (\bigcup_{k=1, l=1}^{n_j, m_k^j} \mathcal{P}_{i_k}^j)$ . In other words, an infinite sequence of sets satisfying criteria i and ii can be constructed such that  $\Lambda \subseteq \bigcap_{j=0}^\infty (\bigcup_{k=1, l=1}^{n_j, m_k^j} \mathcal{P}_{i_k}^j)$ . Finally, if  $\exists [p] \in \bigcap_{j=0}^\infty (\bigcup_{k=1, l=1}^{n_j, m_k^j} \mathcal{P}_{i_k}^j)$  such that  $[p] \notin \Lambda$ , then arguments similar to those in the previous theorem reveal a contradiction.

**Corollary 2.** *Let  $\{\langle \mathcal{N}_k^j \rangle \mid k = 1, \dots, n_j\}$  for stages  $j = 1, 2, \dots$  be successive sets such that (i) each such set comprises an equivalence class of clusters generated by the transitive closure of  $\text{Recurrent}(\cdot, \cdot)$  on the set  $\{\langle \mathcal{N}_k^j \rangle \mid \text{Recurrent}(\langle \mathcal{N}_k^j \rangle, \langle \mathcal{N}_k^j \rangle)\}$ , and (ii)  $\forall j \bigcup_{k=1, l=1}^{n_j, m_k^j} \mathcal{P}_{i_k^j}^j \subseteq \bigcup_{k=1, l=1}^{n_{j-1}, m_k^{j-1}} \mathcal{P}_{i_k^{j-1}}^{j-1}$ . Then  $\bigcap_{j=0}^{\infty} (\bigcup_{k=1, l=1}^{n_j, m_k^j} \mathcal{P}_{i_k^j}^j)$  is a complex set. Conversely, every complex set is representable as such.*

**Proof.**  $\Lambda$  and  $\Lambda'$  are coupled if and only if a sequence of basic sets  $\Lambda, \Lambda_1, \Lambda_2, \dots, \Lambda'$  exists such that each consecutive pair of basic sets shares one or more clusters at every stage. This follows from the observation that given any  $\Lambda$  and its corresponding sequence  $\{\langle \mathcal{N}_k^j \rangle \mid k = 1, \dots, n_j\}$  for  $j = 1, 2, \dots$ , if  $[p] \in \Lambda$ , then for every stage  $j$  there exists a  $\langle \mathcal{N}_{k_0}^j \rangle$  that satisfies  $[p] \in \text{int}(\langle \mathcal{N}_{k_0}^j \rangle)$ , and  $\langle \mathcal{N}_{k_0}^j \rangle \in \{\langle \mathcal{N}_k^j \rangle \mid k = 1, \dots, n_j\}$ . The remainder of the proof follows along the lines of the proof of the previous corollary.

If  $\mathcal{G}^j$  denotes the graph at stage  $j$  and  $\mathcal{H}^j$  is a subgraph of  $\mathcal{G}^j$  such that there are no edges leading from nodes in  $\mathcal{H}^j$  to nodes in  $(\mathcal{G}^j \setminus \mathcal{H}^j)$ , then we note from previous observations that the union of the sets corresponding to the nodes in  $\mathcal{H}^j$  constitutes a trapping region.

We now demonstrate that a complex set  $\Xi$  is an attractor if and only if there is a stage  $j_0$  where no path exists from any node in the equivalence class of clusters associated with  $\Xi$  (as defined in the previous corollary) to a node in an equivalence class of clusters associated with any other complex set  $\Xi'$ . We first note that if such a stage exists, the criterion remains true for all subsequent stages. The criterion guarantees the existence of maximal subgraphs  $\mathcal{H}^j$  for every  $j \geq j_0$  such that (a) every cluster  $\langle \mathcal{N}_k^j \rangle$  in the equivalence class associated with  $\Xi$  lies in  $\mathcal{H}^j$ , (b)  $\mathcal{H}^j$  does not contain any node from an equivalence class of clusters associated with any other complex set  $\Xi'$ , and (c) there are no edges from  $\mathcal{H}^j$  to  $(\mathcal{G}^j \setminus \mathcal{H}^j)$ . If  $W^j$  denotes the union of the sets corresponding to the nodes in  $\mathcal{H}^j$ , the realm of attraction of  $\Xi$  is given by  $\lim_{j \rightarrow \infty} W^j$ .

If, on the contrary, at every stage  $j$  there exists a path from a node in the equivalence class associated with  $\Xi$  to a node in an equivalence class associated with some other complex set  $\Xi'$ , then there is no set  $U$  such that  $\Xi \subset \text{int}(U)$ ,  $\forall \Xi' \neq \Xi \overline{U} \cap \Xi' = \emptyset$ , and  $\Theta(U) \subseteq U$ . If instead such a  $U$  exists, since  $\forall \Xi' \neq \Xi \overline{U} \cap \Xi' = \emptyset$ , given any other complex set  $\Xi'$ , there exists an open neighborhood  $V$  of  $\Xi'$  such that  $U \cap V = \emptyset$ . Moreover, since  $\Theta(U) \subseteq U$ ,  $\forall n \geq 0 \Theta^n(\text{int}(U)) \cap V = \emptyset$ .

In conclusion, we recall that with regard to the dynamics of cortical columns, we demonstrated in section 5 that trajectories (periodic orbits) in the region of the phase-space corresponding to normal operational conditions are, with probability 1, sensitive to initial conditions (unstable). It therefore follows that attractors in this region of the phase-space are almost

surely chaotic. When combined with the observation that the inherently discontinuous nature of  $\Theta$  sanctions the existence of anisotropic attractors, it becomes apparent that the dynamics of cortical columns, under normal operational conditions, is governed by attractors that are not only almost surely chaotic but are also potentially anisotropic.

## 7 Conclusions and Future Research

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The results presented in this article yield a principled resolution of the issue of information coding in recurrent neuronal systems (such as columns in the neocortex): that attractors in the phase-space denote the symbolic states of such systems. While the spatial arrangement of the attractors in the phase-space of certain neuronal systems might prompt the surmise of rate or population coding, such schemes are rendered epiphenomenal from this perspective.

The chaotic and potentially anisotropic nature of the attractors attains principal significance in this context. We first consider the ramifications of the attractors in question being almost surely chaotic. Recall that external input into the system is modeled by introducing additional neurons whose state descriptions match the input identically. Stated formally, the expanded phase-space is given by  $\prod_{i=1}^S \mathbb{I}_{n_i} \times \prod_{i=S+1}^{\mathcal{R}} \mathbb{I}_{n_i}$ , where  $i = 1, \dots, S$  denote the neurons in the system, and  $i = (S + 1), \dots, \mathcal{R}$  denote the input neurons. Since the times at which spikes are generated at the input neurons are determined solely by the external input, the expanded phase-space does not contain hypersurfaces  $P_i^l$  for  $i = (S + 1), \dots, \mathcal{R}$ . Each input corresponds to a unique trajectory  $\hat{\Psi}(t)$  in  $\prod_{i=S+1}^{\mathcal{R}} \mathbb{I}_{n_i}$ . The temporal evolution of the system upon input  $\hat{\Psi}(t)$  is given by the trajectory  $\Psi(t)$  in the expanded phase-space whose projection on  $\prod_{i=S+1}^{\mathcal{R}} \mathbb{I}_{n_i}$  is  $\hat{\Psi}(t)$ .

It is based on this formulation that we demonstrated in section 5 that the dynamics of a cortical column under normal operational conditions, sustained by external input from the thalamus and/or other cortical columns, is sensitive to initial conditions. This implies that even under conditions where the exact input is known, it is impossible to predict, based solely on nominal knowledge of the attractor that the system currently resides in, which attractors the system will visit as its dynamics unfolds, and at what times. In other words, the symbol-level dynamics of a cortical column cannot be modeled as a deterministic automaton.

We now consider the ramifications of the fact that the attractors in question, in addition to being chaotic, are potentially anisotropic. We recall that anisotropic attractors are attracting complex sets that are composed of multiple basic sets. Such attractors are capable of maintaining complex sequence information. The direction from which the system approaches such an attractor determines not only the subset of the constituent basic sets that the system visits, but also the order in which they are visited. In other words,

structure can be discerned in the phase-space of the neuronal system at two levels. First, there is the relationship between the attractors, each of which constitutes a macrosymbolic state of the system, and within each attractor the relationship between the basic sets each of which constitutes a macrosymbolic state of the system.

Our research has generated numerous questions that require investigation. While it is clear that changes in the potential function of the neurons, brought about by long-term potentiation and depression can dramatically change the nature of the dynamics of a neuronal system (creating, destroying, and altering the shape and location of the attractors in the phase-space), the exact nature of these changes is unknown. The nature of the bounds on the number of attractors that a system can maintain, as a function of the number of neurons, their connectivity, and the nature of their potential functions, is also unknown. We plan to address these questions in our future work.

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