

A Practical Approximation Method for Firing Rate Models of Coupled Neural Networks with Correlated Inputs

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Rapid experimental advances now enable simultaneous electrophysiological recording of neural activity at single-cell resolution across large regions of the nervous system. Models of this neural network activity will necessarily increase in size and complexity, thus increasing the computational cost of simulating them and new challenges in analyzing them. Here we present a novel approximation method to approximate the activity and firing statistics of a general firing rate network model (of Wilson-Cowan type) subject to noisy correlated background inputs. The method requires solving a system of algebraic equations and is fast compared to Monte Carlo simulations of coupled stochastic differential equations. We implement the method with several examples of coupled neural networks and show that the results are quantitatively accurate even with moderate coupling strengths and an appreciable amount of heterogeneity in many parameters. This work should be useful for investigating how various neural attributes qualitatively effect the spiking statistics of coupled neural networks. Matlab code implementing the method is freely available at xxx.

I. INTRODUCTION

With advances in neural recording technologies, experimenters can now record simultaneous activity across multiple brain regions at single cell resolution [1–4]. However, it is still a technical challenge to measure the interactions within and across brain regions that govern this multi-region activity. This challenge is heightened by the fact that cortical neurons are heterogeneous and show substantial trial-to-trial variability [5]. Numerous theoretical studies have examined how neural networks can lead to cortex-like dynamics [6–14]; however, most have been limited to a single region, leaving open the question of how inter-region connection strengths contribute to network processing.

One challenge presented by analyzing multi-region neural networks, is the increased number of parameters which must be specified. To survey a high-dimensional parameter space, one must have a way to efficiently simulate (as in [15]) or approximate network statistics (as in [16]). Here we present a novel approximation method for calculating the statistics of a general coupled firing rate model (based on [17]) of neural networks where we: i) assume the *activity* (not the firing) is pairwise normally distributed, ii) take the entire probability distribution of the presynaptic neurons/populations (providing input) into account. Our method is fast, requiring only solving algebraic equations self-consistently rather than simulating

stochastic differential equations. Several example neural networks are considered and compared with Monte Carlo simulations. A specific version of this method was presented in [18] to model the olfactory sensory pathway; here, we derive formulas in a general way which is easy to evaluate and can accommodate heterogeneous networks. We also demonstrate the method’s efficacy on several example networks with much larger dimension (than the networks examined in the previous work).

II. NEURAL NETWORK MODEL

Each cell (or homogeneous population) has a prescribed activity x_j that is modeled by the following equation [17] for $j = 1, 2, \dots, N_c$:

$$\tau_j \frac{dx_j}{dt} = -x_j + \mu_j + \sigma_j \eta_j(t) + \sum_k g_{jk} F_k(x_k(t)) \quad (1)$$

where $F_k(\cdot)$ is a transfer function mapping activity to firing rate (related to the so-called F-I curve) for the k^{th} cell/population. Thus, the instantaneous firing rate of the j^{th} neuron is:

$$F_j(x_j(t)). \quad (2)$$

This type of equation has historically been used to capture the average activity of a population of neurons but from here on out we will use the term “cell” for exposition purposes. All cells receive background noise η_j , the increment of a Wiener process, uncorrelated in time but potentially correlated at each instant: $\langle \eta_j(t) \rangle = 0$,

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$\langle \eta_j(t)\eta_j(t') \rangle = \delta(t-t')$, and $\langle \eta_j(t)\eta_k(t') \rangle = c_{jk}\delta(t-t')$ for $j \neq k$ with $c_{jk} \in (-1, 1)$. The parameters μ_j and σ_j are constants that give the background input mean and input standard deviation, respectively. The parameter g_{jk} represents coupling strength from the presynaptic k^{th} cell and is a signed quantity; $g_{jk} < 0$ represents inhibitory coupling.

We would like to compute the following statistics:

$$\mu(j) := \langle x_j \rangle, \text{mean activity} \quad (3)$$

$$\sigma^2(j) := \langle x_j^2 \rangle - \mu^2(j), \text{variance of activity} \quad (4)$$

$$\begin{aligned} \text{Cov}(j, k) &:= \langle x_j x_k \rangle - \mu(j)\mu(k), \\ &\text{covariance of activity} \end{aligned} \quad (5)$$

$$\nu_j := \langle F_j(x_j) \rangle, \text{firing rate} \quad (6)$$

$$\text{Var}(\nu_j) := \langle F_j^2(x_j) - \nu_j^2 \rangle, \text{variance of spiking} \quad (7)$$

$$\begin{aligned} \text{Cov}(\nu_j, \nu_k) &:= \langle F_j(x_j)F_k(x_k) \rangle - \nu_j\nu_k, \\ &\text{covariance of spiking} \end{aligned} \quad (8)$$

$$\begin{aligned} \rho(\nu_j, \nu_k) &:= \frac{\text{Cov}(\nu_j, \nu_k)}{\sqrt{\text{Var}(\nu_j)\text{Var}(\nu_k)}}, \\ &\text{correlation of spiking} \end{aligned} \quad (9)$$

where the angular brackets $\langle \cdot \rangle$ denote averaging over time and realizations [19]. We will use the following definitions for the following Normal/Gaussian probability density functions (PDF):

$$\varrho_1(y) := \frac{1}{\sqrt{2\pi}} e^{-y^2/2}, \quad (10)$$

the standard normal PDF, and

$$\varrho_{j,k}(y_1, y_2) := \frac{1}{2\pi\sqrt{1-c_{jk}^2}} \exp\left(-\frac{1}{2}\vec{y}^T \begin{pmatrix} 1 & c_{jk} \\ c_{jk} & 1 \end{pmatrix}^{-1} \vec{y}\right), \quad (11)$$

a bivariate normal distribution with $\vec{0}$ mean, unit variance, and covariance c_{jk} .

In the absence of coupling, i.e. $g_{jk} = 0$, Eq (1) would describe a multi-dimensional Ornstein-Uhlenbeck process. Such a process is well-understood: any pair of activity variables, (x_j, x_k) , are bivariate normal random variables [20]. To see this, consider the following two equations without synaptic coupling:

$$\tau_j \frac{dx_j}{dt} = -x_j + \mu_j + \sigma_j \left(\sqrt{1-c_{jk}}\xi_j(t) + \sqrt{c_{jk}}\xi_c(t) \right) \quad (12)$$

$$\tau_k \frac{dx_k}{dt} = -x_k + \mu_k + \sigma_k \left(\sqrt{1-c_{jk}}\xi_k(t) + \sqrt{c_{jk}}\xi_c(t) \right). \quad (13)$$

Note that we have re-written $\eta_{j/k}(t)$ as sums of independent white noise processes $\xi(t)$. Since $x_j(t) = \frac{1}{\tau} \int_0^t e^{-(t-u)/\tau} [\mu_j + \sigma_j \eta_j(u)] du$, we calculate marginal statistics using *Itô* isometries:

$$\mu(j) \equiv \langle x_j \rangle = \mu_j \quad (14)$$

$$\begin{aligned} \sigma^2(j) &\equiv \langle (x_j - \mu(j))^2 \rangle \\ &= \left\langle \frac{\sigma_j^2}{\tau_j^2} \int_0^t \int_0^t e^{-(t-u)/\tau_j} \eta_j(u) e^{-(t-v)/\tau_j} \eta_j(v) du dv \right\rangle \\ &= \frac{\sigma_j^2}{\tau_j^2} \lim_{t \rightarrow \infty} \int_0^t e^{-2(t-u)/\tau_j} du = \frac{\sigma_j^2}{2\tau_j} \end{aligned}$$

A similar calculation shows in general we have:

$$\text{Cov}(j, k) = \frac{c_{jk}}{\tau_j + \tau_k} \sigma_j \sigma_k \quad (15)$$

$$\text{Thus, } (x_j, x_k) \sim \mathbb{N} \left(\begin{pmatrix} \mu_j \\ \mu_k \end{pmatrix}, \begin{pmatrix} \frac{\sigma_j^2}{\tau_j} & \sigma_j \sigma_k \frac{c_{jk}}{\tau_j + \tau_k} \\ \sigma_j \sigma_k \frac{c_{jk}}{\tau_j + \tau_k} & \frac{\sigma_k^2}{\tau_k} \end{pmatrix} \right).$$

Statistics for the firing rates, $F(x_j)$, are inherited from this normal distribution, since the firing rate $F(x_j)$ is simply a nonlinear function of the activity x_j .

When coupling is included, i.e. $g_{jk} \neq 0$ for some indices j and k , it may no longer be true that the activity variables x_j remain normally distributed. However, it is reasonable to suppose that, for sufficiently weak coupling, the deviations from a normal distribution will be small. Furthermore, if the firing rate function F has thresholding and saturating behavior (as does a sigmoidal function), then higher moments of x_j have limited impact on statistics of $F(x_j)$. Thus, our first assumption will be that each pair of activity variables (x_j, x_k) , can be approximated by a bivariate normal, even when coupling is present. We can think of this as a weak coupling assumption, as it holds exactly only with *no* coupling.

III. REDUCTION METHOD

To compute statistics, we start by writing Eq. (1) as a low-pass filter of the right-hand-side:

$$x_j(t) = \frac{1}{\tau_j} \int_0^t e^{-(t-u)/\tau_j} \left[\mu_j + \sigma_j \eta_j(u) + \sum_k g_{jk} F_k(x_k(u)) \right] du, \quad (16)$$

used as the basis for calculating the desired moments of x_j . For example, when $\langle x_j x_k \rangle$ is desired, we use the previous equation for j and k , multiply, then take the expected value $\langle \cdot \rangle$ while letting $t \rightarrow \infty$. The exact statistic is complicated because of the network coupling, so we simplify the calculation(s) as follows:

We only account for direct connections in the formulas for the first and second order statistics, assuming the terms from the indirect connections are either small or already accounted for in the direct connections. For example: although $F_k(x_k(u))$ on the RHS of Eq. (16) *itself* depends on coupling terms of the form $g_{kl} F_l(x_l)$, etc., we will neglect such terms. We further make the following assumptions:

TABLE I. For readability, we define the following quantities. Whenever $j = k$ in the double integrals (e.g., in $\mathcal{N}_{\mathcal{F}}, \mathcal{S}$), the bivariate normal distribution $\varrho_{j,k}$ is replaced with the standard normal distribution ϱ_1 . Note that order of the arguments matters in $\mathcal{N}_{\mathcal{F}}$: $\mathcal{N}_{\mathcal{F}}(j, k) \neq \mathcal{N}_{\mathcal{F}}(k, j)$ in general; all of these quantities depend on the statistics of the activity $\mu(\cdot), \sigma(\cdot)$.

Abbreviation	Definition
$\mathcal{E}_1(k)$	$\int F_k(\sigma(k)y + \mu(k))\varrho_1(y) dy$
$\mathcal{E}_2(k)$	$\int F_k^2(\sigma(k)y + \mu(k))\varrho_1(y) dy$
$\mathcal{V}(k)$	$\int F_k^2(\sigma(k)y + \mu(k))\varrho_1(y) dy - \left(\int F_k(\sigma(k)y + \mu(k))\varrho_1(y) dy\right)^2 = \mathcal{E}_2(k) - [\mathcal{E}_1(k)]^2$
$\mathcal{N}_{\mathcal{F}}(j, k)$	$\iint F_k(\sigma(k)y_1 + \mu(k))\frac{y_2}{\sqrt{2}}\varrho_{j,k}(y_1, y_2) dy_1 dy_2$, if $j \neq k$ $\int F_j(\sigma(j)y + \mu(j))\frac{y}{\sqrt{2}}\varrho_1(y) dy$, if $j = k$
$\mathcal{S}(j, k)$	$\iint F_j(\sigma(j)y_1 + \mu(j))F_k(\sigma(k)y_2 + \mu(k))\varrho_{j,k}(y_1, y_2) dy_1 dy_2$
$\mathcal{C}_{\mathcal{V}}(j, k)$	$\mathcal{S}(j, k) - \mathcal{E}_1(j)\mathcal{E}_1(k)$

$$\left\langle \int_0^t F_k(x_k(u))e^{-(t-u)/\tau_l} du \int_0^t F_k(x_k(v))e^{-(t-v)/\tau_m} dv \right\rangle \approx \frac{\tau_l \tau_m}{\tau_l + \tau_m} \mathcal{E}_2(k) \quad (17)$$

$$\left\langle \int_0^t \sigma_j \eta_j(u) e^{-(t-u)/\tau_l} du \int_0^t F_k(x_k(v)) e^{-(t-v)/\tau_m} dv \right\rangle \approx \frac{\tau_l \tau_m}{\tau_l + \tau_m} \sigma_j \mathcal{N}_{\mathcal{F}}(j, k) \quad (18)$$

$$\left\langle \int_0^t F_j(x_j(u)) e^{-(t-u)/\tau_l} du \int_0^t F_k(x_k(v)) e^{-(t-v)/\tau_m} dv \right\rangle \approx \frac{\tau_l \tau_m}{\tau_l + \tau_m} \mathcal{S}(j, k) \quad (19)$$

See Table I for the definition of the symbols: $\mathcal{E}_2(k), \mathcal{N}_{\mathcal{F}}(j, k), \mathcal{S}(j, k)$.

Each assumption is equivalent to the assumption that two of the random variables of interest are δ -correlated in time; thus avoiding the need to compute autocorrelation functions explicitly. The first assumption, Eq (17), states that $F(x_j(t))$ is δ -correlated with itself; the second, Eq (18), addresses N_j and $F(x_k(t))$, where N_j denotes the random variable $\int_0^t \sigma_j \eta_j(u) e^{-(t-u)/\tau_l} du$, which is by itself normally distributed with mean 0 and variance $\sigma_j^2 \tau_l / 2$. The final assumption, Eq (19), states that $F(x_j(t))$ and $F(x_k(t))$ are δ -correlated. Finally, we make the assumption of ergodicity, that averaging over realizations is the same as averaging over time; e.g. $\langle x_j \rangle = \lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T x_j(t) dt$.

We arrive at the following (approximation) formulas

for the statistics of the activity:

$$\mu(j) = \mu_j + \sum_k g_{jk} \mathcal{E}_1(k) \quad (20)$$

$$\begin{aligned} \sigma^2(j) \tau_j &= \frac{\sigma_j^2}{2} + \sigma_j \sum_k g_{jk} \mathcal{N}_{\mathcal{F}}(j, k) + \frac{1}{2} \sum_k g_{jk}^2 \mathcal{V}(k) \\ &\quad + \sum_{k \neq l} g_{jk} g_{jl} \mathcal{C}_{\mathcal{V}}(k, l) \end{aligned} \quad (21)$$

$$\begin{aligned} Cov(j, k) \frac{\tau_j + \tau_k}{2} &= \frac{1}{2} c_{jk} \sigma_j \sigma_k + \frac{1}{2} \sigma_j \sum_l g_{kl} \mathcal{N}_{\mathcal{F}}(j, l) \\ &\quad + \frac{1}{2} \sigma_k \sum_l g_{jl} \mathcal{N}_{\mathcal{F}}(k, l) + \frac{1}{2} \sum_{l_1, l_2} g_{j, l_1} g_{k, l_2} \mathcal{C}_{\mathcal{V}}(l_1, l_2). \end{aligned} \quad (22)$$

See Table I for the definition of the symbols: $\mathcal{E}_1, \mathcal{N}_{\mathcal{F}}, \mathcal{V}, \mathcal{C}_{\mathcal{V}}$, which all depend on the statistical quantities $\mu(\cdot)$ and $\sigma(\cdot)$ of the activity x_j . Our approximation formulas form a system of $\frac{1}{2}(N_c^2 + 3N_c)$ equations in $\mu(j), \sigma(j), Cov(j, k)$ (in the activity only Eqs. (3)–(5), not the firing) when considering all possible $(j, k) \in \{1, 2, \dots, N_c\}$. This large system of equations, although nonlinear, is simple to solve because it only requires a series of algebraic steps (matrix-vector multiplication with numerical integration, and calculating $F_k(\sigma(k)y + \mu(k))$).

Note that the normal distribution assumptions allow us to conveniently write the average quantities as inte-

grals with respect to standard normal distributions but with shifted integrands, which leads to faster calculations because one does not have to calculate new probability density functions at each step of the iteration.

The resulting formulas can be written compactly with matrices; Eq. (20) for the mean activity $\mu(j)$ can easily be written as a matrix-vector equation and is thus omitted. Let \mathbf{Cov} denote the $N_c \times N_c$ covariance matrix of the activity with $\mathbf{Cov}(j, k) = Cov(j, k)$, \mathbf{G} represent the coupling strengths $\mathbf{G}(j, k) = g_{jk}$, and \mathbf{Cr} denote the correlation matrix of the background noise (i.e. $\mathbf{Cr}(j, k) = \delta_{jk} + c_{jk}(1 - \delta_{jk})$). Then we have

$$\mathbf{Cov} = \mathbf{IT} .* \left(\mathbf{Cov}_0 + \mathbf{GM}_{\mathbf{NF}} + \mathbf{M}'_{\mathbf{NF}}\mathbf{G}' + \mathbf{GM}_{\mathbf{FSq}}\mathbf{G}' \right) \quad (23)$$

where $*$ represents element-wise multiplication, $'$ denotes matrix transposition, and

$$\mathbf{IT}(j, k) = \frac{1}{\tau_j + \tau_k} \quad (24)$$

$$\mathbf{Cov}_0(j, k) = \sigma_j \sigma_k [\delta_{jk} + (1 - \delta_{jk})c_{jk}] \quad (25)$$

$$\mathbf{M}_{\mathbf{NF}}(j, k) = \sigma_k \mathcal{N}_{\mathcal{F}}(k, j) \quad (26)$$

$$\mathbf{M}_{\mathbf{FSq}}(j, k) = \mathcal{C}_{\mathcal{V}}(j, k). \quad (27)$$

where $\mathbb{P}_{j,k}$ is a bivariate normal PDF with zero mean and covariance: $\begin{pmatrix} 1 & \frac{Cov(j,k)}{\sigma(j)\sigma(k)} \\ \frac{Cov(j,k)}{\sigma(j)\sigma(k)} & 1 \end{pmatrix}$. The off-diagonal terms are obtained from the second order statistics of the activity, Eq. (21)–(22).

IV. EXAMPLE NETWORKS AND RESULTS

Network I. We first consider two cells ($N_c = 2$) that are reciprocally coupled without autaptic coupling. For simplicity, we set the intrinsic parameters in the two equations to be identical, with $\tau_j = 1$, $F_j(x) = 0.5(1 + \tanh((x - 0.5)/0.1)) \in [0, 1]$, but the mean and variance of the background input differ: $\mu_1 = 0.15$, $\mu_2 = 4/15 \approx 0.2667$, $\sigma_1 = 2$, $\sigma_2 = 3$. To illustrate the accuracy of our method, we vary two parameters: $g_{12} \in [-2, 2]$ (input strength from x_2 to x_1), and $c_{12} = c_{21} \in [0, 0.8]$, with $g_{21} = 0.4$ fixed.

In Fig. 1, we see that all of the activity *and* firing statistics are accurate compared to Monte Carlo simulations. Fig. 1a shows the mean of x_1 as the input strength g_{12} varies from negative (inhibitory) to positive (excitatory); this statistic is independent of background correlation. Fig. 1b shows the variance of x_1 ; deviations are apparent when the magnitude of the coupling g_{12} is large. The covariance of the activity (Fig. 1c) is also accurate. Even

The matrix I is the $N_c \times N_c$ identity matrix. Note that the matrices $\mathbf{M}_{\mathbf{NF}}$ and $\mathbf{M}_{\mathbf{FSq}}$ have the same nonzero entries as \mathbf{Cr} . The unperturbed covariance (Eq. (25)) can also be expressed in matrix form as:

$$\mathbf{Cov}_0 = (I\vec{\sigma})\mathbf{Cr}(I\vec{\sigma})$$

Once the statistics of the activity: $\mu(j)$, $\sigma^2(j)$, and $Cov(j, k)$ are solved for self-consistently, the firing statistics are solved as follows.

$$\nu_j = \int F_j(\sigma(j)y + \mu(j))\varrho_1(y) dy \quad (28)$$

$$Var(\nu_j) = \int F_j^2(\sigma(j)y + \mu(j))\varrho_1(y) dy - \nu_j^2 \quad (29)$$

$$Cov(\nu_j, \nu_k) = \iint F_j(\sigma(j)y_1 + \mu(j))F_k(\sigma(k)y_2 + \mu(k))\mathbb{P}_{j,k}(y_1, y_2) dy_1 dy_2 - \nu_j \nu_k \quad (30)$$

the statistics of the firing rate are relatively accurate; the mean firing rate $F(x_1)$ (Fig. 1d) is only weakly dependent on background correlation whereas the variance of $F(x_1)$ (Fig. 1e) appears to vary more with background correlation. In Fig. 1f, the strong dependence of the covariance of the firing rate on background correlation is captured by our method. For brevity, we omit the corresponding statistics for x_2 ; the method performs equally well there.

Network II. We next consider an all-to-all coupled network of $N_c = 50$ neurons with heterogeneity in all parameters. The parameter values were selected from specific distributions and gave rise to quenched variability. The transfer function was set to $F_j(\bullet) = 0.5(1 + \tanh((\bullet - x_{rev,j})/x_{sp,j})) \in [0, 1]$, where $x_{rev,j}$ and $x_{sp,j}$ are fixed parameters that depend on the the j^{th} neuron. The distributions of the parameters for this network are:

$$\tau_j \sim \mathbb{N}(1, 0.05^2) \quad (31)$$

$$\mu_j \sim 2\mathbb{U} - 1 \quad (32)$$

$$\sigma_j \sim \mathbb{U} + 1 \quad (33)$$

$$x_{rev,j} \sim \mathbb{N}(0, 0.1^2) \quad (34)$$

$$x_{sp,j} \sim 0.35\mathbb{U} + 0.05 \quad (35)$$

where $\mathbb{U} \in [0, 1]$ is a uniform random variable, and \mathbb{N} is normally distributed with the mean and variance as the arguments. The covariance matrix \mathbf{Cr} of the background

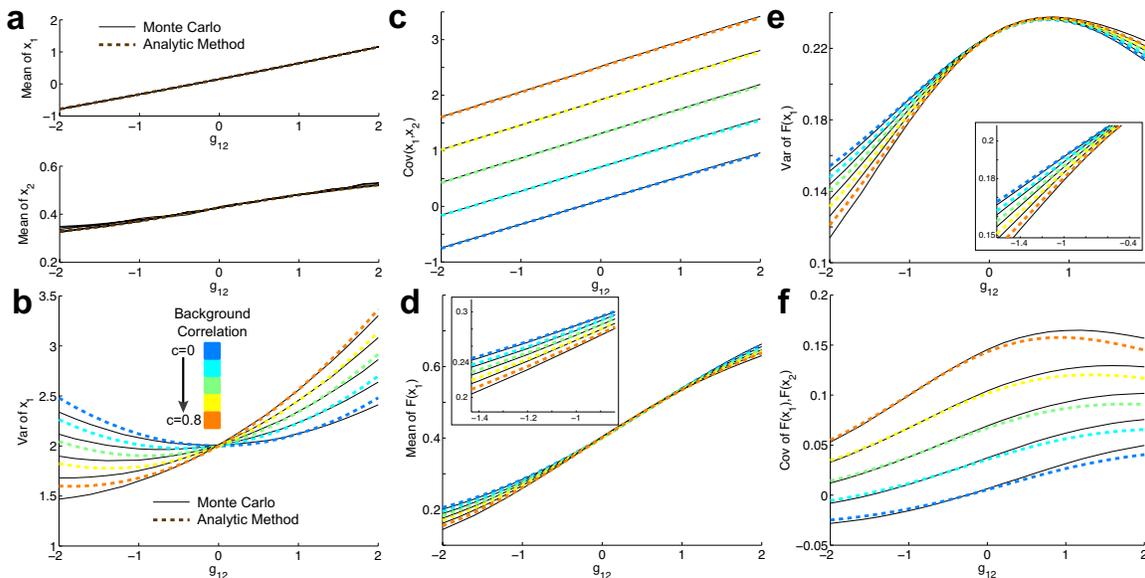


FIG. 1. Illustration of the method on a network with 2 neurons. In all panels, the Monte Carlo simulation results are the thin black solid lines, and the result of the analytic method (Eq. (20)–(22) solved self-consistently, and Eq. (28)–(30)) are the dashed colored lines representing different background correlation levels. All parameters are fixed except g_{12} and $c_{12} = c_{21} =: c$; see main text (**Network I**) for values. (a) The average activity x_1 (top), x_2 (bottom) as a function of g_{12} match very well; here the analytic method is in 1 color (brown) because the result is independent of background correlation. (b) The variance of x_1 , $\sigma^2(1)$, varies with both background correlation and input strength. The match is very good around $g_{12} = 0$ and starts to deviate as $|g_{12}| \rightarrow 2$ because with stronger coupling the normal distribution assumption is severely violated. (c) The covariance of the activity $Cov(1, 2)$. (d) Mean firing rate: $F(\nu_1)$ slightly depends on c ; inset is a zoomed-in picture to show that the method captures the relationship of the curves. (e) Variance of $F(\nu_1)$. (f) The covariance of the firing rate $Cov(F(\nu_1), F(\nu_2))$. The corresponding plots for x_2 (i.e., panels (b), (d), (e)) are not shown because they do not vary as much, however the analytic method accurately captures the results from Monte Carlo simulations.

noise was randomly selected as follows:

$$\mathbf{C}\mathbf{r} = (I\vec{d}_s)\mathbf{A}'\mathbf{A}(I\vec{d}_s) \quad (36)$$

where the entries of the $N_c \times N_c$ matrix \mathbf{A} are independently chosen from a normal distribution: $a_{j,k} \sim \mathbb{N}(0, 0.8^2)$ and \vec{d}_s is the inverse square-root of the diagonal of $\mathbf{A}'\mathbf{A}$; i.e., if we set $\mathbf{B} := \mathbf{A}'\mathbf{A}$ with entries b_{jk} , then $d_s(j) = 1/\sqrt{b_{jj}}$. By construction, $\mathbf{C}\mathbf{r}$ is symmetric positive semi-definite with 1's on the diagonal.

Finally, the entries of the coupling matrix $\mathbf{G}\mathbf{m}$ is randomly chosen, but the parameters of the distribution were varied:

$$\mathbf{G}\mathbf{m}(j, k) \sim \mathbb{N}(0, v_l) \quad (37)$$

where $v_l = (l/10)^2$ for $l = 1, 2, 3, 4$. There are no zero entries in $\mathbf{G}\mathbf{m}$ (i.e. coupling is all-to-all), with both inhibition, excitation, and autaptic (self) coupling.

For each of the four values for the variance of the normal distribution, we chose a single realization of a coupling matrix $\mathbf{G}\mathbf{m}$ and computed first and second-order statistics of x_k and $F(x_k)$. In Fig. 2 we compared analytic vs. Monte Carlo results for each cell or cell pair. Each realization is identified by a different color; in Fig. 2a for example, there are N_c red data points, corresponding to each $\mu(j)$ for $j = 1, \dots, N_c$. Points that are on the

black diagonal line represent perfect matching between Monte Carlo simulations and our method.

First-order statistics $\mu(j)$ and ν_j are well-captured by the analytic method, even for the largest coupling strength (Fig. 2a,b). This excellent agreement is present despite the substantial amount of heterogeneity in these networks: note that $x_j = \mathcal{O}(1)$ and that $F_j \in [0, 1]$, and thus that single-cell firing rates in Fig. 2b have a relatively large range. Second-order statistics (variances and covariances: Fig. 2c-f) are captured well for smaller coupling values (blue and cyan) but become less accurate for the largest coupling value (red). In particular, the analytic method appears to overestimate variance for the largest coupling strength (Fig. 2c).

Network III. Finally we consider a moderately sized network of $N_c = 100$ neurons with quenched heterogeneity in all of the intrinsic parameters, but with more physiological connectivity structure (than Network II). The first 50 neurons are excitatory (**E**) ($g_{jk} \geq 0$ for $k = 1, 2, \dots, 50$) and the last 50 are inhibitory (**I**) ($g_{jk} \leq 0$ for $k = 51, 52, \dots, 100$). We choose a sparse (random)

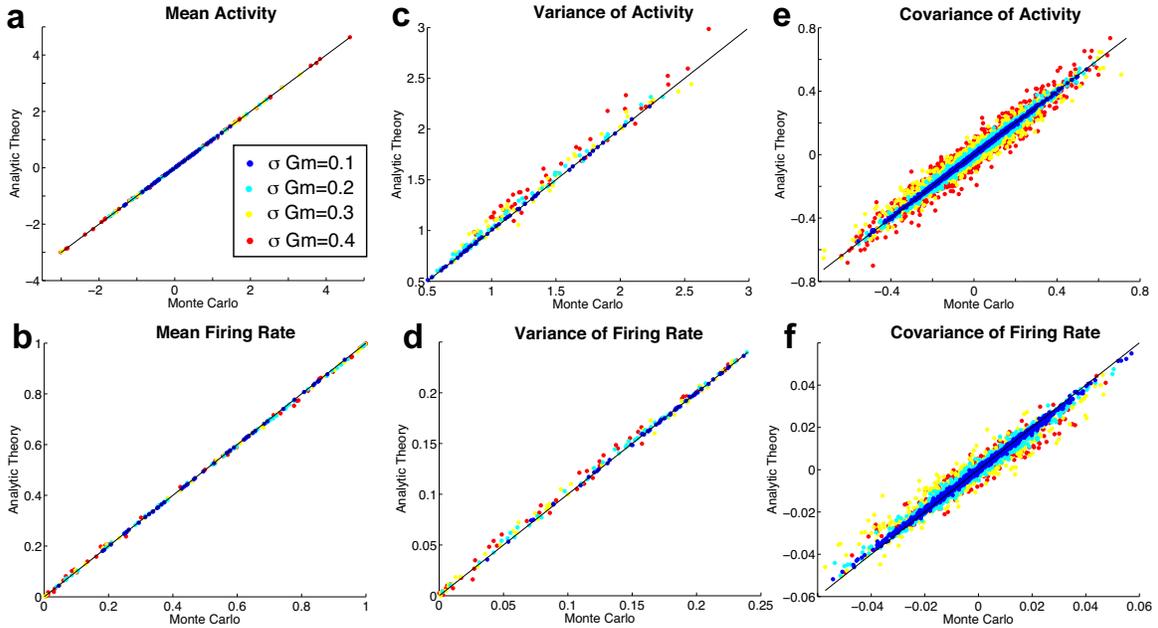


FIG. 2. A network of $N_c = 50$ neurons with heterogeneity in all parameters and all-to-all coupling (**Network II**). See Eq. (31)–(37) for the distributions of the randomly selected parameters. In each panel, four different values of the variance of the distribution of the coupling matrix entries are shown, while the other parameters are held fixed. (a) Comparison of the mean activity $\mu(j)$ calculated via Monte Carlo simulations (horizontal axis) and our reduction method (vertical axis), showing all 50 values for each color (coupling matrix distribution). (b) Similar to (a) but for mean firing rate ν_j . (c) Variance of activity $\sigma^2(j)$. (d) Variance of firing rate $Var(\nu_j)$. (e) Covariance of activity $Cov(j, k)$, showing all $50 \times 49 / 2 = 1225$ values for each coupling matrix. (f) Covariance of the firing rate $Cov(\nu_j, \nu_k)$. The method is accurate but starts to deviate as the overall coupling strength $\|\mathbf{Gm}\|$ increases (from blue to red, more deviations from diagonal line).

background correlation matrix via:

$$c_{jk} = \begin{cases} 1, & \text{if } j = k \\ \mathbb{N}(0.1, 0.1^2), & \text{if } k = j + 1 \text{ and } j = 1, \dots, 49 \\ \mathbb{N}(0.12, 0.1^2), & \text{if } k = j + 1 \text{ and } j = 51, \dots, 99 \\ \mathbb{N}(0.3, 0.1^2), & \text{if } k = 101 - j \text{ and } j = 1, \dots, 100 \\ 0 & \text{otherwise} \end{cases} \quad (38)$$

where as before \mathbb{N} is a Gaussian random variable. That is, each cell shares correlated input with its nearest-neighbors of the same type (excitatory vs. inhibitory), and a single cell of the opposite type, where cell location varies along a one-dimensional line. In a variety of cortical areas, there is evidence that the correlation of neural activity within a population is on average positive with a wide distribution [21–23]; thus we set the distributions of excitatory and inhibitory correlation coefficients to $\mathbb{N}(0.1, 0.1^2)$ and $\mathbb{N}(0.1, 0.12^2)$ respectively (second and third lines of Eq. (38)). Also, there is evidence that E and I neurons are positively correlated (i.e., the synaptic currents are negatively correlated) [24–26], so we set the average background E-I correlation ($\mathbb{N}(0.3, 0.1^2)$, fourth line of Eq. (38)) to a higher value than correlations within E or I (second and third lines respectively). The correlation matrix is tridiagonal with another diagonal band for the E and I correlation; see Fig.3(a) for the

sparsity structure of \mathbf{Cr} .

In order to capture some realistic features of cortical neural networks, we impose sparse but clustered connectivity. Specifically, we have 5 clusters of E cells of size 10 with all-to-all connectivity and no autaptic (self-coupling) connections, and sparse random coupling within the I population (no autaptic connections) and between E and I cells (35% connection probability). See Fig.3(b) for the sparsity structure of \mathbf{Gm} . This is motivated by experimental evidence that E cells show clustered connectivity [27–29], while inhibitory connections have less structure [30].

Synaptic connection strengths were chosen randomly for each realization with the following distributions:

$$\begin{aligned} g_{EE} &= \mathbb{U}/10, \\ g_{EI} &= -\frac{12}{35}\mathbb{U} - \frac{4}{35}, \\ g_{IE} &= \frac{12}{35}\mathbb{U} + \frac{4}{35}, \\ g_{II} &= -\frac{12}{35}\mathbb{U} - \frac{4}{35}, \end{aligned} \quad (39)$$

where again $\mathbb{U} \in [0, 1]$ is a uniform random variable. The value g_{EE} is used for all nonzero E to E connections: g_{jk} with $j, k \in \{1, \dots, 50\}$; g_{EI} is used for all nonzero I to E connections: g_{jk} with $j \in \{1, \dots, 50\}$

and $k \in \{51, \dots, 100\}$; g_{IE} for all nonzero E to I: $j \in \{51, \dots, 100\}$ and $k \in \{1, \dots, 50\}$; similarly for g_{II} .

The distributions for the rest of the parameters were similar to **Network II**, with only inconsequential differences:

$$\tau_j \sim \mathcal{N}(1, 0.075^2) \quad (40)$$

$$\mu_j \sim 2\mathcal{U} - 1 \quad (41)$$

$$\sigma_j \sim \mathcal{U} + 1 \quad (42)$$

$$x_{rev,j} \sim \mathcal{N}(0, 0.1^2) \quad (43)$$

$$x_{sp,j} \sim 0.4\mathcal{U} + 0.05 \quad (44)$$

In Fig. 3(c) and (d) we show the results of the analytic approximation compared to Monte Carlo simulations for both the activity and firing rates, respectively. In each panel, we have combined the mean, variance and covariance and, as in Fig. 2, a data point is plotted for each cell (for means and variances) or cell pair (for covariances). Also, we show data from two (2) instances of the network, labeled A and B; for each instance a new realization of the coupling matrix \mathbf{Gm} and the coupling parameters (Eq. (39)) are generated (see Fig. 3 caption for values), but each of the other randomly selected parameters were kept fixed. Points that are on the black diagonal line represent a perfect match between Monte Carlo simulations and our method. As with **Network II**, the analytic method accurately captures the statistics cell-by-cell, despite an appreciable degree of heterogeneity.

Finally, we test how well our method approximates firing rate *correlation*, which is an important normalized measure of trial-to-trial variability (or noise correlations). The Pearson's correlation coefficient is the predominant measure: $\rho(\nu_j, \nu_k) = Cov(\nu_j, \nu_k) / \sqrt{Var(\nu_j, \nu_k)}$, i.e. the ratio of two quantities which we must estimate using the analytic method. In Fig. 4, we show comparisons between the analytic method and Monte Carlo simulations for **Network II** and **Network III**. The method is accurate for a wide range of correlations; Fig. 4a shows correlations as low as -0.3 and as high as 0.3 . Thus, the viability of our approximation is not limited to small correlation values, but can robustly capture the full range of correlation values observed in cortical neurons [5, 31].

V. DISCUSSION

There has been a long history of analytic reduction methods for neural network models, both to enhance efficiency in simulation and to aid mathematical analyses. Here, we summarize some of this literature and its relationship to the work presented here.

Many authors have analyzed *mean-field* equations, in which they derive equations for population-averaged activity, usually in the limit of large system size. The dynamics of single neurons within such a population may be described either by master equations [12, 32, 33], stochastic differential equations [14, 34], or generalized linear models [35]. We have not attempted that here, in that we

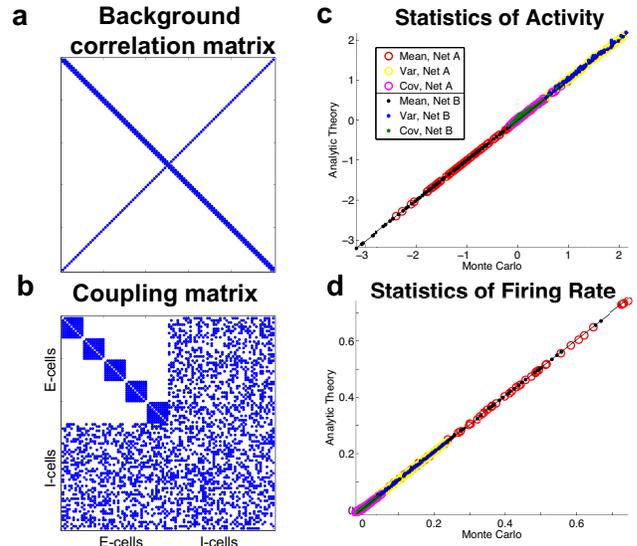


FIG. 3. A network of $N_c = 100$ neurons with heterogeneity in all parameters, but sparse background correlation and clustered and random connectivity (**Network III**). See Eq. (38)–(44) for the distributions of the randomly selected parameters. Sparsity structure of the background correlation matrix \mathbf{Cr} (a) and coupling matrix \mathbf{Gm} (b). (c) Comparing all of the statistics of the activity for 2 realizations of the network: coupling parameters for network A are: $(g_{EE}, g_{EI}, g_{IE}, g_{II}) = (0.079, -0.24, 0.17, -0.31)$ and coupling parameters for network B are: $(g_{EE}, g_{EI}, g_{IE}, g_{II}) = (0.049, -0.38, 0.16, -0.17)$. As in Fig. 2, all 100 mean and variance values are plotted, as well as all 4950 covariance values. (d) Similar to (c) but for the firing rates.

have made no attempt to reduce the number of degrees of freedom. Rather, we start with a system of coupled stochastic differential equations, each of which may represent either a single neuron or a population, and sought to quickly and accurately estimate statistics of the coupled system. Importantly, the unperturbed state in our system is not one in which all neurons are independent; instead we perturb from a state with background noise correlations. Thus, we anticipate this approximation can be used to probe a range of neural networks, in which correlations can be significant and activity-modulated.

While the coupled firing rate models we study here were not derived as a mean field limit of a spiking network, our results presented can still yield insight into spiking networks. Our previous work [18] used the qualitative principles and intuitions gained from a simple firing rate model to characterize relationships between the analogous parameters in a full spiking model of a multi-region olfactory network. In that paper, a small system with simple coupling and background correlations was studied, whereas this paper treats networks of arbitrary size, and arbitrary coupling and input correlation structures. The work here is thus a generalization of the calculations in [18].

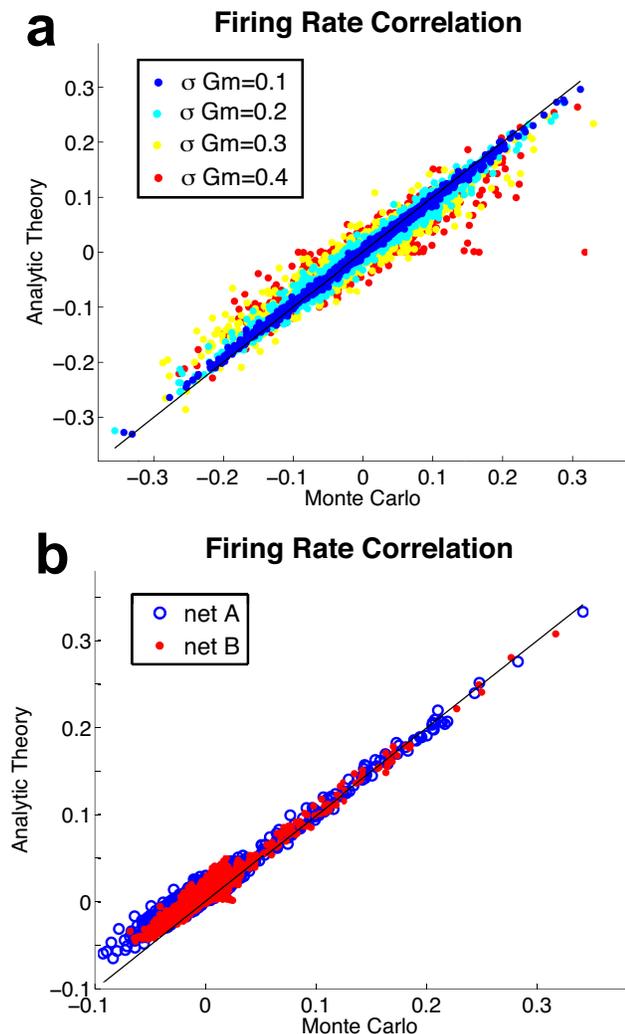


FIG. 4. Comparisons of the spike count correlation computed by our method and Monte Carlo simulations. (a) Comparing the 4 regimes in **Network II**. The results are accurate because the points predominately lie on the diagonal line. As we saw in Fig. 2, as the relative coupling strength increases, the estimation of the spike count correlation is not as accurate. (b) Comparing the 2 networks in **Network III**. In both cases, the method performs well even though *both* the numerator and denominator are estimated via the method. All $N_c(N_c - 1)/2$ firing rate correlation values are plotted for each network.

In other models, $F(\cdot)$ represents the function that maps firing rate to synaptic input. Here, we assume that the effective synaptic input $g_{jk}F_j$ is a fixed scaling of the firing rate F_j . In other biophysical models the effective synaptic input may be a more complex transformation of the firing rate (e.g., an alpha function convolved with firing rate): the methods presented here can easily be altered to account for this. To do this, the only change would be to use $S_j(F_j)$ in Eq. (1) instead of F_j .

Our method relies on the assumption that statistics are stationary in time; this assumption allows a set of statistics to be solved self-consistently. Thus we have not addressed complex network dynamics, such as oscillations. However, this limitation is not specific to our method, but is also in related work. Previously developed approximation methods may fail when the system undergoes a bifurcation [32, 33], and truncation methods (or moment closure methods) are known to fail in certain parameter regimes [36]. When the set of self-consistent equations cannot be solved, there may be other methods available to characterize the oscillatory dynamics (see [37] where this is done for the adaptive quadratic integrate-and-fire model). Considering how to accurately and quickly capture firing statistics when in this regime is an important topic of future work.

Time-varying statistics are not considered here and is beyond the scope of this study. Such an approach often requires deriving an ODE of the desired quantities [33–35, 38] or some other dynamical equation(s) [39] that must be solved numerically.

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