Field-theoretic approach to fluctuation effects in neural networks

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A well-defined stochastic theory for neural activity, which permits the calculation of arbitrary statistical moments and equations governing them, is a potentially valuable tool for theoretical neuroscience. We produce such a theory by analyzing the dynamics of neural activity using field theoretic methods for nonequilibrium statistical processes. Assuming that neural network activity is Markovian, we construct the effective spike model, which describes both neural fluctuations and response. This analysis leads to a systematic expansion of corrections to mean field theory, which for the effective spike model is a simple version of the Wilson-Cowan equation. We argue that neural activity governed by this model exhibits a dynamical phase transition which is in the universality class of directed percolation. More general models (which may incorporate refractoriness) can exhibit other universality classes, such as dynamic isotropic percolation. Because of the extremely high connectivity in typical networks, it is expected that higher-order terms in the systematic expansion are small for experimentally accessible measurements, and thus, consistent with measurements in neocortical slice preparations, we expect mean field exponents for the transition. We provide a quantitative criterion for the relative magnitude of each term in the systematic expansion, analogous to the Ginsburg criterion. Experimental identification of dynamic universality classes *in vivo* is an outstanding and important question for neuroscience.

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I. INTRODUCTION

It has proven difficult to produce an analytic theory for the treatment of fluctuations in the neural activity of neocortex. It is clear, however, that mean field models are inadequate [1]. Consistent with this fact, there is little detailed understanding of the role correlated activity plays in the brain, although such correlations have been associated with expectant and attendant states in behaving animals [2,3].

The neocortex contains on the order of 10^{10} neurons, each supporting up to 10^4 synaptic contacts. This enormous connectivity suggests that a statistical approach might be appropriate. We present a theory developed with the methods of stochastic field theory applied to nonequilibrium statistical mechanics [4,5]. The formalism for this theory is based primarily on the assumption that neural dynamics is Markovian, although this can be relaxed. The derivation of the master equation for this process is based on an analysis of neurophysiology. The intuition behind the resulting theory is that the action potentials or "spikes" emitted by neurons are akin to the molecular density in a chemical kinetic reaction. The expectation value of the field, $\langle \varphi(x,t) \rangle$, describes the density of spikes that still influence the network at the point (x,t). It is a measure of neural "activity."

The use of field theory solves the "closure" problem typically seen in statistical theories by making available the loop expansion, which allows for a systematic calculation of corrections to the mean field behavior. In the cortex the degree of connectivity is expected to be very high, and thus an analog of the Ginsburg criterion tells us that the loop expansion should be useful at finite order. Likewise, the theory makes available expansions for the correlation functions. Often, a field theory approach is used in order to facilitate renormalization group techniques for describing the critical behavior of a system. Indeed, we will still find a use for renormalization arguments.

While a field theorist might find this a novel use of an established technique, much of the aim of this paper is to provide a framework in which the practicing theoretical neuroscientist can approach an analysis of fluctuations in neural systems. Since this community is not, by and large, familiar with field theory, there is some background discussion.

II. STOCHASTIC MODELS OF NEURAL ACTIVITY

A. The effective spike model

Consider a network of N neurons. The configuration of each neuron is given by the number of "effective" spikes n_i that neuron i has emitted. There is a weight function w_{ij} describing the relative innervation of neuron i by neuron j. The probability per unit time that a neuron will emit another spike, i.e., transition from the state n_i to the state n_i+1, is given by the firing rate function $f(s)$, which depends upon the input s to the neuron. We imagine this input to be due to both an external input I and the recurrent input from other neurons, $\Sigma_j w_{ij} n_j$. We also include a decay rate α to account for the fact that spikes are effective only for a time interval of approximately $1/\alpha$. This decay can be interpreted as either a potential failure of postsynaptic firing or the time constant of the synapse.

In total, the variable n_i describes the number of spikes which are still affecting the dynamics of the system. Outside

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of interactions, each spike has a lifetime of approximately $1/\alpha$. When the system undergoes a transition such that $n_i \to n_i - 1$, it means that a spike at neuron i, say the earliest one fired, is no longer having an effect upon the dynamics. Similarly, the transition $n_i \to n_i + 1$ means that neuron i has fired (again).

This model is a Markov process, which enables the representation of its dynamics by a master equation

$$\frac{dP(\vec{n},t)}{dt} = \sum_i \alpha(n_i+1)P(\vec{n}_{i+},t) - \alpha n_i P(\vec{n},t) + f\left(\sum_j w_{ij} n_j + I\right) \times [P(\vec{n}_{i-},t) - P(\vec{n},t)]. \quad (1)$$

The component n_i of $\vec{n}$ is the number of effective spikes that have been emitted by neuron i. $P(\vec{n},t)$ is the probability of the network having the configuration described by $\vec{n}$ at time t. The special configurations $\vec{n}_{i+}$ and $\vec{n}_{i-}$ are equal to configuration $\vec{n}$ except that the ith component is $n_i \pm 1$, respectively.

This model makes standard assumptions to facilitate the use of nonequilibrium statistical mechanics. In particular, in addition to the Markov assumption, the neurons are all assumed identical, with identical α and $f(s)$, although this can and will be relaxed. We also assume that w_{ij} is a function only of $|i-j|$, i.e., the pattern of innervation is the same for every neuron.

We wish to compute either the probability distribution $P(\vec{n},t)$ or, equivalently, its moments

$$\langle n_i(t) n_j(t') n_k(t'') \cdots \rangle, \quad (2)$$

where the expectation value is over all statistical realizations of the Markov process. Note that we are abusing notation by adding a time argument to $n_i(t)$. This indicates that we are interested in the expectation value of n_i at time t. In particular, let us define

$$a_i(t) = \langle n_i(t) \rangle = \sum_{\vec{n}} n_i P(\vec{n},t). \quad (3)$$

$a_i(t)$ is a measure of the activity in the network. In general, this is calculated using a mean field approximation. The standard approach is to derive equations governing the time evolution of the mean and ignore the effects of higher-order correlations such as $\langle n_i(t) n_j(t') \rangle$ (as shown below, for the effective spike model this produces the Wilson-Cowan equation). Using the machinery of stochastic field theory, we will demonstrate how to calculate these quantities and the equations governing their evolution.

Because it does not account for refractory effects, we expect this model to have difficulties with modeling high firing rates. In particular, any given neuron could fire arbitrarily fast in an arbitrarily small amount of time. An approximate substitute is to choose the firing rate function $f(s)$ to be saturating. It is possible to account for refractory effects by, for example, adding a temporal component to the weight function, i.e., a delay; the input to the neuron is given by the states some number of time steps in the past. Technically, this is no longer a Markov process if it involves the state of the network at more than one time step. This is not a problem for the formalism, but for now we will keep the mechanics simple by assuming the Markov property. Finally, we would like to point out that $f(s)$ need not be smooth, and the extensions to the Wilson-Cowan equations apply for $f(s)$ which are almost everywhere differentiable. However, our renormalization arguments later will depend upon smoothness.

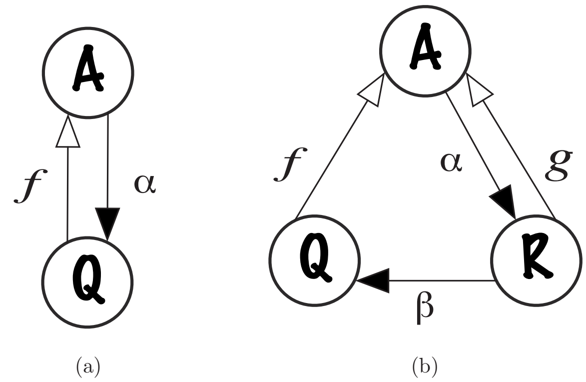

FIG. 1. Graphical representations of Cowan dynamics for the (a) two- and (b) three-state neural models. A, Q, and R represent active, quiescent, and refractory states, respectively. The arrows represent possible transitions with the indicated transition rates. Open arrows indicate that the corresponding rate is potentially dependent on the state of the network, i.e., the activity of the other neurons in the network, with firing rate functions f and g.

B. Older models

The effective spike model grew out of older models introduced by Cowan. In [6], Cowan introduced an approximate Markov process to describe the statistics of neurons considered as objects with a fixed set of basis states. In the simplest case, a neuron can be considered "active" or "quiescent." A refinement of this considers that neurons can also occupy a "refractory" state. These states are taken from an analysis of the neuron's firing behavior. When an action potential is triggered, there is a brief period in which the cell membrane is depolarized (the active state) after which it becomes hyperpolarized (the refractory state, which makes it more difficult for the neuron to fire), before returning to rest (the quiescent state) to await another depolarizing event. Whether one wishes to account for the refractory state depends upon the time scales under consideration.

The full state of a given neuron is defined by the probability that it is in any of the basis states. Likewise, the dynamics are defined by a master equation along with firing rate functions which gave the probability for a neuron to change state given the states of the other neurons in the network. State diagrams for two- and three-state neurons are given in Fig. 1. In equilibrium statistical physics, models such as Glauber dynamics or similar for the Ising or Potts models are the obvious parallels, with the central distinguishing feature being the absence of detailed balance.

The Cowan models are perhaps more satisfying because they are closer to the biology of real neurons, albeit still stochastic. In turn we can connect the effective spike model to the Cowan models. A qualitative method of arriving at the effective spike model from the dynamics defined by Cowan is to consider the states of low activity (i.e., where most of the neurons are quiescent). The quiescent state then serves as a "thermal bath" of sorts for the active states. In the thermodynamic limit ($N \to \infty$), there are an infinite number of neurons within a small region. If we look at time scales such that refractory effects are negligible, the primary variable of relevance is the number of active neurons in a given region of the network. The effective spikes of the spike model can be interpreted as the number of neurons active within a small region at a given time. The decay constant α then describes the length of time each spike remains active before being reabsorbed by the quiescent bath.

In Appendix C, after we have introduced the technology used to analyze the effective spike model, we give a brief discussion of how the Cowan models are analyzed in similar fashion and how they can be reduced to the effective spike model.

III. FIELD THEORY FOR THE EFFECTIVE SPIKE MODEL

Using the master equation (1), it is straightforward to derive a stochastic field theory describing the continuum and "thermodynamic" ($N \to \infty$) limits of this model. The explicit derivation is given in the appendices. There are two basic steps to this process. First, one formulates an operator representation of the configurations available to the system, i.e., the states with probability distribution $P(\vec{n},t)$ and of the master equation. This is shown in Appendix A. Second, one uses the coherent state representation to transform the operators into the final field variables. This is shown in Appendix B. The end result is a generating functional $Z[J,\tilde{J}]$ [Eq. (11)] for moments of two fields $\varphi(x,t)$ and $\tilde{\varphi}(x,t)$ [i.e., functional derivatives of Z produce moments of $\varphi(x,t)$ and $\tilde{\varphi}(x,t)$]. These fields are related to the physical quantities of interest via

$$\left\langle \prod_i n(x_i,t_i) \right\rangle = \left\langle \prod_i [\tilde{\varphi}(x_i,t_i)\varphi(x_i,t_i) + \varphi(x_i,t_i)] \right\rangle. \quad (4)$$

We have promoted the neural index into an argument x. The index i in this context refers to points (i.e., the neuron at location x_i) in whose correlations we are interested. Loosely speaking, one can think of $\varphi(x,t)$ as the variable describing $n(x,t)$, and $\tilde{\varphi}(x,t)$ as describing the network's response to perturbations (it is often called the "response field").[1] $\tilde{\varphi}(x,t)$ has the property that

$$\left\langle \prod_i \tilde{\varphi}(x_i,t_i) \prod_j \varphi(x_j,t_j) \right\rangle = 0 \quad (5)$$

if there is at least one i such that $t_i \geq t_j$ for all j. In particular, we have

$$a(x,t) = \langle n(x,t) \rangle = \langle \varphi(x,t) \rangle \quad (6)$$

and (if $t_1 > t_2$)

$$\langle n(x_1,t_1)n(x_2,t_2)\rangle = \langle \varphi(x_1,t_1)\varphi(x_2,t_2)\rangle + \langle \varphi(x_1,t_1)\tilde{\varphi}(x_2,t_2)\rangle a(x_2,t_2). \quad (7)$$

The correlation function

$$\Delta(x_1,t_1;x_2,t_2) = \langle \varphi(x_1,t_1)\tilde{\varphi}(x_2,t_2)\rangle \quad (8)$$

is called the propagator and describes the network's linear response. It has the property

$$\lim_{t \to t'_+} \Delta(x_1,t;x_2,t') = \delta(x_1 - x_2) \quad (9)$$

so that the equal-time two-point correlator is given by

$$\langle n(x_1,t)n(x_2,t)\rangle = \langle \varphi(x_1,t)\varphi(x_2,t)\rangle + \delta(x_1 - x_2)a(x_2,t). \quad (10)$$

The generating functional $Z[J,\tilde{J}]$ is given by the following path integral (see Appendix B) over $\varphi(x,t)$ and $\tilde{\varphi}(x,t)$:

$$Z[J,\tilde{J}] = \int \mathcal{D}\varphi\, \mathcal{D}\tilde{\varphi}\, e^{-S[\varphi,\tilde{\varphi}] + J\cdot\tilde{\varphi} + \tilde{J}\cdot\varphi}, \quad (11)$$

where $\mathcal{D}$ indicates a functional integration measure; we are using the notation

$$\tilde{J}\cdot\varphi = \int d^dx\, dt\, \tilde{J}(x,t)\varphi(x,t) \quad (12)$$

(we have allowed the domain of x to have d dimensions; see below). The "action" $S[\varphi,\tilde{\varphi}]$ is defined as

$$S[\varphi(x,t),\tilde{\varphi}(x,t)] = \int_{-\infty}^{\infty} d^dx \left(\int_0^t dt\, \tilde{\varphi}\partial_t\varphi + \alpha\tilde{\varphi}\varphi - \tilde{\varphi} f(w \star [\tilde{\varphi}\varphi + \varphi] + I) \right) - \int_{-\infty}^{\infty} d^dx\, \bar{n}(x)\tilde{\varphi}(x,0). \quad (13)$$

There is an initial state operator in this action proportional to $\bar{n}(x)$ (see Appendix A) and $\star$ denotes a convolution. It corresponds to the assumption that the network starts out in an uncorrelated state where each neuron x has a Poisson distribution of spikes with mean $\bar{n}(x)$. Other such initial state operators will correspond to different initial (possibly correlated) states.

We should add a word concerning the dimension d. Although we did not mention it in the discussion of the model, it is crucial in the thermodynamic and continuum limits, and has measurable effects. For example, the emergent patterns from a bifurcation will be affected by the dimension d. We have left it arbitrary, but we expect d to take the value 2 or 3 (or possibly in between to allow for a fractal lattice). Real cortex is of course three dimensional, but certain applications may be adequately described by a two-dimensional network (i.e., the correlation length may be longer than the extent of the cortex in a particular dimension). In the event that interactions are simply between nearest neighbors, d characterizes the number of neighbors any given neuron will have.

[1] More precisely, the fields $\varphi(x,t)$ and $\tilde{\varphi}(x,t)$ are related to $n(x,t)$ and a new field $\tilde{n}(x,t)$ via $1+\tilde{\varphi}(x,t) = \exp[\tilde{n}(x,t)]$ and $\varphi(x,t) = n(x,t)\exp[-\tilde{n}(x,t)]$. One could formulate the theory in terms of $n(x,t)$ and $\tilde{n}(x,t)$, but the action would be more complicated.

The opposite extreme of all-to-all homogeneous coupling produces an effectively high-dimensional system. We consider connectivity that is short range relative to the total system size.

The generating functional (11) contains all of the statistical information about the system. In principle, one must simply calculate $Z[J(x,t),\tilde{J}(x,t)]$ for any model. Realistically, this is possible for only the simplest of systems. Typically, one evaluates the generating functional via a perturbation series. The action is separated into the piece bilinear in $\varphi(x,t)$ and $\tilde{\varphi}(x,t)$, called the "free" action, and the remainder, called the "interacting" action:

$$S[\varphi,\tilde{\varphi}] = S_f[\varphi,\tilde{\varphi}] + S_i[\varphi,\tilde{\varphi}]. \tag{14}$$

This allows us to define the linear operator $\mathcal{L}$ as follows:

$$S_f[\varphi,\tilde{\varphi}] = \tilde{\varphi}(x,t)\mathcal{L}[\varphi(x,t)], \tag{15}$$

as well as the propagator $\Delta(x,t)$,

$$\mathcal{L}[\Delta(x-x',t-t')] = \delta(x-x')\,\delta(t-t'). \tag{16}$$

In other words, $\Delta(x,t)$ is the Green's function for the differential operator $\mathcal{L}$. This allows us to define a perturbation expansion using the remainder of the action S_i,

$$Z[J(x,t),\tilde{J}(x,t)] = \int \mathcal{D}\varphi\,\mathcal{D}\tilde{\varphi} \sum_{n=0}^{\infty} \frac{(-S_i[\varphi,\tilde{\varphi}])^n}{n!} e^{-S_f[\varphi,\tilde{\varphi}]+J\cdot\tilde{\varphi}+\tilde{J}\cdot\varphi}. \tag{17}$$

We can rewrite this as

$$Z[J(x,t),\tilde{J}(x,t)] = \sum_{n=0}^{\infty} \frac{(-S_i[\delta/\delta\tilde{J},\delta/\delta J])^n}{n!} \times \int \mathcal{D}\varphi\,\mathcal{D}\tilde{\varphi}\, e^{-S_f[\varphi,\tilde{\varphi}]+J\cdot\tilde{\varphi}+\tilde{J}\cdot\varphi}, \tag{18}$$

where we have replaced the arguments of S_i with functional derivatives in order to write the generating functional as an expansion of moments of a Gaussian path integral:

$$Z_f[J(x,t),\tilde{J}(x,t)] = \int \mathcal{D}\varphi\,\mathcal{D}\tilde{\varphi}\, e^{-S_f[\varphi,\tilde{\varphi}]+J\cdot\tilde{\varphi}+\tilde{J}\cdot\varphi}. \tag{19}$$

We can compute the generating functional Z_f via completing the square,

$$\varphi(x,t) \rightarrow \varphi(x,t) + \Delta\cdot J,$$

FIG. 2. Feynman graph for the propagator. Time increases from left to right so that $t' < t$.

$$\tilde{\varphi}(x,t) \rightarrow \tilde{\varphi}(x,t) + \tilde{J}\cdot\Delta, \tag{20}$$

and so

$$Z_f[J(x,t),\tilde{J}(x,t)] = \int \mathcal{D}\varphi\,\mathcal{D}\tilde{\varphi}\, e^{-S_f[\varphi,\tilde{\varphi}]+\tilde{J}\cdot\Delta\cdot J} = Z_f[0,0]e^{\tilde{J}\cdot\Delta\cdot J}. \tag{21}$$

$Z_f[0,0]$ is a normalization factor. This produces the following series:

$$Z[J(x,t),\tilde{J}(x,t)] = \sum_{n=0}^{\infty} \frac{(-S_i[\delta/\delta\tilde{J},\delta/\delta J])^n}{n!} Z_f[0,0]e^{\tilde{J}\cdot\Delta\cdot J}. \tag{22}$$

In this series all moments generated by $Z[J,\tilde{J}]$ are expressed as products of moments of a Gaussian measure. This expression allows us to construct Feynman diagram representations of the moments of the distribution. If $S_i=0$ we are left with the simple generating functional

$$Z[J(x,t),\tilde{J}(x,t)] = Z_f[0,0]e^{\tilde{J}\cdot\Delta\cdot J}, \tag{23}$$

which tells us that

$$\langle\varphi(x,t)\tilde{\varphi}(x',t')\rangle = \frac{1}{Z_f[0,0]} \frac{\delta}{\delta\tilde{J}(x,t)} \frac{\delta}{\delta J(x',t')} Z[J(x,t),\tilde{J}(x,t)] = \Delta(x-x',t-t'), \tag{24}$$

which we can represent by a straight line connecting points (x',t') and (x,t). In these diagrams time implicitly moves to the left, so that $t' < t$ in Fig. 2. The terms in S_i produce vertices with n "incoming" lines and m "outgoing" lines depending on the factors of φ and $\tilde{\varphi}$ respectively. For example, if $S_i = g\int d^dx\,dt\,\varphi\tilde{\varphi}^2$, then the perturbation series for $\langle\varphi(x_1,t_1)\varphi(x_2,t_2)\tilde{\varphi}(x_3,t_3)\rangle$ looks like (to first order in g)

$$\begin{aligned}\langle\varphi(x_1,t_1)\varphi(x_2,t_2)\tilde{\varphi}(x_3,t_3)\rangle &= \frac{1}{Z_f[0,0]} \frac{\delta}{\delta\tilde{J}(x_1,t_1)} \frac{\delta}{\delta\tilde{J}(x_2,t_2)} \frac{\delta}{\delta J(x_3,t_3)} Z \\ &= g \frac{\delta}{\delta\tilde{J}(x_1,t_1)} \frac{\delta}{\delta\tilde{J}(x_2,t_2)} \frac{\delta}{\delta J(x_3,t_3)} \int d^dz\,ds \frac{\delta}{\delta\tilde{J}(z,s)} \left(\frac{\delta}{\delta J(z,s)}\right)^2 e^{\tilde{J}\cdot\Delta\cdot J} = g\int d^dz\,ds\,\Delta(x_1-z,t_1-s)\Delta(x_2 \\ &\quad - z,t_2-s)\Delta(z-x_3,s-t_3).\end{aligned} \tag{25}$$

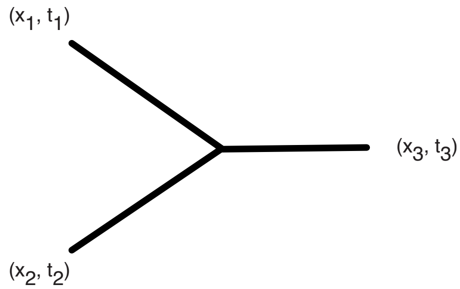

FIG. 3. Feynman graph for the moment $\langle\varphi(x_1,t_1)\varphi(x_2,t_2)\tilde{\varphi}(x_3,t_3)\rangle$.

This is pictured in Fig. 3. Initial state terms do not have an integration over time (like the previous example vertex). Additionally, they only have "outgoing" lines, i.e., factors of $\tilde{\varphi}$. We will consider only initial state terms linear in $\tilde{\varphi}$, but the generalization is straightforward. We denote them with bold dots in the figures to represent the initial time. For example, if $S_i=\int d^dx\,\tilde{\varphi}(x,0)\rho(x)$, i.e., there is only an initial state term, then the exact calculation of the mean is given by

$$\langle\varphi(x,t)\rangle=\int dz\,\Delta(x-z,t)\rho(z). \tag{26}$$

$\rho(x)$ is the initial condition for $\langle\varphi(x,t)\rangle$. This graph is shown in Fig. 4. In later graphs we will not explicitly label the coordinates (x,t).

In our case the vertices given by S_i are somewhat more complicated. We introduce the notation that $f^{(n)}$ is the nth derivative of f. The tree-level propagator is given by

$$(\partial_t+\alpha)\Delta(x,t;x',t')-\int dx\,f^{(1)}(I)w(x-x'')\Delta(x'',t;x',t') = \delta(x-x')\delta(t-t') \tag{27}$$

and the vertices are given by an expansion of $f(x)$ about $x=I$ as

$$\mathcal{V}_{mn}=\int d^dx\,dt\frac{f^{(n)}(I)}{n!}\tilde{\varphi}[w\star\tilde{\varphi}\varphi]^m[w\star\varphi]^n\binom{n}{m}, \tag{28}$$

which represents n incoming lines and $m+1$ outgoing lines (the $n=1,m=0$ term has already been incorporated into the propagator). In addition, the initial state terms will contribute vertices with $n=0$ for any m. Graphs are constructed by taking products of vertices and replacing pairs of factors $\varphi,\tilde{\varphi}$ by factors of the propagator Δ. If the vertex is part of the initial state operator, we represent it with a bold dot. In the following, we will be interested in *vacuum* graphs. Vacuum graphs are those in which all factors of φ have been paired with a factor of $\tilde{\varphi}$, and vice versa, in addition to being one-particle irreducible. One-particle irreducible means that the graphs cannot be rendered disconnected by cutting only a single line. The first few terms in the series for $\langle\varphi(x,t)\rangle$ using only the $m=0$, $n=2$ vertex are shown in Fig. 5. One can see that this series is quite unwieldy.

FIG. 4. Feynman graph for the mean with no interactions and a simple linear initial condition, represented by the bold dot.

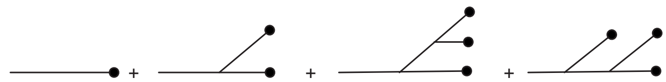

FIG. 5. First four terms in the perturbation expansion of $\langle\varphi(x,t)\rangle$ using only the vertex $\mathcal{V}_{02}$. The dots represent the initial condition operator. Time moves from right to left.

IV. THE EFFECTIVE ACTION AND THE LOOP EXPANSION

The perturbation expansion (22) is adequate in the case of weak coupling. However, in order to systematically characterize fluctuations, the loop expansion is more useful. The loop expansion is a reorganization of the perturbative expansion according to the topology of the graphs in each term. In particular, the loop expansion collects together diagrams with a given number of loops. Equivalently, the loop expansion is a systematic expansion of the generating functional using the method of steepest descents. Each order in this expansion couples higher moments into the dynamics. Introduce the parameter h into $Z[J(x,t),\tilde{J}(x,t)]$ (h serves only as a bookkeeping parameter and must be set to 1 for physical calculations),

$$Z[J(x,t),\tilde{J}(x,t)]=\int\mathcal{D}\varphi\,\mathcal{D}\tilde{\varphi}\,e^{(-S[\varphi,\tilde{\varphi}]+J\cdot\tilde{\varphi}+\tilde{J}\cdot\varphi)/h} \tag{29}$$

An expansion of a given moment in powers of h is equivalent to an expansion in the number of loops in a Feynman graph perturbation expansion. The correlation functions at tree level (0 loops) have the following h dependence:

$$\langle\varphi^n\tilde{\varphi}^m\rangle\sim h^{n+m-1}. \tag{30}$$

Each order in the loop expansion has an additional factor of h. Note that $a(x,t)=\langle\varphi(x,t)\rangle\sim h^0$ and $\tilde{a}(x,t)=\langle\tilde{\varphi}(x,t)\rangle\sim h^0$ [7].

Summing the diagrams in the perturbation series that contribute to $\langle\varphi(x,t)\rangle$ but contain no loops yields the solution to the equations described as mean field theory. Incorporating higher-order effects is a matter of including diagrams with some number of loops. The existence of an initial state operator complicates the explicit representation of this series by adding an infinite number of graphs even at tree level. In order to calculate even the one-loop correction to $\langle\varphi(x,t)\rangle$, we would need to sum the infinite series consisting of the mean field diagrams with one loop inserted in all possible ways.

It is simpler to remove this complication by shifting the field operators $\varphi(x,t)$ by the first moment:

$$\varphi(x,t)\to\varphi(x,t)+a(x,t),$$

$$\tilde{\varphi}(x,t)\to\tilde{\varphi}(x,t)+\tilde{a}(x,t), \tag{31}$$

where

$$a(x,t) = \langle \varphi(x,t) \rangle,$$

$$\tilde{a}(x,t) = \langle \tilde{\varphi}(x,t) \rangle. \tag{32}$$

$a(x,t)$ is *not* the solution of the Wilson-Cowan equation. It is the true mean value of the theory, including all fluctuation effects. The solution of the Wilson-Cowan equation will be an approximation of this.

After performing this shift, the action (including source terms J, $\tilde{J}$) now looks like

$$S[a,\tilde{a};\varphi,\tilde{\varphi}] = S_0[a,\tilde{a}] + S_F[a,\tilde{a};\varphi,\tilde{\varphi}] + J \cdot (\tilde{a} + \tilde{\varphi}) + \tilde{J} \cdot (a + \varphi), \tag{33}$$

where

$$S_0[a(x,t),\tilde{a}(x,t)] = \int_{-\infty}^{\infty} d^d x \left(\int_0^t dt\, \tilde{a}\partial_t a + \alpha \tilde{a} a - \tilde{a} f(w \star [\tilde{a}a + a] + I) \right) - \int_{-\infty}^{\infty} d^d x\, \bar{n}(x)\tilde{a}(x,0), \tag{34}$$

$$S_F[a,\tilde{a};\varphi(x,t),\tilde{\varphi}(x,t)] = \int_{-\infty}^{\infty} d^d x \left(\int_0^t dt\, \tilde{\varphi}\partial_t \varphi + \alpha \tilde{\varphi}\varphi - \tilde{\varphi} f(w \star [\tilde{\varphi}\varphi + \varphi] + I) \right) + (\tilde{\varphi} + \tilde{a}) \times \sum_n \frac{f^{(n)}(w \star [\tilde{a}a + a] + I)}{n!} [w \star \{\tilde{a}\varphi + \tilde{\varphi}a + \tilde{\varphi}\varphi + \varphi\}]^n - \int_{-\infty}^{\infty} d^d x\, \bar{n}(x)\tilde{\varphi}(x,0). \tag{35}$$

For generic $J,\tilde{J}$, this action still has linear source terms for the fields $\varphi,\tilde{\varphi}$, including the initial state. This term represents corrections to the mean arising from stochastic effects. These corrections will appear at all orders of perturbation theory, so that it would seem we have only compounded the problem. However, since we have stipulated that $a(x,t)$ represents the true mean (including all stochastic effects) we can rid ourselves of this difficulty as well by using the effective action.

The generating functional for connected graphs (or the cumulant generating functional) is simply $W[J,\tilde{J}] = h \ln Z$. This gives us

$$hW[J,\tilde{J}] = -S_0 - J \cdot \tilde{a} - \tilde{J} \cdot a + h \ln Z_F, \tag{36}$$

where Z_F is the generating functional with respect to S_F.

Legendre transforming W gives us the effective action

$$\Gamma[a,\tilde{a}] = -hW[J,\tilde{J}] + a \cdot \tilde{J} + \tilde{a} \cdot J, \tag{37}$$

along with the condition

$$\frac{\delta \Gamma}{\delta a(x,t)} = \tilde{J}(x,t),$$

$$\frac{\delta \Gamma}{\delta \tilde{a}(x,t)} = J(x,t), \tag{38}$$

and so

$$\Gamma[a,\tilde{a}] = S_0[a,\tilde{a}] + h \ln Z_F|_{\delta\Gamma/\delta a = \tilde{J};\, \delta\Gamma/\delta\tilde{a} = J}, \tag{39}$$

where the above condition on $J,\tilde{J}$ is imposed upon Z_F. Since $\delta\Gamma/\delta a(x,t)$ and $\delta\Gamma/\delta\tilde{a}(x,t)$ are the linear source terms, setting $J,\tilde{J}=0$ removes them from the stochastic part of the action, including the linear initial state operators. Had we assumed nonlinear initial state operators, they would not be eliminated, but they would not cause the same trouble, as they would produce loop corrections (attaching a nonlinear initial state operator to a diagram will produce a loop). $a(x,t)$ is the true mean of the theory with this choice, since we must have

$$h \frac{\delta W}{\delta \tilde{J}(x,t)} = a(x,t). \tag{40}$$

The diagrammatic expansion of Γ is not plagued by initial state and linear source terms. The equations of motion are given by

$$\frac{\delta \Gamma}{\delta a} = 0,$$

$$\frac{\delta \Gamma}{\delta \tilde{a}} = 0. \tag{41}$$

The vertices for the Feynman diagrams that constitute the loop expansion of the effective action are of the form (28), with the addition of all possible vertices, where $\tilde{a}$ and a have been substituted for $\tilde{\varphi}$ and φ, respectively. The propagator is given below in Eq. (47). The expansion is given by the sum of the vacuum diagrams with respect to $\varphi,\tilde{\varphi}$. Recall from above that vacuum diagrams are those that contain no external $\varphi,\tilde{\varphi}$ lines and are one-particle irreducible, i.e., they cannot be disconnected by removing only a single line. The one-particle reducible graphs are precisely those which are eliminated via the conditions in Eq. (38) [7].

A. Mean field theory

Before we consider the effects of fluctuations, we define mean field theory. The mean field theory corresponding to the action S is defined as the $h \to 0$ limit of the theory. It is the lowest order in the steepest descent approximation. In other words, the mean field $a(x,t) = \langle \varphi(x,t) \rangle$ is given only by the tree level perturbation expansion. All loops and higher moments are set to 0. This is equivalent to the theory defined by the zero-loop approximation of the effective action (although not the zero-loop approximation of the generating functional $Z[J,\tilde{J}]$).

Since the zero-loop effective action is simply $\Gamma_0[a(x,t),\tilde{a}(x,t)] = S_0[a,\tilde{a}]$ (hence the subscript), the mean field theory of the effective spike model is given by

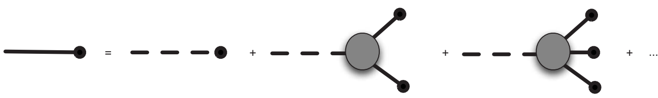

FIG. 6. Equation of motion for $a(x,t)$, exact to all orders. Shown are the linear, quadratic, and cubic parts of the equation. The gray circles represent the proper vertices which are given by the loop expansion of the effective action. Solid lines indicate $a(x,t)$ to all orders; dotted lines indicate the propagator from Eq. (47).

$$0 = \frac{\delta S[a,\tilde{a}]}{\delta \tilde{a}(x,t)} = (\partial_t + \alpha)a(x,t) - f(w \star [\tilde{a}(x,t)a(x,t) + a(x,t)] + I) - \int d^d x'' \tilde{a}(x'',t) f^{(1)}(w \star [\tilde{a}(x'',t)a(x'',t) + a(x'',t)] + I) w(x''-x) a(x,t), \quad (42)$$

$$0 = \frac{\delta S[a,\tilde{a}]}{\delta a(x,t)} = (-\partial_t + \alpha)\tilde{a}(x,t) - \int d^d x'' \tilde{a}(x'',t) \times f^{(1)}(w \star [\tilde{a}(x'',t)a(x'',t) + a(x'',t)] + I) w(x''-x)[\tilde{a}(x,t) + 1], \quad (43)$$

where we have the initial conditions $a(x,0)=\bar{n}(x)$ and $\tilde{a}(x,0)=0$. The second initial condition implies that $\tilde{a}(x,t)=0$ [which we already knew from Eq. (5)]. Using this result we have

$$\partial_t a_0(x,t) + \alpha a_0(x,t) - f(w \star a_0(x,t) + I) = 0 \quad (44)$$

and $\tilde{a}_0(x,t)=0$ with the initial condition $a_0(x,0)=\bar{n}(x)$. We have introduced the notation $a_0,\tilde{a}_0$ to indicate that the calculation is done to zero loops. Equation (44) is a simple form of the Wilson-Cowan equation.

B. Loop corrections to Wilson-Cowan equation

Calculating loop corrections to the effective action provides a means of attaining systematic corrections to the Wilson-Cowan equation. Although taking into account all possible diagrams generated by the action S_F would be a daunting task, the result $\tilde{a}(x,t)=0$ greatly simplifies our consideration. The only diagrams that will contribute to the mean field equation are those with precisely one factor of $\tilde{a}(x,t)$; higher-order terms in $\tilde{a}$ will become zero. More precisely, we need to evaluate the sum of the $(1,n)$ proper vertices $\Gamma^{(1,n)}$ for all n [the notation (m,n) indicates the vertex that has m outgoing and n incoming lines].

The one-loop contribution is rather simple. It is indicated graphically in Figs. 6 and 7. The vertices that contribute to the mean equation are

$$-\int dx\, dt\, \tilde{a}(x,t) \frac{f^{(2)}(w \star a(x,t) + I)}{2} [w \star \varphi(x,t)]^2 \quad (45)$$

and

$$-\int dx\, dt\, \tilde{\varphi}(x,t) f^{(1)}(w \star a(x,t) + I) w \star [\tilde{\varphi}(x,t) a(x,t)]. \quad (46)$$

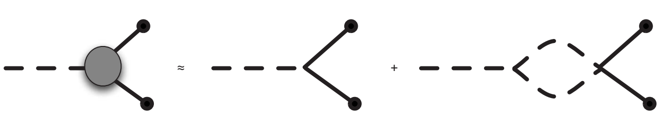

FIG. 7. One-loop approximation to the quadratic term in the equation for $a(x,t)$. There are similar diagrams for the cubic and higher terms as well, all of which sum (along with the linear term) to give the term $\mathcal{N}$ in Eq. (49).

In order to connect these vertices we need the propagator. It is given by the bilinear part of S_F. It is

$$(-\partial_t + \alpha)\Delta(x-x',t-t') - f^{(1)}(x,t) \int dx'' w(x-x'')\Delta(x''-x',t-t') = \delta(x-x')\delta(t-t'), \quad (47)$$

where we have used the abbreviated notation $f^{(n)}(x,t) = f^{(n)}(w \star a(x,t) + I)$. The one-loop contribution to the Wilson-Cowan equation is therefore

$$-\mathcal{N}[a,\Delta] = \int dx_1 dx_2 dx' dt' dx'' f^{(2)}(x,t) w(x-x_1) w(x-x_2) \times f^{(1)}(x',t') w(x'-x'') \Delta(x_1-x',t-t') \Delta(x_2-x'',t-t') a(x'',t'). \quad (48)$$

Thus we have the one-loop Wilson-Cowan equation

$$\partial_t a_1(x,t) + \alpha a_1(x,t) - f(w \star a_1(x,t) + I) + h\mathcal{N}[a_1,\Delta] = 0 \quad (49)$$

along with Eq. (47) (with $a=a_1$). Further loop corrections can be obtained as a simple application of the Feynman rules. No new equations will be added. From this point of view, the loop expansion provides a natural closure of the moment hierarchy normally associated with stochastic systems. To incorporate higher-order statistical effects into the equations, one simply needs to calculate to a higher order in h, i.e., evaluate more loop contributions to Eq. (49). As it stands, Eq. (49) amounts to a "semiclassical" evaluation of the Wilson-Cowan equation.

C. Mean field criterion

In order for the loop expansion to be valid and useful to finite order, we need some justification for claiming that the relative magnitude of the loop effects is diminished higher in the expansion. In equilibrium statistical mechanics, the Ginsburg criterion provides a condition for when loop effects become comparable to mean field effects and hence gives a criterion for when the loop expansion begins to break down at finite order.

To derive an analog of this condition, we wish to know when the one-loop correction to the propagator becomes of the same order as the tree-level propagator. The propagator is the solution to the linearized Wilson-Cowan equation; likewise the "one-loop" propagator is the solution to the linearization of Eq. (49). The diagram for this is shown in Fig. 8. For simplicity, we are considering perturbations around a

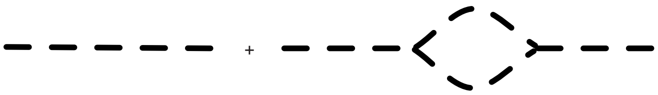

FIG. 8. Lowest-order contributions to $\Gamma^{(1,1)}[0,0]$. When the one-loop contribution is of the same magnitude as the mean field propagator, mean field theory is no longer dependable.

homogeneous equilibrium solution $a_1(x,t)=a_1$. The assumption that the mean field contribution is dominant implies

$$\alpha - f'\hat{w}(p) \gg \frac{f''f'}{2}\int \frac{d^dq}{(2\pi)^d}\frac{\hat{w}(q)^2\hat{w}(p-q)}{[2\alpha - f'\hat{w}(q) - f'\hat{w}(p-q)]}, \tag{50}$$

where we have introduced the notation $\hat{w}(p)$ to describe the Fourier transform of $w(x)$. The left-hand side is the mean field contribution while the right-hand side is the one-loop diagram of Fig. 8. For specificity we make the assumption that the weight function $\hat{w}(p)$ is peaked at $p=0$. There is then a bifurcation at a critical point determined at mean field order by $\alpha = f'\hat{w}(0)$. We can rescale the integral in (50) to extract the infrared ($|q|\to 0$) singular behavior [note that it is well behaved in the ultraviolet ($|q|\to\infty$) because of the weight function, if not by a neural lattice cutoff]. Near criticality, the dominant contribution to the integral comes from

$$\int \frac{d^dq}{(2\pi)^d}\frac{\hat{w}(0)^3}{[2\alpha - 2f'\hat{w}(0) + f'w_2q^2]} \tag{51}$$

where w_n is the nth moment of the distribution $w(x)$. In the limit $\alpha \to f'\hat{w}(0)$, this integral is divergent ("infrared singular") for $d<4$ (as is to be expected from the discussion below on the directed percolation phase transition). Scaling the integration variable to $q' = l_d q$ allows us to write the condition as (after some algebra)

$$\left(\frac{w_2}{w_0}\right)^2 \gg \frac{|f''|w_0A[f',w_4,\ldots]}{f'}l_d^{4-d} \tag{52}$$

where

$$l_d^2 = \frac{f'w_2}{2(\alpha - f'w_0)} \tag{53}$$

is the diffusion length. The factor $A[f',w_4,\ldots]$ comes from the regularized integral in (50). In the absorbing state, the diffusion length is the length to which spikes will propagate before decaying. Loop corrections become comparable to the tree-level contributions as this length becomes comparable to the spatial extent of the cortical interactions. Physically speaking, far from criticality, fluctuations do not have a chance to propagate because perturbations away from the mean relax quickly. Near criticality, small perturbations can propagate throughout the system, leading to fluctuation-dominated behavior. Note in particular that as $f''\to 0$, condition (52) is never violated. Because of the high connectivity and long range of interactions in the cortex, we expect that this criterion is satisfied for realistic networks.

This result implies that a loop expansion is useful and relevant as long as one is interested in behavior away from a bifurcation, or critical, point. Near the onset of an instability, the loop expansion breaks down at finite order, and one must make use of renormalization arguments.

Comparing this criterion to the well-known Ginsburg criterion from equilibrium statistical mechanics, we see that the form is identical, although the diffusion length is replaced by the correlation length.

D. Higher-order correlations

Having both provided the equation governing the mean field and justified the truncation of the loop expansion away from critical points, we now wish to illustrate the calculation of higher-order correlations to finite order in the loop expansion. In particular, we will provide a recipe for calculating all moments at tree level. The discussion of the preceding section suggests that a tree-level computation of higher moments should be quite adequate for many purposes. Recall also that in the loop expansion the tree level for the correlations is at higher order than the mean, e.g., the two-point correlation is at $O(h)$, while the mean is $O(1)$. A consistent expansion requires considering all moments to the same power in h. Consequently, a one-loop expansion in the mean corresponds to a tree-level calculation of the two-point function. Feynman diagrams permit us to compute any such tree-level correlation in terms of the mean field from Eq. (44) and the propagator in Eq. (47).

The action for the deviations from the mean is given by Z_F. The vertices are those given by the action S_F while the propagator is that from Eq. (47). For these vertices, we can freely set $\tilde{a}=0$. As an example, the vertex which contributes at tree level to $\langle(\varphi-a)^2\rangle$, $\Gamma^{(2,0)}$, is

$$\int dx\, dt\, \tilde{\varphi}(x,t)f^{(1)}(x,t)w \star [\tilde{\varphi}(x,t)a]. \tag{54}$$

Defining $C(x_1,t_1;x_2,t_2)=\langle[\varphi(x_1,t_1)-a(x_1,t_1)][\varphi(x_2,t_2)-a(x_2,t_2)]\rangle$, this means that

$$\begin{aligned}C(x_1,t_1;x_2,t_2) = {}& h\int dx\, dx'dt\, \Delta(x_1-x,t_1-t)\Delta(x_2-x',t_2 - t)f^{(1)}(x,t)w(x-x')a(x',t)\\ &+ h\int dx\, dx'dt\, \Delta(x_1-x',t_1-t)\Delta(x_2-x,t_2 - t)f^{(1)}(x,t)w(x-x')a(x',t).\end{aligned} \tag{55}$$

$C(x_1,t_1;x_2,t_2)$ is shown graphically in Fig. 9. It is straightforward to use the Feynman rules to construct the corresponding moments $\langle(\Delta\varphi)^n\rangle$. Note that we can use the function $C(x_1,t_1;x_2,t_2)$ to write the one-loop correction to the Wilson-Cowan equation (48) in the following form:

$$h\mathcal{N}[a,\Delta] = h\frac{1}{2}\int dx_1dx_2f^{(2)}(x,t)w(x-x_1)w(x-x_2)C(x_1,t;x_2,t). \tag{56}$$

The one-loop Wilson-Cowan equations are then

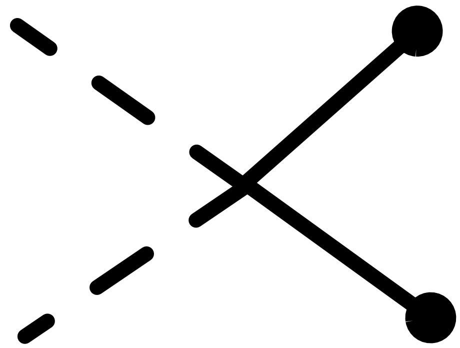

FIG. 9. Tree-level graph for the two-point correlation function $C(x_1,t_1;x_2,t_2)$. It should be compared with the diagram of the loop correction to $a(x,t)$ in Fig. 7.

$$\partial_t a_1(x,t) + \alpha a_1(x,t) - f(w \star a_1(x,t)) + h\frac{1}{2}\int dx_1 dx_2 \times f^{(2)}(x,t)w(x-x_1)w(x-x_2)C(x_1,t;x_2,t). \quad (57)$$

In the same manner, higher terms in the loop expansion can be written as couplings of the mean with higher moment functions.

V. RENORMALIZATION AND CRITICALITY

We now analyze the critical behavior of the effective spike model. As mentioned above, the loop expansion begins to break down as $f'w_0 \to \alpha$. This corresponds to the situation wherein the tendency of a neuron to be excited by depolarization is balanced by the decay of the spike rate. It can be thought of as a "balance condition" between excitation and inhibition, since inhibition cannot be distinguished from the effects of α in the effective spike model.

Qualitatively we can say that the breakdown of the loop expansion corresponds to the situation wherein the branching and aggregating processes are beginning to balance one another. These processes are due to vertices that generate the two-point correlation and couple it to the mean field at one-loop order. If we make the following transformation on the fields:

$$\tilde{\varphi}(x,t) \to \sqrt{\frac{2f'}{w_0|f''|}}\tilde{\varphi}(x,t),$$

$$\varphi(x,t) \to \left(\sqrt{\frac{2f'}{w_0|f''|}}\right)^{-1}\varphi(x,t), \quad (58)$$

the magnitudes of the coefficients of the branching and aggregating vertices are equal. In addition, if f'' is opposite in sign to f' (which corresponds to a saturation of the weight function) the vertices will have opposite sign. The transformed fields now have dimensions of $[\varphi]=[\tilde{\varphi}]=d/2$ (meaning φ^2 will have dimensions of a density). In addition, the fact that the propagator approaches that of diffusion at large time suggests that time should carry dimension $[t]=-2$. Removing all irrelevant operators (those whose coefficients naively scale to 0 as we scale to large system sizes) in $d\leq 4$ we have

$$S[\varphi,\tilde{\varphi}] = \int dt\, d^dx[\tilde{\varphi}\partial_t\varphi - D\tilde{\varphi}\nabla^2\varphi + \mu\tilde{\varphi}\varphi + g(\varphi^2\tilde{\varphi} - \tilde{\varphi}^2\varphi)] \quad (59)$$

where we have defined renormalized parameters for the diffusion constant D, decay (or growth) μ, and coupling g. This is the action for the Reggeon field theory, shown to be in the same universality class as directed percolation [8]. An extensive review of directed percolation can be found in [9]. The minus sign between the cubic terms is a reflection of the saturating firing rate function and is necessary for the existence of an ultraviolet fixed point, otherwise the argument breaks down. We are making the reasonable assumption here that the renormalized action will show this saturating character given that $f(x)$ saturates. Resting neocortex should therefore exhibit a directed percolation phase transition from the absorbing (nonfluctuating) fully quiescent state to a spontaneously active state. This means that the scaling properties of the cortex should be identical with those of directed percolation. This transition occurs as the parameter μ moves through zero from above. The bare (i.e., unrenormalized) value of this parameter is $\mu_0=\alpha-f'w_0$. Altering the relative degree of excitation and inhibition changes the value of w_0, resulting in one method of achieving the phase transition in practice. Note also that this action has a time reversal symmetry $\phi(x,t)\to\tilde{\phi}(x,-t)$. This is an emergent symmetry near the critical point.

The directed percolation phase transition (and, in general, all nonequilibrium dynamical phase transitions) is characterized by four exponents β,β',ν,z. These are defined as

$$\langle\varphi(x,t)\rangle \sim \mu^{\beta},$$

$$\xi_\perp \sim \mu^{-\nu},$$

$$\xi_\parallel \sim \mu^{-\nu z},$$

$$P_\infty \sim \mu^{\beta'}. \quad (60)$$

$\langle\varphi\rangle$ here represents the supercritical equilibrium expectation value. $\xi_{\perp,\parallel}$ are the spatial and temporal correlation lengths, respectively. P_∞ is the probability that a randomly chosen site will belong to a cluster of infinite temporal extent. The time reversal symmetry of directed percolation implies $\beta=\beta'$. The mean field values of these exponents are

$$\beta=1,$$

$$\nu=\frac{1}{2},$$

$$z=2. \quad (61)$$

We have stated that $d\leq 4$ above. Strictly speaking, the upper critical dimension for directed percolation is $d_c=4$. For $d>4$, the loop corrections are no longer infrared divergent and thus do not dominate the activity. In this regime, mean field theory will describe the scaling behavior. Physically, the probability of aggregating essentially vanishes and the dynamics is that of a branching process. The role dimension plays in directed percolation is to determine the number of neighbors each lattice point will have. In the cortical case, the weight function determines the number of neighbors a neuron has. As determined by the criterion in Eq. (52), the loop corrections will not affect the mean field scaling until the diffusion length is sufficiently large. Realistically, in cortex, therefore, this theory predicts the mean field scaling of directed percolation for near-critical systems.

The smoothness of $f(s)$ is important to the renormalization argument. While the theory is well defined with discontinuous $f(s)$, the argument for criticality breaks down with, for example, a step function, which would cause all of the bare vertices [i.e., the coefficients of the interactions for the unrenormalized action (13)] to diverge. It is interesting to note that, in a previous version of neural dynamics, Cowan [6] identified his two-state neural Hamiltonian as being a generalization of the Regge spin Hamiltonian, a reformulation of Reggeon field theory [10].

Evidence consistent with this prediction has already been observed in cortex. Beggs and Plenz [11] have made microelectrode array recordings in rat cerebral cortex which manifest a behavior they term "neuronal avalanches." These avalanches have precisely the character of directed percolation clusters and exhibit critical power law behavior. They measure an avalanche size distribution (equivalent to the cluster mass distribution of directed percolation) with an exponent of $-3/2$. It is the distribution given by

$$P(S)=\left\langle \delta\left(\int d^dx\, dt\, \varphi(x,t)-S\right)\exp[\tilde{\varphi}(0,0)]\right\rangle \quad (62)$$

where $\bar{n}$ in the action is set to zero. The exponential term represents an initial condition of precisely one active site at the origin. The avalanche size is the integrated activity in both space and time. The δ function limits the path integration of the field theory to those configurations of avalanche size S. The prediction of directed percolation near criticality gives the following scaling:

$$P(S)=S^{1-\tau}g(\mu S^{\sigma}) \quad (63)$$

where τ and σ are

$$\tau=2+\frac{\beta}{(d+z)\nu-\beta},$$

$$\sigma=\frac{1}{(d+z)\nu-\beta}. \quad (64)$$

Using mean field values of the exponents we get

$$\tau=\frac{5}{2},$$

$$\sigma=\frac{1}{2}, \quad (65)$$

and so $P(S)\sim S^{-3/2}$. The effective spike model predicts the correct avalanche size distribution.

The effective spike model makes some rather severe assumptions about the network. In particular, the homogeneity of the network dynamics may not be adequate for realistic systems. For descriptions of cortex, there should be some degree of disorder associated with both the decay constant α and the weight function. It has been shown that, although quenched spatial and temporal disorder each separately have severe repercussions upon the universal behavior of directed percolation, spatiotemporally quenched disorder does not affect the universality class [9]. The disorder we expect from the nervous system is due to both spatial inhomogeneities and plasticity, which together constitute spatiotemporal disorder.

Altering the definition of the dynamics in fundamental ways will produce different universality classes. Naturally, universality implies that a wide range of models will produce the same critical behavior. In particular, however, the incorporation of refractory effects in a certain way will result in the universality class of dynamic isotropic percolation rather than directed percolation. Dynamic isotropic percolation produces the same prediction for the avalanche size distribution.

VI. DISCUSSION

We have presented a field theory for neural dynamics derived solely from the assumption of the Markov property and using neurophysiology to formulate the relevant master equation. This theory facilitates the calculation of all of the statistics in a well-defined expansion whose truncation is justified due to the high connectivity of cortical interactions. Also, we can now easily ask how the model responds to correlated input; the equations are a straightforward extension of those presented above. Furthermore, the fact that the firing rate function must saturate suggests a renormalization argument which allows for the characterization of the fluctuations near criticality. The effective spike model suggests that the resulting phase transition is in the directed percolation universality class, although dynamic isotropic percolation is another candidate implied by plausible neural dynamics, i.e., refractoriness. It remains to characterize the extent of finite size effects in the effective spike model.

It is important to emphasize that this approach naturally solves the closure problem. In essence, one exchanges the closure problem for an approximation problem. The vital difference is that in the present formalism one has a means of estimating at what point the loop expansion will break down. In addition one has recourse to the renormalization group when it does.

This model has predictions that are consistent with observations of fluctuations in neocortex. We have already described the Beggs and Plenz observation of critical branching behavior in a neocortical slice [11]. Segev *et al.* also studied neural tissue cultures and found power laws in interspike and interburst intervals [12]. In the arena of simulations, the Tsodyks-Sejnowski computations of networks obeying a balancing condition [13] exhibit the same qualitative behavior as the Beggs and Plenz data, although Tsodyks and Sejnowski did not measure critical exponents.

Of course, the prediction of the $-3/2$ power law for avalanche distributions is not new [14–16], and there has been plenty of work on modeling avalanches in neural networks [17,18]. In particular, Eurich *et al.* have presented an avalanche model which admits an analytic calculation of the avalanche size distribution for an all-to-all uniform connected network of finite size. As stated, our goal was to produce a formulation of neural network dynamics which builds upon the established Wilson-Cowan approach by systematically incorporating fluctuation effects. For example, not only do we have an extension of the Wilson-Cowan equation but our method also permits the calculation of correlation functions, or "multineuron" distribution functions, and facilitates the study of the dynamics of these correlation functions. In addition, our method of analysis has allowed us to refrain from making certain simplifying assumptions about the connectivity; in particular, we do not require the network to be all-to-all uniformly coupled, so that our formalism admits the study of pattern formation. From this point of view, the goal of our work has been the determination of the semi-classical Wilson-Cowan equations (47) and (49), and a systematic means of enhancing the approximation derived from the loop expansion.

A side effect of the field theoretic approach is the identification of a directed percolation fixed point in our model, and a nice connection between the Wilson-Cowan-derived literature (see, for example, [19]) and the avalanche modeling literature through the predicted avalanche size distribution. It is important to emphasize that our work identifies the criticality in cortex as a manifestation of a directed percolation phase transition, the tuning of which is governed by the magnitude of the intercortical interactions. From an experimental point of view, the question now regards the identification of the correct nonequilibrium phase transition that governs criticality in the cortex. In turn, this will inform the theorist about which classes of models are appropriate for neural dynamics. For example, if experiment determines that dynamic isotropic percolation is the correct universality class, then the large class of models which exhibit directed percolation as their only phase transition are fundamentally inappropriate. In our view the universality class being studied in much of the avalanche literature is in fact tuned directed percolation, with the tuning parameter sometimes difficult to find. This view of self-organized criticality has been expressed before [20,21]. In keeping with this interpretation, the avalanche results of Beggs and Plenz are dependent upon a small effective input. A large input would have a similar effect to a large magnetic field on a critical Ising network. In cortex, where the inputs are expected to be somewhat larger than in a prepared slice, we no longer expect avalanche behavior. This is also consistent with results observed in cortex [22], where *in vivo* data produces no activity recognizable as avalanche behavior.

Self-organization in a more general sense, however, may actually play an important role in neocortex. It has been shown that the strength of synaptic contacts adapts to the average firing rate [23]. In particular, increased firing reduces the synaptic strength whereas decreased firing increases it. Such a mechanism could provide neocortical dynamics with a tendency to move towards a critical point by providing a means of tuning the parameter w_0, for example.

The potential importance of criticality in neural dynamics is evident upon considering its computational significance. In the absorbing state, activity is too transient to be useful to an "upstream" network, although the response will be local and the character of the stimulus can be distinguished. Likewise, in the active state (or in the growth phase of branching) the response will quickly trigger a stereotypical pattern, providing a response that is useless for discriminating stimuli. The critical state is precisely the region in which stimuli can be distinguished (they retain a degree of locality) in addition to possessing a degree of stability for use in computation. This stability is due to critical slowing down as the decay or growth exponent tends to zero. Beggs and Plenz have similarly remarked that critical behavior may serve to balance the competing requirements of stability and information transmission [11].

The work presented here also suggests that epileptic seizures are manifestations of directed percolation phase transitions. Epileptic conditions are associated with changes in the susceptibility of neocortex. In particular, in lesioned areas, the connectivity tends to increase as a result of neural growth around the lesion. In our view, this serves to increase w_0, driving the system toward the active region. The importance of the saturation of the firing rate function here is that, in real tissue, a single epileptic seizure does not completely destroy neocortex, although damage is incurred over time. This would be the outcome were the network completely linear. The active state in directed percolation produces spontaneous neocortical activity in the absence of stimuli.

We would like to emphasize the concept of universality which we have implicitly introduced in a neural context. If indeed the concept of criticality is important for cortical function, then several biologically relevant questions arise. Principally, what is the function of criticality itself? Beyond this, however, we must ask what role any given universality class plays in neural dynamics. Universality suggests that detailed interactions are unimportant for those functions that may depend upon criticality. As such, a host of simple models may be expected to account for a range of phenomena. Whether one model more accurately represents the detailed biological dynamics may then say more about the evolutionary path by which that system was realized than about the actual function. The first step in this regard is to identify the dynamic universality classes present in the cortex.

It is important to understand that more detailed biological models may introduce different sets of relevant operators and thus potentially alter or remove the universal behavior we have described, although the results of Beggs and Plenz are a strong point in favor of the ubiquitous directed percolation universality class. We have already mentioned that spatially or temporally quenched disorder removes the universality of the model, whereas spatiotemporal noise preserves it. It is also important to understand that universality in the cortex does not preclude the importance of nonuniversal properties, which likely affect many cortical phenomena, otherwise the entire understanding of the cortex could be reduced to the field theory governing a single universality class. As a simple example, much of the cortex operates within a regime with strong, correlated inputs. While our theory is equipped to handle this, universality governs the behavior of spontaneous or near-spontaneous cortex. The importance of criticality from this regard may be to identify classes of theories, namely, those which exhibit the correct universal behavior.

Much traditional work in theoretical neuroscience involves analysis of mean field equations. Not only have we expanded this structure by advocating a statistical approach, we have connected it to the concepts of criticality and universality in the cortex. In summary, we have demonstrated that both fluctuations and correlations in neocortical activity can be accounted for using field theoretic methods of nonequilibrium statistical mechanics, may play an important role in facilitating information processing, and may also influence the emergence of pathological states.

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APPENDIX A: OPERATOR REPRESENTATION OF THE EFFECTIVE SPIKE MODEL

Following Doi [24,25] and Peliti [26] we can introduce creation-annihilation operators for each neuron:

$$[\Phi_i, \Phi_j^\dagger] = \delta_{ij} \tag{A1}$$

These operators generate a state space by acting on the "vacuum" state $|0\rangle$, with $\Phi_i|0\rangle=0$. Inner products in this space are defined by $\langle 0|0\rangle=1$ and the commutation relations. The dual vector to $\Phi_i^\dagger|0\rangle$ is $\langle 0|\Phi_i$. These operators allow us to "count" the number of spikes at each neuron by using the number operator $\Phi_i^\dagger\Phi_i$ and the following representation of each configuration $\vec{n}$:

$$|\vec{n}\rangle = \prod_i \Phi_i^{\dagger n_i}|0\rangle. \tag{A2}$$

We have

$$\Phi_i^\dagger\Phi_i|\vec{n}\rangle = n_i|\vec{n}\rangle \tag{A3}$$

as can be derived from the commutation relation (A1). We can then use this to define states of the network,

$$|\phi(t)\rangle = \sum_{\vec{n}} P(\vec{n},t)\prod_i \Phi_i^{\dagger n_i}|0\rangle = \sum_{\vec{n}} P(\vec{n},t)|\vec{n}\rangle, \tag{A4}$$

where $P(\vec{n},t)$ is the probability distribution given in the master equation (1) and the sum is over all configurations $\vec{n}$.

If we introduce the "projection" state

$$|p\rangle = \exp\left(\sum_i \Phi_i^\dagger\right)|0\rangle, \tag{A5}$$

we can compute expectation values. In particular,

$$\langle p|\Phi_i^\dagger\Phi_i|\phi(t)\rangle = \sum_{\vec{n}} n_i P(\vec{n},t) = \langle n_i(t)\rangle. \tag{A6}$$

Similarly, for products of the number operator, we have

$$\langle p|\Phi_i^\dagger\Phi_i\Phi_j^\dagger\Phi_j\Phi_k^\dagger\Phi_k\cdots|\phi(t)\rangle = \langle n_i(t)n_j(t)n_k(t)\cdots\rangle. \tag{A7}$$

The previous equation can also be generalized so that each neuron is considered at a different point in time, i.e.,

$$\langle n_i(t)n_j(t')n_k(t'')\cdots\rangle, \tag{A8}$$

since the governing equation for $P(\vec{n},t)$ is first order in time.

By acting with ∂_t on the state $|\phi(t)\rangle$, we can construct a representation of the master equation:

$$\begin{aligned}\partial_t|\phi(t)\rangle &= \sum_{\vec{n}} \partial_t P(\vec{n},t)|\vec{n}\rangle = \sum_i \alpha(n_i+1)P(\vec{n}_{i+},t) - \alpha n_i P(\vec{n},t) \\ &\quad + f\left(\sum_j w_{ij}n_j + I\right)[P(\vec{n}_{i-},t) - P(\vec{n},t)]|\vec{n}\rangle \\ &= \left[\sum_i \alpha(\Phi_i - \Phi_i^\dagger\Phi_i) + f_{NO}\left(\sum_j w_{ij}\Phi_j^\dagger\Phi_j + I\right)(\Phi_i^\dagger \right. \\ &\quad \left. - 1)\right]|\phi(t)\rangle,\end{aligned} \tag{A9}$$

where we have used the master equation (1), and where the subscript NO indicates that f is defined by its Taylor expansion about I, where the operators are normal ordered at each order in the series (all creation operators are placed to the right of all annihilation operators). The master equation is thereby written in the form

$$\partial_t|\phi(t)\rangle = -\hat{H}|\phi(t)\rangle \tag{A10}$$

with Hamiltonian

$$\hat{H} = \left[\sum_i \alpha(\Phi_i^\dagger\Phi_i - \Phi_i) + f_{NO}\left(\sum_j w_{ij}\Phi_j^\dagger\Phi_j + I\right)(1-\Phi_i^\dagger)\right]. \tag{A11}$$

As a convenience, we can commute the operator $\exp(\Sigma_i\Phi_i^\dagger)$ all the way to the right in expectation values. This allows us to define all expectation values as vacuum expectation values. The projection state operator would appear as a final condition operator for $\tilde{\phi}$ in the action of the field theory. This procedure allows us to get rid of this operator. Using the commutation relation, we see that this is equivalent to performing the shift

$$\Phi_i^\dagger \to \Phi_i^\dagger + 1. \tag{A12}$$

The number operator becomes

$$\Phi_i^\dagger\Phi_i \to \Phi_i^\dagger\Phi_i + \Phi_i. \tag{A13}$$

Now expectation values are given by

$$\langle 0|(\Phi_i^\dagger\Phi_i+\Phi_i)(\Phi_j^\dagger\Phi_j+\Phi_j)(\Phi_k^\dagger\Phi_k+\Phi_k)\cdots|\phi(t)\rangle = \langle n_i(t)n_j(t)n_k(t)\cdots\rangle. \tag{A14}$$

The Hamiltonian $\hat{H}$ is now given by

$$\hat{H}=\left[\sum_i \alpha\Phi_i^\dagger\Phi_i - f_{NO}\left(\sum_j w_{ij}\Phi_j^\dagger\Phi_j + I\right)\Phi_i^\dagger\right]. \tag{A15}$$

An initial state that is Poisson distributed with mean $\bar{n}_i$ would be

$$|\phi(0)\rangle = e^{-\bar{n}_i}\prod_i\sum_k \frac{\bar{n}_i^k}{k!}\Phi_i^{\dagger k}|0\rangle = \exp\left(\sum_i(-\bar{n}_i+\bar{n}_i\Phi_i^\dagger)\right)|0\rangle. \tag{A16}$$

After shifting it becomes

$$|\phi(0)\rangle = \exp\left(\sum_i \bar{n}_i\Phi_i^\dagger\right)|0\rangle = \hat{I}|0\rangle, \tag{A17}$$

which defines the initial state operator $\hat{I}$.

APPENDIX B: COHERENT STATE PATH INTEGRALS

1. Definition and properties of coherent states

Coherent states have the form

$$|\vec{\varphi}\rangle = \exp\left(\sum_i \varphi_i\Phi_i^\dagger\right)|0\rangle. \tag{B1}$$

The vector $\vec{\varphi}$ has components φ_i, which are eigenvalues of the annihilation operator,

$$\Phi_i|\vec{\varphi}\rangle = \varphi_i|\vec{\varphi}\rangle. \tag{B2}$$

These eigenvalues φ_i are complex numbers; we use a tilde to denote the conjugate variable $\tilde{\varphi}_i$. They obey the completeness relation

$$\int\prod_i d\varphi_i d\tilde{\varphi}_i \exp\left(-\sum_i|\varphi_i|^2\right)|\vec{\varphi}\rangle\langle\vec{\varphi}| = 1. \tag{B3}$$

The integration of φ_i follows the real line, whereas the integration of $\tilde{\varphi}$ is carried out along the imaginary axis. Because of property (B2) the coherent state representation of a normal ordered operator is obtained very simply:

$$\langle\vec{\psi}|\Phi_i^\dagger\Phi_i|\vec{\varphi}\rangle = \tilde{\psi}_i\varphi_i\langle\vec{\psi}|\vec{\varphi}\rangle = \tilde{\psi}_i\varphi_i\exp(\vec{\tilde{\psi}}\cdot\vec{\varphi}). \tag{B4}$$

We will define the coherent state representation of a (normal ordered) operator $\hat{O}$ to be

$$\mathcal{O}[\vec{\psi},\vec{\varphi}] = \langle\vec{\psi}|\hat{O}|\vec{\varphi}\rangle\exp(-\vec{\tilde{\psi}}\cdot\vec{\varphi}). \tag{B5}$$

2. Path integrals

We can use the coherent state representation to transform the operator representation of the master equation (A10) into a path integral over the coherent state eigenvalues $\varphi,\tilde{\varphi}$. We can write the solution to the master equation in the form

$$|\phi(t)\rangle = e^{-\hat{H}t}|\phi(0)\rangle. \tag{B6}$$

We divide the time evolution into N_t small steps of length Δt using the formula

$$e^{-\hat{H}t} = \lim_{N_t\to\infty}\left(1-\frac{\hat{H}t}{N_t}\right)^{N_t}. \tag{B7}$$

After each time step t_i, we insert a complete set of coherent states using the completeness relation (B3). Taking the expectation value by forming the inner product with $|0\rangle$ (or $|p\rangle$ in the nonshifted representation) and taking the limit $N_t\to\infty$, we get the path integral

$$1=\langle 0|\phi(t)\rangle = \int\prod_i \mathcal{D}\varphi_i\mathcal{D}\tilde{\varphi}_i\exp-\left(\sum_i\int dt\,\tilde{\varphi}_i(t)\partial_t\varphi_i(t) - \mathcal{H}(\tilde{\varphi}_i(t),\varphi_i(t))\right)\mathcal{I}[\tilde{\varphi}] \tag{B8}$$

where $\mathcal{H}$ and $\mathcal{I}$ are the coherent state representations of the Hamiltonian and the initial state operator. By adding the terms $\int dt\Sigma_i J_i\tilde{\varphi}_i$ and $\int dt\Sigma_i\tilde{J}_i\varphi_i$ to the exponential, this becomes a generating functional for the moments of φ_i and $\tilde{\varphi}_i$. Using the Hamiltonian and initial state operators from Appendix B and taking the continuum limit in the neuron label i, we have the action defined in Eq. (13).

Because the action is first order in time, the propagator will have the step function as a factor:

$$\langle\varphi(x,t)\tilde{\varphi}(x',t')\rangle \propto \Theta(t-t'). \tag{B9}$$

The action above is defined with the convention that $\Theta(0)=0$. This can be seen either as a result of the fact that operators which go into $\hat{H}$ must be normal ordered (choosing $\Theta(0)=1$ produces exactly the normal ordering factor in the propagator) or as equivalent to the Ito prescription for defining stochastic integrals.

From Eq. (A14) we see that the moments of the quantity $n(x,t)$ are given by moments of

$$\tilde{\varphi}(x,t)\varphi(x,t)+\varphi(x,t). \tag{B10}$$

The first moment is therefore

$$\langle n(x,t)\rangle = \langle\varphi(x,t)\rangle \tag{B11}$$

because of the $\Theta(0)$ prescription. Care must be taken if the time points coincide. The second moment comes from the operator

$$\Phi_i^\dagger\Phi_i\Phi_j^\dagger\Phi_j = \Phi_i^\dagger\Phi_j^\dagger\Phi_i\Phi_j + \Phi_i^\dagger\Phi_j\delta_{ij}, \tag{B12}$$

which becomes upon shifting

$$(\Phi_i^\dagger+1)(\Phi_j^\dagger+1)\Phi_i\Phi_j + (\Phi_i^\dagger+1)\Phi_j\delta_{ij}, \tag{B13}$$

implying that the equal-time two-point correlation function is given by

$$\langle n(x,t)n(y,t)\rangle = \langle \varphi(x,t)\varphi(y,t)\rangle + \delta(x-y)\langle \varphi(x,t)\rangle. \tag{B14}$$

One would come to the same conclusion by taking the time points separate, using (B10), and taking the limit as the time points approach each other.

APPENDIX C: THE COWAN MODELS

The Cowan models are analyzed in a similar fashion to the effective spike model. For the representation, each of the neural states, active, quiescent, and refractory, is assigned a basis state for each neuron. The state of the system is the tensor product of all such states over each neuron, provided that one and only one neuron is at each spatial point, i.e., the probability of finding a neuron in some state at each point is precisely 1. The same coherent state procedure results in an action with a separate field for each state of the neurons, the expectation value of which gives the probability for a neuron to be in that state.

The action for a network of two-state neurons is

$$\begin{aligned}\mathcal{S}(\psi,\phi) = \int_{-\infty}^{\infty} dt\, d^dx\{&\tilde{\psi}(x,t)\partial_t\psi(x,t) + \tilde{\phi}(x,t)\partial_t\phi(x,t) \\ &+ \alpha[|\psi(x,t)|^2 - \tilde{\phi}(x,t)\psi(x,t)] + [|\phi(x,t)|^2 \\ &- \tilde{\psi}(x,t)\phi(x,t)]f(w\star[|\psi(x,t)|^2 + \psi(x,t)])\} \\ &+ \int d^dx[p(x)\tilde{\psi}(x,0) + q(x)\tilde{\phi}(x,0)].\end{aligned} \tag{C1}$$

The fields ψ and ϕ here stand for the active and refractory neural fields. $p(x)$ and $q(x)$ are the initial densities and $p(x)+q(x)=1$.

Likewise, the action for the three-state neurons is given by

$$\begin{aligned}\mathcal{S}(\psi,\phi,\pi) = \int_{-\infty}^{\infty} dt\, d^dx\{&\tilde{\psi}(x,t)\partial_t\psi(x,t) + \tilde{\phi}(x,t)\partial_t\phi(x,t) \\ &+ \tilde{\pi}(x,t)\partial_t\pi(x,t) + \alpha[|\psi(x,t)|^2 - \tilde{\pi}(x,t)\psi(x,t)] \\ &+ \beta[|\pi(x,t)|^2 - \tilde{\phi}(x,t)\pi(x,t)] + [|\phi(x,t)|^2 \\ &- \tilde{\psi}(x,t)\phi(x,t)]f(w\star[|\psi(x,t)|^2 + \psi(x,t)]) \\ &+ [|\pi(x,t)|^2 - \tilde{\psi}(x,t)\pi(x,t)]g(w\star[|\psi(x,t)|^2 \\ &+ \psi(x,t)])\} + \int d^dx[p(x)\tilde{\psi}(x,0) + q(x)\tilde{\phi}(x,0) \\ &+ r(x)\tilde{\pi}(x,0)].\end{aligned} \tag{C2}$$

The extra field π represents the refractory neurons and $r(x)$ its initial density. Now we have the requirement that $p(x)+q(x)+r(x)=1$. The extra firing function $g(s)$ accounts for the possibility of refractory neurons entering the active state.

Since the action is quadratic in those fields corresponding to the quiescent and refractory states, they can be integrated out to arrive at an action for just the active neurons. Provided that we assume the majority of the neurons are quiescent and neglect the non-local temporal effects, we get the action of the effective spike model with some effective firing rate function $f(s)$ (in general different from that in the above two actions).

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