

Firing statistics and correlations in spiking neurons: A level-crossing approach

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(Received 8 April 2011; revised manuscript received 7 July 2011; published 17 October 2011)

We present a time-dependent level-crossing theory for linear dynamical systems perturbed by colored Gaussian noise. We apply these results to approximate the firing statistics of conductance-based integrate-and-fire neurons receiving excitatory and inhibitory Poissonian inputs. Analytical expressions are obtained for three key quantities characterizing the neuronal response to time-varying inputs: the mean firing rate, the linear response to sinusoidally modulated inputs, and the pairwise spike correlation for neurons receiving correlated inputs. The theory yields tractable results that are shown to accurately match numerical simulations and provides useful tools for the analysis of interconnected neuronal populations.

DOI: [10.1103/PhysRevE.84.041919](https://doi.org/10.1103/PhysRevE.84.041919)

PACS number(s): 87.19.lj, 05.10.Gg, 87.19.1l

I. INTRODUCTION

Understanding the dynamics of interconnected networks of neurons is of fundamental importance in theoretical neuroscience. An essential step in solving this problem is to determine the input-output relationship of individual neurons given an underlying biophysical model. For white-noise-driven integrate-and-fire (IF) neurons this problem is generally tractable (e.g., [1–4]), but efforts to integrate key aspects of neuronal signaling into the IF formalism have added to its complexity. First, synaptic input consists of discrete action potentials, which results in non-Gaussian voltage distributions and affects firing statistics [5–8]. Second, synaptic communication is mediated by two separate (excitatory and inhibitory) systems with distinct kinetics. The majority of theoretical studies include only one synaptic type and assume either fast (e.g., [9–11]) or slow [11,12] kinetics compared with the membrane integration time, but experimental evidence suggests that these time scales are often comparable [13]. Finally, neurons sharing presynaptic partners exhibit correlations in their synaptic input. While network models typically assume sparse connectivity for which correlations are negligible, recent reports suggest important functional roles for this type of “noise” correlation [14,15]. For IF neurons, obtaining the input-output relationship essentially involves computing moments of the first passage time (FPT) to threshold, but analytical solutions are rarely possible. Here, we show that for membrane-to-synaptic time constant ratios of the order of unity, level-crossing statistics provide good approximations to the FPT while retaining sufficient tractability to incorporate additional biological detail. Analytical expressions are given for the mean firing rate, pairwise spike correlation, and linear response to sinusoidally modulated inputs, which compare favorably with numerical simulations of conductance-based IF neurons. The method thus provides a complete set of input-output properties needed for an analysis at the network level. Although the focus of the present paper is on neuroscience applications, the theory is rather general and applies to any linear system perturbed by colored Gaussian noise; our results may therefore find applications in other fields.

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II. MODEL DEFINITION

A neuron, with capacitance C and charged at a voltage V , obeys the current-balance equation

$$C\dot{V} + I_L = I_{\text{syn}} + I_{\text{ext}}, \quad (1)$$

where $I_L = G_L(V - E_L)$ is a transmembrane “leak” current of conductance G_L such that $C/G_L = 20$ ms and reversal potential $E_L = -65$ mV, and I_{ext} is an external current. The synaptic current I_{syn} comprises excitatory and inhibitory conductances $I_{\text{syn}} = G_e(E_e - V) + G_i(E_i - V)$ with reversals $E_e = 0$ and $E_i = -80$ mV. Synaptic channels activate rapidly but close with a characteristic time particular to excitation ($\tau_e = 3$ ms) or inhibition ($\tau_i = 10$ ms). The assumption that these conductances are activated stochastically with a short autocorrelation allows a Langevin equation to be written, $\tau_\alpha \dot{G}_\alpha = \bar{G}_\alpha - G_\alpha + \sigma_\alpha \sqrt{2\tau_\alpha} \xi_\alpha$ for $\alpha \in \{e, i\}$, where $\bar{G}_\alpha(t)$ and $\sigma_\alpha(t)$ represent the tonic and fluctuating components driving the synaptic conductance. The general form of this equation can be related to a family of underlying models; in our simulations a process is considered in which synaptic conductances increase by an amount J_α at a rate $R_\alpha(t)$ with intermediate exponential decay with characteristic time τ_α . The diffusion limit of this process assigns $\bar{G}_\alpha = J_\alpha \tau_\alpha R_\alpha$ and $\sigma_\alpha = J_\alpha \sqrt{\tau_\alpha R_\alpha / 2}$. Finally, a mechanism for an action potential is introduced: if the voltage exceeds $V_\theta \approx -50$ mV, a spike is emitted and the voltage is immediately reset to $V_r = -60$ mV.

The equations for V and G_α constitute a stochastic process with multiplicative noise. Expansion of Eq. (1) to leading order in the fluctuating synaptic conductances [5] yields an additive Gaussian approximation for the voltage:

$$\dot{v} = \tau_v^{-1}(E_0 - v) + x(E_e - \langle v \rangle) + y(E_i - \langle v \rangle) + \mu, \quad (2)$$

$$\tau_e \dot{x} = -x + \sqrt{2\sigma_e^2 \tau_e} \xi_e, \quad (3)$$

$$\tau_i \dot{y} = -y + \sqrt{2\sigma_i^2 \tau_i} \xi_i, \quad (4)$$

where angular brackets denote ensemble averages, and lowercase letters distinguish the Gaussian approximation from the original conductance-based model. The time scale $\tau_v = C/G$, total conductance $G = G_L + \langle G_e \rangle + \langle G_i \rangle$, and driving term $E_0 = (G_L E_L + \langle G_e \rangle E_e + \langle G_i \rangle E_i)/G$ are all potentially time dependent. The variables x and y scale with the fluctuations of

synaptic conductances, $x = (G_e - \langle G_e \rangle)/C$ and $y = (G_i - \langle G_i \rangle)/C$, and $\mu = I_{\text{ext}}/C$. Excitatory and inhibitory inputs may be cross correlated, so that $\langle \xi_e(t)\xi_i(t') \rangle = c_{ei}\delta(t-t')$ with a correlation coefficient $|c_{ei}| \leq 1$.

III. FIRING RATE

An ensemble of statistically identical neurons, described by Eqs. (2)–(4) but each with different realizations of the noise terms $\xi_\alpha(t)$, is now considered. Although a general solution for the mean firing rate is not possible, we show here that for $\tau_\alpha/\tau_v \approx 1$ the firing rate is well approximated by the rate of upward threshold crossings of the free system (i.e., ignoring the reset). For a continuous process $u(t)$, the rate r of upcrossings of a level $u = u_\theta$ is given by the Rice formula [16], $r = \int_0^\infty |\dot{u}| p(u_\theta, \dot{u}) d\dot{u}$, where $p(u, \dot{u})$ is the joint distribution of u and \dot{u} . For a Gaussian process $v(t)$, this yields

$$r = \frac{1}{2\pi} \frac{[\sigma_v]_\theta}{\sigma_v} e^{-(v_\theta - \langle v \rangle)^2 / (2\sigma_v^2)} [e^{-\beta^2} + \sqrt{\pi} \beta (1 + \text{erf} \beta)], \quad (5)$$

where σ denotes the standard deviation, $\beta = \langle \dot{v} \rangle_\theta / (\sqrt{2}[\sigma_v]_\theta)$, and the subscript θ indicates quantities evaluated conditional on $v = v_\theta$. These conditional statistics can be expressed from the marginal statistics as $\langle \dot{v} \rangle_\theta = \langle \dot{v} \rangle + [\text{cov}(v, \dot{v})/\sigma_v^2](v_\theta - \langle v \rangle)$ and $[\sigma_v^2]_\theta = \sigma_v^2 - \text{cov}(v, \dot{v})^2/\sigma_v^2$. In general, for time-dependent inputs, the moments of v and \dot{v} are obtained by solving a system of ordinary differential equations (see Appendix A for details); for stationary inputs, Eq. (5) reduces to [17–19]

$$r^{\text{stat}} = \frac{1}{2\pi} \frac{\sigma_v}{\sigma_v} e^{-v_\theta^2 / (2\sigma_v^2)}, \quad (6)$$

and in the weakly nonstationary case, a Taylor expansion in β yields $r = r^{\text{stat}}[1 + \sqrt{\pi}\beta]$. Consistent with previous reports

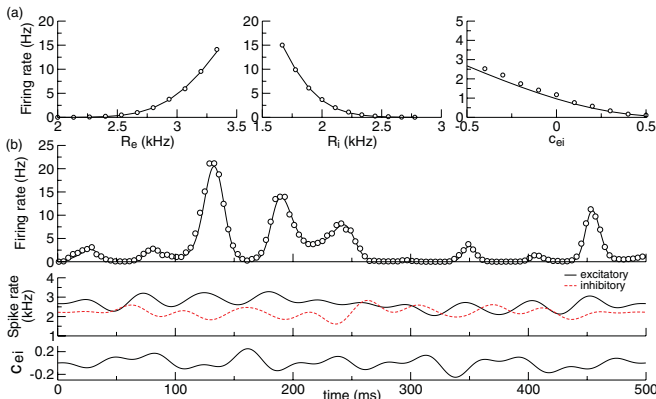


FIG. 1. (Color online) (a) Steady-state firing rate of the IF model. Solid line, Eq. (6). Symbols, numerical simulation. Parameters are $J_e = 6.3$ nS, $J_i = 4.5$ nS, $E_0 = -55$ mV, $v_\theta = -48$ mV, $v_r = -60$ mV, $\tau_v = 5$ ms, $\tau_e = 3$ ms, $\tau_i = 10$ ms, and where not otherwise mentioned, $R_e = 2.66$ kHz, $R_i = 2.22$ kHz, and $c_{ei} = 0$. (b) Firing-rate response to time-varying inputs. Top: Solid line, Eq. (5); symbols, numerical simulation. Middle: Input spike rates, with mean $R_{e0} = 2.66$ kHz for excitation and $R_{i0} = 2.22$ kHz for inhibition. Bottom: Instantaneous correlation coefficient between excitatory and inhibitory inputs. Other parameters identical to those in (a).

[20–22], r scales with the mean rate of change of voltage and is thus proportional to any (small) applied current in Eq. (1). Comparison of Eq. (5) with numerical simulations shows that the level-crossing rate provides an excellent approximation to the firing rate of the thresholded IF model (Fig. 1). Although some deviations are seen in the stationary case, the theory captures especially well variations of the firing rate [Fig. 1(b)], an aspect particularly relevant for neuronal signaling.

IV. FREQUENCY RESPONSE

Another interesting application of Eq. (5) is to compute the firing-rate response to sinusoidally modulated inputs. While the frequency response of white-noise-driven IF neurons has been calculated previously [1,10,23,24], only asymptotic results are known for the case of filtered noise [10,24]; the level-crossing approach allows approximation of the amplitude and phase of the response in the full frequency range. In response to a perturbation $\sim \varepsilon e^{i\omega t}$ ($\varepsilon \ll 1$), the statistical moments in Eq. (5) undergo periodic modulations with frequency ω . The threshold crossing rate Eq. (5) can be written as $r = r_0 + \varepsilon r_1 e^{i\omega t}$ to first order in ε , with

$$\begin{aligned} \frac{r_1}{r_0} = & \sqrt{\frac{\pi}{2[\sigma_v^2]_0}} \left(\langle \dot{v} \rangle_1 + v_\theta \frac{[\text{cov}(v, \dot{v})]_1}{[\sigma_v^2]_0} \right) + v_\theta \frac{\langle v \rangle_1}{[\sigma_v^2]_0} \\ & + \frac{1}{2} \left(v_\theta^2 \frac{[\sigma_v^2]_1}{[\sigma_v^4]_0} + \frac{[\sigma_v^2]_1}{[\sigma_v^2]_0} - \frac{[\sigma_v^2]_1}{[\sigma_v^2]_0} \right), \end{aligned} \quad (7)$$

where the subscripts indicate zeroth- and first-order corrections in ε . Let us first consider as in [10] a current-based description for both the synaptic input and the perturbation, i.e., we set $\langle v \rangle = E_0$ and $\mu = \varepsilon \mu_0 e^{i\omega t}$ in Eq. (2). In this case, only the mean values in (5) are affected, and we obtain $r_1/r_0 = \mu_0 \tau_v \{v_\theta / [\sigma_v^2]_0 + i\omega \sqrt{\pi} / (2[\sigma_v^2]_0)\} / (1 + i\omega \tau_v)$. Consistent with [10], this expression converges to a real limit $\mu_0 \sqrt{\pi} / \sigma_v^2$ as $\omega \rightarrow \infty$, reflecting the ability of IF neurons to respond to arbitrarily fast changes in input current (e.g., [21]). For the case of perturbations arising from changes in presynaptic firing rates, modulations of the second moments in (5) must be included, leading to more complex expressions for r_1 . In general (see Appendix B), to linear order the correction to the firing rate may be written as the sum of excitatory and inhibitory components, $r_1 = r_1^e - r_1^i$, which can be calculated using (7) and are found to decay monotonically with increasing frequency. However, due to the distinct filtering time constants, the superposition of excitatory and inhibitory modulations generally leads to nonmonotonic response profiles (Fig. 2): if r_1^e dominates at low frequencies, the faster decay of r_1^i leads to a peak in the response; conversely, if r_1^i dominates for small ω the response may be suppressed around the frequency where r_1^e and r_1^i intersect. When $r_1^e \simeq r_1^i$ at low frequency, the two contributions cancel and the neuron behaves as a bandpass filter. These results illustrate how distinct integration time scales for excitation and inhibition can lead to nontrivial responses at the postsynaptic level. The occurrence of zero-phase lags at finite frequencies, which are not observed in the case of a single synaptic type (or, equivalently, when τ_e and τ_i are identical), also bears possible implications for the generation of self-sustained network oscillations.

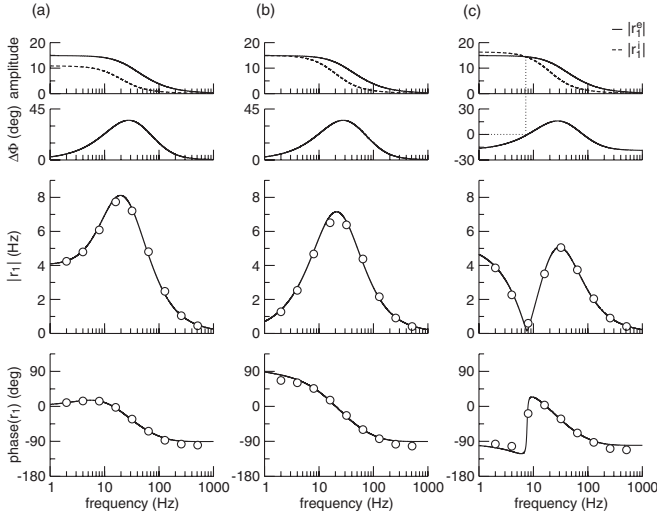


FIG. 2. Frequency response of the IF model to sinusoidal modulations in presynaptic excitatory and inhibitory firing rates. The response is illustrated in three typical cases: at low frequency, $r_1^e > r_1^i$ (a), $r_1^e = r_1^i$ (b), or $r_1^e < r_1^i$ (c). Top two graphs: The components of the firing-rate response due to excitatory (r_1^e) and inhibitory (r_1^i) modulations are shown as functions of the frequency of the modulation. The summed response is determined from the amplitude (top graph) and the phase difference (bottom graph) of the two components. Bottom two graphs: Amplitude $|r_1|$ and phase lag $\text{phase}(r_1)$ of the summed firing-rate response (solid line, theory; symbols, numerical simulation). For (c) a phase difference of 29° is introduced between excitatory and inhibitory modulations to maximize the trough.

V. CROSS CORRELATIONS

The Rice formula for the level-crossing rate can be extended to approximate spike correlations in populations of neurons. The probability density of two neurons crossing their firing thresholds simultaneously, which we call the joint firing rate, is given by a double integral $r_{12} = \int_0^\infty \int_0^\infty |\dot{v}_1 \dot{v}_2| p(v_{\theta 1}, v_{\theta 2}, \dot{v}_1, \dot{v}_2) d\dot{v}_1 d\dot{v}_2$, where the subscripts 1, 2 refer to the neuron number. If both neurons have identical membrane time constants, this integral can be evaluated in closed form in the stationary case [18]; the result is $r_{12}^{\text{stat}} = p_\theta \sigma_{\dot{v}_1} \sigma_{\dot{v}_2} / (2\pi) [\sqrt{1 - \rho^2} + 2\rho \arctan \sqrt{(1 + \rho)/(1 - \rho)}]$. Here, p_θ is the marginal probability density that the two neurons are found at their firing threshold and is given by a two-dimensional Gaussian, and we have defined the correlation coefficient $\rho = \text{cov}(\dot{v}_1, \dot{v}_2) / (\sigma_{\dot{v}_1} \sigma_{\dot{v}_2})$. If the two neurons have distinct membrane time constants and/or if the inputs are time dependent, the joint firing rate can no longer be evaluated in closed form. A Taylor expansion can be made for weakly nonstationary inputs, which yields

$$r_{12} = p_\theta \frac{[\sigma_{\dot{v}_1}]_\theta [\sigma_{\dot{v}_2}]_\theta}{2\pi} \left(\sqrt{\pi} (\beta_1 + \beta_2) (1 + \rho_\theta) + (1 + \beta_1^2 + \beta_2^2) \times \sqrt{1 - \rho_\theta^2} + (2\rho_\theta + 4\beta_1\beta_2) \arctan \sqrt{\frac{1 + \rho_\theta}{1 - \rho_\theta}} \right) \quad (8)$$

to second order in β_1, β_2 , where $\beta_k = \langle \dot{v}_k \rangle_\theta / (\sqrt{2} [\sigma_{\dot{v}_k}]_\theta)$, and the subscript θ indicates here that a quantity is evaluated conditional on both neurons being at their firing threshold.

To illustrate the use of Eq. (8), we consider an example in which two neuronal populations receive common inputs. Each population consists of P identical, unconnected neurons receiving inputs from an external source; the excitatory input to each neuron consists of a background part that is uncorrelated across neurons and a shared part that is identical for all neurons within the population. The shared inputs to the two populations may also be cross correlated, resulting in a correlation coefficient c_{ee} between the total input to any two neurons in different populations. Similar definitions are also assumed for the inhibitory inputs. The number of output spikes for population 1 during a time interval Δt has a mean $N_1 = Pr_1 \Delta t$, where r_1 is calculated from Eq. (5), and a variance $\sigma_{N_1}^2 = Pr_1 \Delta t + P(P-1)(r_{11} - r_1^2) \Delta t^2$, where r_{11} is the joint firing rate for population 1, obtained from Eq. (8). The correlation coefficient between the outputs of the two populations is

$$c_{\text{out}} = \frac{\left(\frac{P}{P-1}\right)(r_{12} - r_1 r_2)}{\sqrt{\left[r_{11} - r_1^2 + \frac{r_1}{(P-1)\Delta t}\right] \left[r_{22} - r_2^2 + \frac{r_2}{(P-1)\Delta t}\right]}}, \quad (9)$$

where r_{12} is the joint firing rate for a pair of neurons in different populations, obtained from Eq. (8) with appropriate parameters. It is worth remarking that, while the terms dependent on the time step in Eq. (9) vanish in the limit of large populations, they may remain significant even for relatively large populations because the correlative terms $r_{ii} - r_i^2$ are generally of the order of the square of the firing rate, which is itself a small quantity. Figure 3 shows the result of numerical simulations for two populations of $P = 1000$ neurons, illustrating how output spike correlations are affected by changes in input correlations. As can be expected from previous reports (e.g., [25]), the pooled spike trains of the two populations exhibit strong correlations of the same order of magnitude as the correlations in the inputs. However, since the output correlation depends on both input correlations and the individual firing rates of the two populations, its precise time course is difficult to anticipate in the case of time-varying inputs. The results of Fig. 3 show that the theory provides an accurate prediction of the evolution of the correlation coefficient under time-dependent stimulus.

A. Implications for synchrony

The development of synchronization in layered feedforward networks has been reported theoretically (e.g., [26,27]) and experimentally [28]. Here, we use the results of the previous section to calculate the Fano factor of the pooled output of a population, which provides a quantitative measure of synchrony at the level of pairwise correlations. The Fano factor is given by $F = \sigma_N^2 / \langle N \rangle$, where N is the number of spikes fired in a small time interval Δt . For a large number P of independent neurons, N approximates a Poisson process with mean and variance $\langle N \rangle = \sigma_N^2 = Pr \Delta t$, leading to a Fano factor $F = 1$. A larger $F > 1$ indicates an increased probability of observing either high or low numbers of spikes in Δt , i.e., an increased frequency of synchronous (spiking or quiescent) events. For correlated neurons,

$$F = 1 + \frac{r_{11} - r^2}{r} (P-1) \Delta t, \quad (10)$$

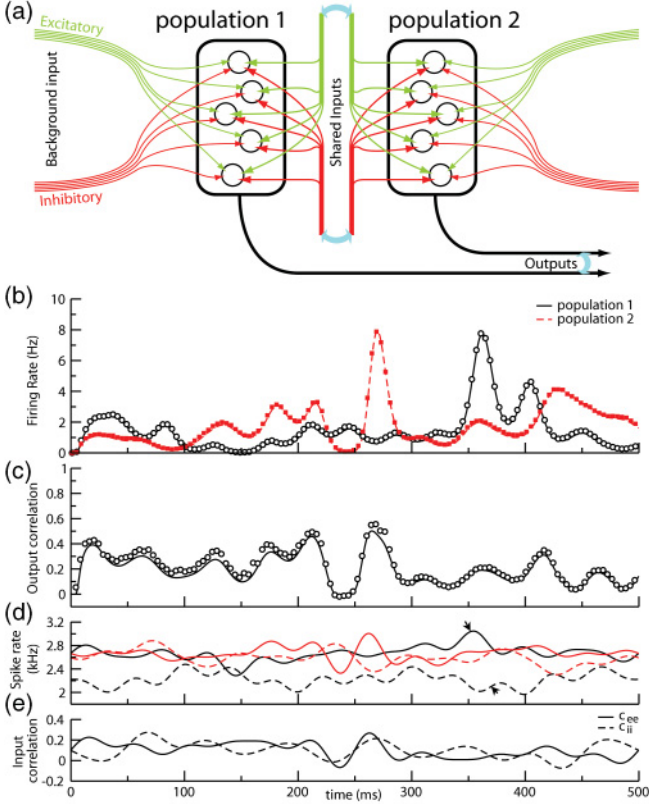


FIG. 3. (Color online) Response of correlated neuronal populations. (a) Schematic representation of the network. In addition to background inputs that are uncorrelated across neurons, each population receives shared inputs that are identical for all neurons. Shared inputs to population 1 and 2 are also cross correlated (indicated by blue arrows). (b) Firing rate of population 1 (solid line with open circles) and 2 (dashed line with squares). Lines, Eq. (5); symbols, numerical simulations. Parameters for population 1 are $\tau_v = 5$ ms, $J_e = 7.3$ nS, $J_i = 4.5$ nS, $v_\theta = -53$ mV, $v_r = -60$ mV, and for population 2 $\tau_v = 4.65$ ms, $J_e = 7.5$ nS, $J_i = 5.4$ nS, $v_\theta = -50$ mV, $v_r = -60$ mV. (c) Cross-correlation coefficient of the outputs of the two populations [solid line, expression (9); symbols, numerical simulation]. (d) Excitatory (solid lines) and inhibitory (dashed lines) input firing rates (population 2 data marked with arrow). (e) Cross-correlation coefficients between excitatory (solid) and inhibitory (dashed) inputs.

where r_{11} is the joint firing rate of the population. Positive correlations in the inputs increase the Fano factor, indicating an increase in synchrony. As an illustration, we consider a similar scenario as in the previous section but consisting of only one population [Fig. 4(a)]. The input initially consists only of background input, so that neurons fire independently ($F = 1$). At time $t = 250$ ms, the shared inputs activate and the background input is weakened to keep the mean firing rate constant [Fig. 4(b), top]. Although the firing rate does not change, input through the shared connections drives correlated spiking that is reflected by an approximately fivefold increase in the Fano factor [Fig. 4(b), bottom]. After the shared input is switched off at $t = 750$ ms, the network quickly returns to its initial state. The increase in synchrony indicated by the Fano factor is clearly visible in the raster plots in Figs. 4(c)–4(e),

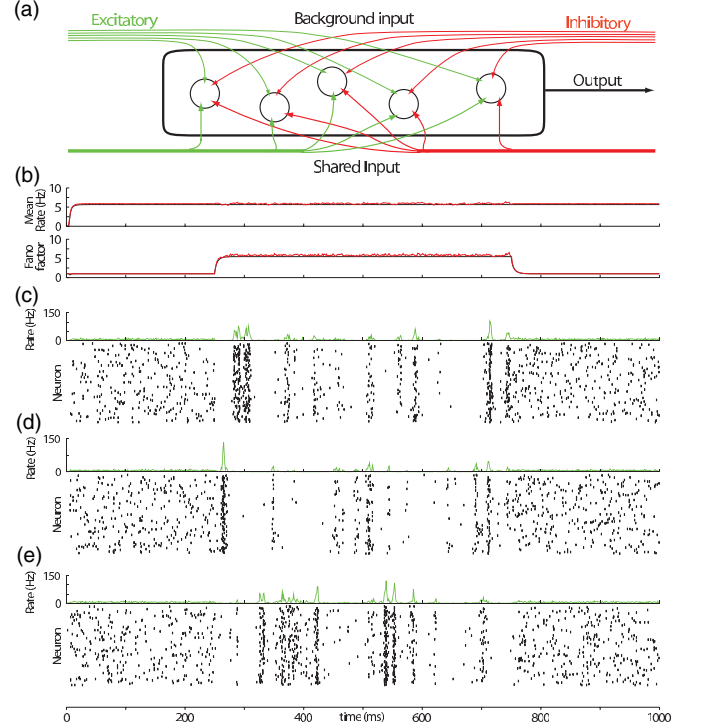


FIG. 4. (Color online) Synchronized spiking from pairwise correlations. (a) Schematic representation of the network. In addition to background inputs that are uncorrelated across neurons, the population is subjected to common inputs that are shared by all neurons. (b) Mean firing rate and Fano factor of the pooled output of the population. Black dashed lines, theory [top, Eq. (5); bottom, Eq. (10)]. Red solid lines, numerical simulation. Shared inputs with constant spike rate are activated between $t = 250$ and 750 ms; background activity is adjusted to maintain a constant overall firing rate. (c)–(e) Population firing rate (green solid line in top graphs) for three single runs of the numerical simulation. Raster plots showing the spikes of 200 randomly chosen neurons are also shown, in which synchronous events are clearly seen.

where the spiking activity of 200 randomly chosen neurons is shown for three different realizations of the simulation.

VI. RANGE OF VALIDITY

In order to study the range of validity of the level-crossing approximation, we first note that, in the case of a single synaptic type ($y \equiv 0$), for stationary inputs the system (2)–(4) can be cast in the following form:

$$\frac{dv}{dt} = \dot{v}, \quad \frac{d\dot{v}}{dt} = -\gamma_e \dot{v} - \omega_e v + \sqrt{2\gamma_e T_e} \xi_e(t), \quad (11)$$

where $\gamma_e = \tau_e^{-1} + \tau_v^{-1}$, $\omega_e = (\tau_v \tau_e)^{-1}$, and $T_e = \sigma_e^2 / [\tau_v (\tau_e + \tau_v)]$. This system describes the motion of a Brownian particle in a quadratic potential $U(v) = \frac{1}{2} \omega_e v^2$ with friction coefficient γ_e and temperature T_e . The problem of escape over a potential barrier for systems of the form (11) has been studied for several decades (e.g., [29]), and in the case of a quadratic potential, it is known that for the thresholded model also, (6) is the correct result for $\gamma_e = O(1)$, to first order in T_e [30]. In the case of two synaptic inputs, the membrane voltage consists of the sum of two contributions, $v = v_e + v_i$, where v_e and v_i each obey

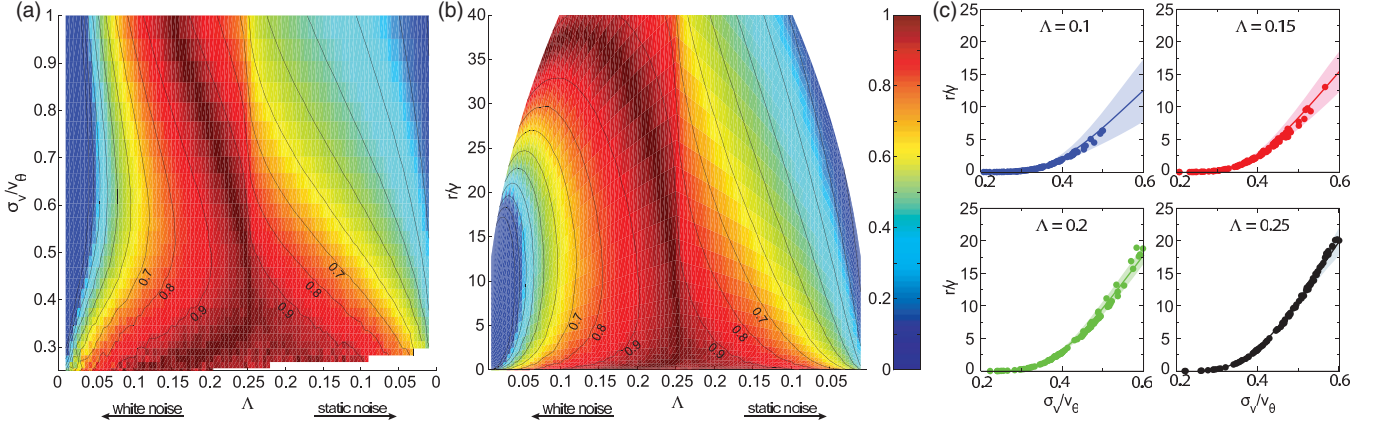


FIG. 5. (Color online) Range of validity of the level-crossing approximation. (a) Two-dimensional plot of the accuracy of the approximation as a function of the dimensionless parameters Λ and σ_v/v_θ , for the case of the two-dimensional system (11). The accuracy is plotted for the two limits $\tau_e \rightarrow 0$ (white noise limit) and $+\infty$ (static noise limit). The plot is color coded according to the scale bar on the right. Level curves are also shown as black solid lines. (b) The accuracy is represented here as a function of Λ and the dimensionless firing rate r/γ . (c) The accuracy of the approximation in the case of the three-dimensional system (2)–(4) is shown for four different values of the parameter Λ . Solid lines show the theoretical prediction, and shaded regions correspond to the accuracy expected from the analysis in (b). Symbols show the result of 100 numerical simulations with randomly chosen parameters.

a dynamics of the form (11) with corresponding parameters γ_i , ω_i , and T_i for the inhibitory part. The system (2)–(4) can be written as

$$\frac{dv}{dt} = \dot{v}, \quad \frac{d\dot{v}}{dt} = -\gamma\dot{v} - \omega v + \sqrt{2\gamma T}\xi(t) + z \quad (12)$$

with a new white noise $\xi(t)$, and effective parameters defined as $T = \tilde{T}_e + \tilde{T}_i$, with modified temperatures $\tilde{T}_k = (\sigma_k^2 - \tilde{\sigma}^2)/[\tau_v(\tau_k + \tau_v)]$, where $\tilde{\sigma}^2 = 2c_{ei}\sigma_e\sigma_i\sqrt{\tau_e\tau_i}/(\tau_e + \tau_i)$, $\gamma = (\gamma_e\tilde{T}_e + \gamma_i\tilde{T}_i)/T$, and ω is defined such that $T/\omega = \tilde{T}_e/\omega_e + \tilde{T}_i/\omega_i$. The new variable z is defined such that $\text{cov}(v, z) = \text{cov}(\dot{v}, z) = 0$ in the steady state and satisfies a linear equation of the form $dz/dt = \beta_1 z + \beta_2 v + \beta_3 \dot{v} + \beta_4 \xi'$ with constant parameters β_k and a second white noise ξ' . Because in the steady state z is independent of both v and \dot{v} , we may take the average of (12) given v and \dot{v} , and assume that the conditional mean $\langle z|v, \dot{v} \rangle \ll 1$, to obtain an approximate two-dimensional description of the system near equilibrium, Eq. (12) with $z \equiv 0$. This can be further simplified by switching to dimensionless variables, $t \rightarrow \gamma t$, $v \rightarrow v/\sigma_v$, which yields

$$\frac{dv}{dt} = \dot{v}, \quad \frac{d\dot{v}}{dt} = -\dot{v} - \Lambda v + \sqrt{2\Lambda}\xi(t) \quad (13)$$

with a unique dimensionless parameter $\Lambda = \omega/\gamma^2 \in (0, \frac{1}{4})$, and where ξ is a unit white noise in the dimensionless time. This formulation allows us to study the validity of the level-crossing method in a two-dimensional space defined by Λ and the dimensionless threshold v_θ/σ_v . To do so, we numerically simulate the reduced system (13), systematically varying the parameters Λ and v_θ/σ_v , and compare the resulting firing rate r_{sim} with the theoretical prediction r_{th} of the level-crossing method. We then compute the accuracy as $1 - |r_{\text{sim}} - r_{\text{th}}|/r_{\text{th}}$. As can be seen from Figs. 5(a) and 5(b), the accuracy is maximal near $\Lambda \simeq \frac{1}{4}$, which corresponds to the case of identical time constants ($\tau_{e,i} = \tau_v$). Although the approximation breaks down in the limit where $\tau_{e,i} \rightarrow 0$ (white noise limit) or $+\infty$ (static noise limit), it remains highly

accurate for $\Lambda \gtrsim 0.2$, corresponding to synaptic time constants in the range of $\sim 0.4\tau_v$ to $2.6\tau_v$. In order to check the validity of the reduced equation (13) for the thresholded system, we then simulate the three-dimensional system (2)–(4) for fixed values of Λ by selecting random values for the parameters $\tau_{e,i}$ and $\sigma_{e,i}$, and verify that the results match the accuracy expected from the analysis of the reduced system [Fig. 5(c)]. The breakdown of the approximation for $\tau_{e,i} \rightarrow 0, +\infty$ can be explained by the fact that in these two limits, voltage trajectories following a threshold crossing do not return near the stable equilibrium before crossing the threshold again. For very short synaptic time constants, this is due to the fact that voltage fluctuations become so rapid that the probability of multiple threshold crossings in a small time interval becomes very high. In the limit of long synaptic time constants, after a threshold crossing the input can remain above threshold for a sufficiently long time for ballistic firing to occur. These two different mechanisms explain the asymmetry in the plots of Figs. 5(a) and 5(b) (it is readily checked that the symmetry is recovered if the synaptic input is reset after each action potential). These results show that the level-crossing rate provides a good approximation to the firing rate in the steady-state case as long as the synaptic filtering time constants remain of the same order of magnitude as the membrane time constant. In the case of time-varying inputs, this is expected to hold as long as the voltage distribution remains subthreshold and the firing rate is much lower than the typical relaxation time of the voltage ($r/\gamma \ll 1$). Applicability to the case of conductance-based Poissonian synaptic drive is justified when the usual conditions of validity of the effective time-constant approximation are met (i.e., high input rates and small postsynaptic conductance increase; see, e.g. [5]).

VII. DISCUSSION

We have shown how level-crossing rates can be used to approximate the firing statistics of thresholded integrate-

and-fire neurons. Using this approach, we derived analytical expressions for three key aspects of the response: the mean firing rate, the linear response to sinusoidally modulated inputs, and the pairwise cross correlation between neurons receiving correlated inputs. The theory was developed for both stationary and time-dependent stimulus conditions and shown to accurately match the results of numerical simulations of integrate-and-fire neurons receiving filtered Poissonian synaptic drive. Using similar methods, other authors have recently suggested threshold-crossing models as an alternative to the standard integrate-and-fire description [17,18], in which the nonlinear reset mechanism precludes detailed analytical treatment. Our results provide a quantitative link between these two descriptions, as well as the range of parameters under which similar firing statistics are obtained. In particular, we have found that the synaptic filtering time constant is a crucial parameter for the validity of the level-crossing method. We have also shown that the level-crossing method can be extended to the case of time-dependent inputs, an aspect that has not been previously investigated, to our knowledge.

Although we have treated here only the case of unconnected populations, the theory captures the time-dependent aspects of the response and provides the required quantities for a self-consistent treatment of recurrent networks. Specifically, by using expressions (5) and (8) to express the mean, variance, and cross correlations of excitatory and inhibitory synaptic conductances, a closed system of equations can be obtained that corresponds to a mean-field description of the network. Analyzing this type of model could give interesting insights into the way synaptic filtering affects network dynamics. Moreover, because correlations naturally arise in recurrent networks as a result of shared connections, their effect on firing rates [Fig. 1(a)] and synchronization (Fig. 4) suggest that these may play a crucial role in determining the stable states of a network. The frequency response of individual neurons (Fig. 3), which was found to exhibit a richer structure when distinct excitatory and inhibitory time scales are considered, also suggests that stable oscillatory states may be possible that are not present in purely excitatory networks.

Our results could be generalized in several ways. For example, it should be possible to obtain perturbative corrections for the effects of the voltage reset that follows the emission of spikes. Although our analysis of cross correlations is restricted to pairwise correlations, higher-order correlations could also be calculated using the same formalism. The case of non-Gaussian voltage distributions could be treated using expansions in Hermite polynomials, for example a Hedgeworth expansion [31].

Note added in proof. We have recently learned of a closely related article [33] dealing with the dynamical response of threshold-crossing neurons.

ACKNOWLEDGMENTS

Magnus J. E. Richardson is thanked for initiating early research that led to this paper. The author also acknowledges useful discussions with Wulfram Gerstner, Liam Paninski,

and Srdjan Ostojic. This work was supported by Grant No. PBELP3-127907 from the Swiss National Science Foundation.

APPENDIX A: FIRING RATE

1. Level-crossing rates for Gaussian processes

We detail here the calculation of level-crossing rates for Gaussian processes. For concreteness, we start with the IF model (2)–(4) as an example. Due to the linearity of this system, and because x and y are Gaussian random variables, $v(t)$ and its derivative $\dot{v}(t)$ are also Gaussian random variables. The rate of upward crossings of the threshold v_θ is given by [16]

$$r = \int_0^\infty |\dot{v}| p(v_\theta, \dot{v}) d\dot{v}, \quad (\text{A1})$$

where $p(v, \dot{v})$ is the marginal probability density of v and \dot{v} . Since in general these two variables are not independent, we rewrite $p(v_\theta, \dot{v})$ using Bayes' rule as $p(v_\theta)p(\dot{v}|v_\theta)$, where

$$p(v_\theta) = \frac{1}{\sqrt{2\pi}\sigma_v} e^{-(v_\theta - \langle v \rangle)^2 / (2\sigma_v^2)}, \quad (\text{A2})$$

$$p(\dot{v}|v_\theta) = \frac{1}{\sqrt{2\pi}[\sigma_{\dot{v}}]_\theta} e^{-(\dot{v} - \langle \dot{v} \rangle_\theta)^2 / (2[\sigma_{\dot{v}}]_\theta^2)}, \quad (\text{A3})$$

where the conditional moments $\langle \dot{v} \rangle_\theta$ and $[\sigma_{\dot{v}}]_\theta^2$ are yet to be determined. Insertion of (A2) and (A3) into (A1) yields

$$\begin{aligned} r &= \frac{1}{2\pi\sigma_v[\sigma_{\dot{v}}]_\theta} e^{-(v_\theta - \langle v \rangle)^2 / (2\sigma_v^2)} \int_0^\infty \dot{v} e^{-(\dot{v} - \langle \dot{v} \rangle_\theta)^2 / (2[\sigma_{\dot{v}}]_\theta^2)} d\dot{v} \\ &= \frac{1}{2\pi} \frac{[\sigma_{\dot{v}}]_\theta}{\sigma_v} e^{-(v_\theta - \langle v \rangle)^2 / (2\sigma_v^2)} [e^{-\beta^2} + \sqrt{\pi}\beta(1 + \text{erf}\beta)], \end{aligned}$$

where $\beta = \langle \dot{v} \rangle_\theta / (\sqrt{2}[\sigma_{\dot{v}}]_\theta)$. To determine the conditional moments, we define a new variable $z = \dot{v} + \alpha v$ that is independent of v , i.e., $\langle zv \rangle = \langle z \rangle \langle v \rangle$, which is achieved for $\alpha = -\text{cov}(v, \dot{v}) / \sigma_v^2$. Due to independence, we have $\langle z \rangle_\theta = \langle z \rangle$, where

$$\begin{aligned} \langle z \rangle_\theta &= \langle \dot{v} \rangle_\theta + \alpha v_\theta, \\ \langle z \rangle &= \langle \dot{v} \rangle + \alpha \langle v \rangle. \end{aligned}$$

This is solved for $\langle \dot{v} \rangle_\theta$,

$$\langle \dot{v} \rangle_\theta = \langle \dot{v} \rangle + \frac{\text{cov}(v, \dot{v})}{\sigma_v^2} (v_\theta - \langle v \rangle). \quad (\text{A4})$$

Similarly, for the variance we have $[\sigma_z^2]_\theta = \sigma_z^2$, where

$$\begin{aligned} [\sigma_z^2]_\theta &= [\sigma_{\dot{v}}^2]_\theta, \\ \sigma_z^2 &= \sigma_{\dot{v}}^2 + 2\alpha \text{cov}(v, \dot{v}) + \alpha^2 \sigma_v^2, \end{aligned}$$

which gives

$$[\sigma_{\dot{v}}^2]_\theta = \sigma_{\dot{v}}^2 - \frac{\text{cov}(v, \dot{v})^2}{\sigma_v^2}. \quad (\text{A5})$$

2. Moments for time-dependent input

To determine the moments of v and \dot{v} for arbitrary inputs, we rewrite the system (2)–(4) in vector form as

$$d\vec{z}/dt = A\vec{z} + \vec{\mu} + B\vec{\xi}(t), \quad (\text{A6})$$

where $\vec{\xi}$ is a multidimensional white noise, and

$$\vec{z}(t) = (v(t), x(t), y(t))^T,$$

$$A(\langle v(t) \rangle, t) = \begin{pmatrix} -1/\tau_v(t) & E_e - \langle v(t) \rangle & E_i - \langle v(t) \rangle \\ 0 & -1/\tau_e & 0 \\ 0 & 0 & -1/\tau_i \end{pmatrix},$$

$$B(t) = \begin{pmatrix} 0 & 0 & 0 \\ 0 & \sigma_e(t)\sqrt{2(1-c_{ei}(t)^2)/\tau_e} & \sigma_e(t)c_{ei}(t)\sqrt{2/\tau_e} \\ 0 & 0 & \sigma_i(t)\sqrt{2/\tau_i} \end{pmatrix},$$

$$\vec{\mu}(t) = (E_0(t)/\tau_v(t) + I_{\text{ext}}(t)/C, 0, 0)^T,$$

where $c_{ei}(t)$ is the correlation coefficient between excitatory and inhibitory inputs, such that $\langle \xi_e(t)\xi_i(t+\tau) \rangle = c_{ei}(t)\delta(\tau)$. Taking moments of Eq. (A6) yields ordinary differential equations for the mean $\langle \vec{z}(t) \rangle$ and covariance matrix $C_{ij}(t) = \langle z_i(t)z_j(t) \rangle - \langle z_i(t) \rangle \langle z_j(t) \rangle$. These equations are in general implicit due to the dependence of the matrix A on the mean voltage, but can be solved iteratively using standard numerical methods. However, after a short initial transient $\langle x \rangle = \langle y \rangle = 0$, the equation for the first moment becomes explicit:

$$\frac{d}{dt} \langle v(t) \rangle = [E_0(t) - \langle v(t) \rangle]/\tau_v(t) + I_{\text{ext}}(t)/C,$$

which can be integrated to give

$$\langle v(t) \rangle - \langle v(t_0) \rangle = \int_{t_0}^t e^{-\int_s^t \frac{du}{\tau_v(u)}} \left(\frac{E_0(s)}{\tau_v(s)} + \frac{I_{\text{ext}}(s)}{C} \right) ds.$$

This yields the explicit form of $A(t)$, which can then be substituted in the equation for the second moments,

$$\frac{d}{dt} C = AC + CA^T + BB^T,$$

which becomes solvable (see, e.g., [32] for an explicit solution). The moments of \dot{v} are then obtained using $\langle \dot{v} \rangle = (A\langle \vec{x} \rangle)_1$, $\sigma_v^2 = (ACA^T)_{11}$, and $\text{cov}(v, \dot{v}) = (AC)_{11}$. It is also worth noting that both equations simplify in the weakly nonstationary case, where $\langle v(t) \rangle \simeq \text{const}$, so that $\langle v \rangle$ can be substituted by $E_0 + \tau_v I_{\text{ext}}/C$ in the expression for A .

In the stationary case, we have

$$\langle v \rangle = E_0 + \tau_v I_{\text{ext}}/C,$$

$$\langle \dot{v} \rangle = 0,$$

$$\sigma_v^2 = (\sigma_e^2 \bar{E}_e^2 + \tilde{\sigma}^2 \bar{E}_e \bar{E}_i) \frac{\tau_v^2 \tau_e}{\tau_v + \tau_e} + (\sigma_i^2 \bar{E}_i^2 + \tilde{\sigma}^2 \bar{E}_i \bar{E}_e) \frac{\tau_v^2 \tau_i}{\tau_v + \tau_i},$$

$$\sigma_{\dot{v}}^2 = (\sigma_e^2 \bar{E}_e^2 + \tilde{\sigma}^2 \bar{E}_e \bar{E}_i) \frac{\tau_v}{\tau_v + \tau_e} + (\sigma_i^2 \bar{E}_i^2 + \tilde{\sigma}^2 \bar{E}_i \bar{E}_e) \frac{\tau_v}{\tau_v + \tau_i},$$

where $\bar{E}_{e,i} = E_{e,i} - \langle v \rangle$ and $\tilde{\sigma}^2 = \langle xy \rangle = 2c_{ei}\sigma_e\sigma_i\sqrt{\tau_e\tau_i}/(\tau_e + \tau_i)$.

APPENDIX B: FREQUENCY RESPONSE

When a perturbation $f(t) = \varepsilon e^{i\omega t}$ is injected into the system (2)–(4), the dynamical variables respond by oscillating with the same frequency ω as the perturbation. In this section, we calculate the modulation of the firing rate when a perturbation of the form $f(t)$ is injected on top of a background stationary input. For simplicity, we assume $c_{ei} = 0$, but the case of correlated inputs can be treated in the same way. We adopt here

the following notation: for any statistical variable z , we write $z(t) = z_0 + \varepsilon z_1 e^{i\omega t}$, where z_0 is the value of $z(t)$ for $\varepsilon = 0$, and z_1 is the first-order correction in ε due to the perturbation $f(t)$. The determination of the firing-rate response requires the calculation of the first and second moments appearing in Eq. (5), which we therefore expand as

$$\langle v(t) \rangle = \langle v \rangle_0 + \varepsilon \langle v \rangle_1 e^{i\omega t}, \quad (\text{B1})$$

$$\langle \dot{v}(t) \rangle = \langle \dot{v} \rangle_0 + \varepsilon \langle \dot{v} \rangle_1 e^{i\omega t}, \quad (\text{B2})$$

$$\sigma_v^2(t) = [\sigma_v^2]_0 + \varepsilon [\sigma_v^2]_1 e^{i\omega t}, \quad (\text{B3})$$

$$\sigma_{\dot{v}}^2(t) = [\sigma_{\dot{v}}^2]_0 + \varepsilon [\sigma_{\dot{v}}^2]_1 e^{i\omega t}, \quad (\text{B4})$$

$$\text{cov}(v(t)\dot{v}(t)) = [\text{cov}(v, \dot{v})]_0 + \varepsilon [\text{cov}(v, \dot{v})]_1 e^{i\omega t}. \quad (\text{B5})$$

Substituting (B1)–(B5) in (5) and expanding to first order in ε yields the firing rate in the form $r(t) = r_0 + \varepsilon r_1 e^{i\omega t}$, with r_1/r_0 given by Eq. (7). This can be rewritten, using $\text{cov}(v, \dot{v})_1 = \frac{1}{2}i\omega[\sigma_v^2]_1$, as

$$\frac{r_1}{r_0} = \left[\sqrt{\frac{\pi}{2[\sigma_v^2]_0}} \langle \dot{v} \rangle_1 + v_\theta \frac{\langle v \rangle_1}{[\sigma_v^2]_0} \right] + \frac{1}{2} \left[\frac{[\sigma_v^2]_1}{[\sigma_v^2]_0} \left(\frac{v_\theta^2}{[\sigma_v^2]_0} - 1 + i\omega v_\theta \sqrt{\frac{\pi}{2[\sigma_v^2]_0}} \right) + \frac{[\sigma_v^2]_1}{[\sigma_v^2]_0} \right]. \quad (\text{B6})$$

Explicit expressions for the moments appearing in (B6) are given below for two specific scenarios.

1. Response to modulations in input current

We first consider the case where the perturbation is injected as an external current, i.e., we set $I_{\text{ext}} = \varepsilon I_0 e^{i\omega t}$ in (1). Substituting $(v - E_0) \rightarrow v$ and rescaling the reversal potentials accordingly, the system (2)–(4) becomes

$$\dot{v} = -\tau_v^{-1}v + x(\bar{E}_e - \langle v \rangle) + y(\bar{E}_i - \langle v \rangle) + \varepsilon \mu_0 e^{i\omega t}, \quad (\text{B7})$$

$$\tau_e \dot{x} = -x + \sqrt{2\sigma_e^2 \tau_e} \xi_e, \quad (\text{B8})$$

$$\tau_i \dot{y} = -y + \sqrt{2\sigma_i^2 \tau_i} \xi_i, \quad (\text{B9})$$

where $\bar{E}_{e,i} = E_{e,i} - E_0$ and $\mu_0 = I_0/C$. Taking the average of (B7) and integrating, we obtain

$$\langle v(t) \rangle = \int_{-\infty}^t e^{-(t-s)/\tau_v} \varepsilon e^{i\omega s} ds = \varepsilon \mu_0 \tau_v \frac{e^{i\omega t}}{1 + i\omega \tau_v}, \quad (\text{B10})$$

so that $\langle v \rangle_0 = 0$ and $\langle v \rangle_1 = \mu_0 \tau_v (1 + i\omega \tau_v)^{-1}$. Differentiating (B10), we get $\langle \dot{v} \rangle_0 = 0$ and $\langle \dot{v} \rangle_1 = i\omega \mu_0 \tau_v (1 + i\omega \tau_v)^{-1}$. By taking second moments of (B7)–(B9), we obtain through similar calculations

$$[\sigma_v^2]_0 = \sigma_e^2 \bar{E}_e^2 \frac{\tau_v^2 \tau_e}{\tau_v + \tau_e} + \sigma_i^2 \bar{E}_i^2 \frac{\tau_v^2 \tau_i}{\tau_v + \tau_i}, \quad (\text{B11})$$

$$[\sigma_v^2]_1 = -\sigma_e^2 \bar{E}_e \mu_0 \frac{\tau_v^3 \tau_e}{\tau_v + \tau_e} k_v k_{vv} (1 + k_{ve}) \quad (\text{B12})$$

$$-\sigma_i^2 \bar{E}_i \mu_0 \frac{\tau_v^3 \tau_i}{\tau_v + \tau_i} k_v k_{vv} (1 + k_{vi}), \quad (\text{B13})$$

$$[\sigma_{\dot{v}}^2]_0 = \sigma_e^2 \bar{E}_e^2 \frac{\tau_v}{\tau_v + \tau_e} + \sigma_i^2 \bar{E}_i^2 \frac{\tau_v}{\tau_v + \tau_i}, \quad (\text{B14})$$

$$[\sigma_v^2]_1 = -\sigma_e^2 \bar{E}_e \mu_0 \frac{\tau_v^2}{\tau_v + \tau_e} k_{vv}(1 + k_v k_{ve}) \quad (\text{B15})$$

$$-\sigma_i^2 \bar{E}_i \mu_0 \frac{\tau_v^2}{\tau_v + \tau_i} k_{vv}(1 + k_v k_{vi}), \quad (\text{B16})$$

where we have defined

$$k_\alpha = (1 + i\omega\tau_\alpha)^{-1} \quad \text{and} \quad k_{\alpha\beta} = \left[1 + i\omega \left(\frac{1}{\tau_\alpha} + \frac{1}{\tau_\beta} \right)^{-1} \right]^{-1} \quad (\text{B17})$$

for $\alpha, \beta \in \{v, e, i\}$. The firing-rate modulation can then be obtained by inserting these expressions in (B6). Note that as $\omega \rightarrow \infty$, only $\langle \dot{v} \rangle_1$ remains finite, so that the firing-rate modulation converges to a real limit,

$$\frac{r_1}{r_0} \rightarrow \mu_0 \sqrt{\frac{\pi}{2[\sigma_v^2]_0}} \quad (\omega \rightarrow \infty). \quad (\text{B18})$$

For the case where synaptic inputs are modeled as postsynaptic currents, i.e., replacing $\langle v \rangle$ by E_0 in Eq. (B7), the first-order corrections to the variances (B13) and (B16) vanish, and the expression for the firing rate simplifies as

$$\frac{r_1}{r_0} = \mu_0 \tau_v \frac{\frac{v_\theta}{[\sigma_v^2]_0} + i\omega \sqrt{\frac{\pi}{2[\sigma_v^2]_0}}}{1 + i\omega\tau_v}$$

which has the same high-frequency behavior as (B18).

A. Response to modulations in presynaptic firing rates

We now consider the case where the modulations arise from changes in presynaptic firing frequencies. We rewrite the equation for the excitatory synaptic conductance,

$$\tau_e \dot{G}_e = -G_e + c_e \tau_e N_e(t), \quad (\text{B19})$$

where $N_e(t) = \sum \delta(t - t_f)$ is a Poisson process representing the sum of excitatory presynaptic spikes. A modulation in presynaptic excitatory rate is described by $\langle N_e(t) \rangle = \sigma_{N_e}^2 = R_{e0} + \varepsilon_e R_{e1} e^{i\omega t}$. We can then write $\langle G_e(t) \rangle = \langle G_e \rangle_0 + \varepsilon_e \langle G_e \rangle_1 e^{i\omega t}$ and $\sigma_{G_e}^2(t) = [\sigma_{G_e}^2]_0 + \varepsilon_e [\sigma_{G_e}^2]_1 e^{i\omega t}$, where

$$\begin{aligned} \langle G_e \rangle_0 &= c_e \tau_e R_{e0}, \\ \langle G_e \rangle_1 &= c_e \tau_e R_{e1} k_e, \\ [\sigma_{G_e}^2]_0 &= \frac{1}{2} c_e^2 \tau_e R_{e0}, \\ [\sigma_{G_e}^2]_1 &= \frac{1}{2} c_e^2 \tau_e R_{e1} k_e, \end{aligned}$$

with k_e defined as in (B17). Similar equations are assumed for the inhibitory part, with parameter ε_i and frequency ω' . Inserting into (2)–(4), substituting $(v - E_0) \rightarrow v$, and rescaling the reversal potentials accordingly yields

$$\begin{aligned} \dot{v} &= -(\tau_v^{-1} + \varepsilon_e \langle g_e \rangle_1 e^{i\omega t} + \varepsilon_i \langle g_i \rangle_1 e^{i\omega' t}) v \\ &\quad + \varepsilon_e \langle g_e \rangle_1 e^{i\omega t} \bar{E}_e + \varepsilon_i \langle g_i \rangle_1 e^{i\omega' t} \bar{E}_i \\ &\quad + x(\bar{E}_e - \varepsilon_e \langle v \rangle_1 e^{i\omega t}) + y(\bar{E}_i - \varepsilon_i \langle v \rangle_1 e^{i\omega' t}), \end{aligned} \quad (\text{B20})$$

$$\tau_e \dot{x} = -x + \sqrt{2\tau_e([\sigma_e^2]_0 + \varepsilon_e [\sigma_e^2]_1 e^{i\omega t})} \xi_e(t), \quad (\text{B21})$$

$$\tau_i \dot{y} = -y + \sqrt{2\tau_i([\sigma_i^2]_0 + \varepsilon_i [\sigma_i^2]_1 e^{i\omega' t})} \xi_i(t), \quad (\text{B22})$$

to first order in $\varepsilon_e, \varepsilon_i$, where $g_{e,i} = G_{e,i}/C$. By taking the average of Eq. (B20), we obtain $\langle v(t) \rangle = \langle v \rangle_0 + \varepsilon_e \langle v \rangle_1^e e^{i\omega t} + \varepsilon_i \langle v \rangle_1^i e^{i\omega' t}$, where

$$\begin{aligned} \langle v \rangle_0 &= 0, \\ \langle v \rangle_1^e &= \tau_v k_v \langle g_e \rangle_1 \bar{E}_e, \\ \langle v \rangle_1^i &= \tau_v k_v \langle g_i \rangle_1 \bar{E}_i. \end{aligned}$$

Similarly, we have for the variance $\sigma_v^2(t) = [\sigma_v^2]_0^e + [\sigma_v^2]_0^i + \varepsilon_e [\sigma_v^2]_1^e e^{i\omega t} + \varepsilon_i [\sigma_v^2]_1^i e^{i\omega' t}$, where

$$\begin{aligned} [\sigma_v^2]_0^e &= \sigma_e^2 \bar{E}_e^2 \tau_v^2 \frac{\tau_e}{\tau_v + \tau_e}, \\ [\sigma_v^2]_1^e &= [\sigma_v^2]_0^e k_{xx} k_{vv} k_{ve} \\ &\quad + [\sigma_v^2]_0^e \left(k_{vv}(1 + k_{ve}) \left[\frac{\langle g_e \rangle_1}{i\omega} - \frac{\langle v \rangle_1^e}{\bar{E}_e} \right] - \frac{\langle g_e \rangle_1}{i\omega} \right) \\ &\quad + [\sigma_v^2]_0^i \left(k_{vv}(1 + k_{vi}) \left[\frac{\langle g_e \rangle_1}{i\omega} - \frac{\langle v \rangle_1^e}{\bar{E}_e} \right] - \frac{\langle g_e \rangle_1}{i\omega} \right). \end{aligned}$$

The inhibitory terms $[\sigma_v^2]_0^i$ and $[\sigma_v^2]_1^i$ are obtained by switching the indices $e \leftrightarrow i$ and $\omega \leftrightarrow \omega'$ in the above expressions. For the covariance, $\text{cov}(v(t)x(t)) = \text{cov}(v, x)_0 + \varepsilon_e \text{cov}(v, x)_1^e e^{i\omega t} + \varepsilon_i \text{cov}(v, x)_1^i e^{i\omega' t}$, with

$$\begin{aligned} \text{cov}(v, x)_0 &= \sigma_e^2 \bar{E}_e \tau_v \frac{\tau_e}{\tau_v + \tau_e}, \\ \text{cov}(v, x)_1^e &= \text{cov}(v, x)_0^e k_{ee} k_{ve} \\ &\quad + \text{cov}(v, x)_0^e \left[k_{ve} \left(\frac{\langle g_e \rangle_1}{i\omega} - \frac{\langle v \rangle_1^e}{\bar{E}_e} \right) - \frac{\langle g_e \rangle_1}{i\omega} \right], \\ \text{cov}(v, x)_1^i &= \text{cov}(v, x)_0^i \left[k'_{ve} \left(\frac{\langle g_i \rangle_1}{i\omega'} - \frac{\langle v \rangle_1^i}{\bar{E}_e} \right) - \frac{\langle g_i \rangle_1}{i\omega'} \right], \end{aligned}$$

where k'_{ve} is defined by Eq. (B17) with ω replaced by ω' . The other covariance $\text{cov}(v, y)$ is obtained from the above expressions by switching the indices $e \leftrightarrow i$ and $\omega \leftrightarrow \omega'$. The variance of \dot{v} is given by $\sigma_{\dot{v}}^2(t) = [\sigma_{\dot{v}}^2]_0^e + [\sigma_{\dot{v}}^2]_0^i + \varepsilon_e [\sigma_{\dot{v}}^2]_1^e e^{i\omega t} + \varepsilon_i [\sigma_{\dot{v}}^2]_1^i e^{i\omega' t}$, with

$$\begin{aligned} [\sigma_{\dot{v}}^2]_0^e &= \frac{[\sigma_v^2]_0^e}{\tau_v^2} + [\sigma_e^2]_0 \bar{E}_e^2 - 2 \frac{\bar{E}_e}{\tau_v} \text{cov}(v, x)_0, \\ [\sigma_{\dot{v}}^2]_1^e &= \frac{[\sigma_v^2]_1^e}{\tau_v^2} + [\sigma_e^2]_1 \bar{E}_e^2 + 2 \frac{\langle g_e \rangle_1}{\tau_v} [\sigma_v^2]_0 \\ &\quad - 2 \langle v \rangle_1^e \bar{E}_e [\sigma_e^2]_0 - 2 \frac{\bar{E}_e}{\tau_v} \text{cov}(v, x)_1^e \\ &\quad + 2 \left(\frac{\langle v \rangle_1^e}{\tau_v} - \langle g_e \rangle_1 \bar{E}_e \right) \text{cov}(v, x)_0 \\ &\quad - 2 \langle v \rangle_1^e \bar{E}_i [\sigma_i^2]_0 - 2 \frac{\bar{E}_i}{\tau_v} \text{cov}(v, y)_1^e \\ &\quad + 2 \left(\frac{\langle v \rangle_1^e}{\tau_v} - \langle g_e \rangle_1 \bar{E}_e \right) \text{cov}(v, y)_0, \end{aligned}$$

and with similar expressions for $[\sigma_{\dot{v}}^2]_0^i$ and $[\sigma_{\dot{v}}^2]_1^i$ with indices $e \leftrightarrow i$ and $\omega \leftrightarrow \omega'$ switched. These expressions are then inserted into (B6) to obtain the firing-rate modulation r_1 .

APPENDIX C: CROSS CORRELATIONS

We now consider a pair of neurons receiving cross-correlated inputs:

$$\dot{v}_1 = \tau_1^{-1}(E_1 - v_1) + x_1(E_e - \langle v_1 \rangle) + y_1(E_i - \langle v_1 \rangle), \quad (\text{C1})$$

$$\tau_e \dot{x}_1 = -x_1 + \sqrt{2\sigma_{x_1}^2} \tau_e \xi_e, \quad (\text{C2})$$

$$\tau_i \dot{y}_1 = -y_1 + \sqrt{2\sigma_{y_1}^2} \tau_i \xi_i, \quad (\text{C3})$$

$$\dot{v}_2 = \tau_2^{-1}(E_2 - v_2) + x_2(E_e - \langle v_2 \rangle) + y_2(E_i - \langle v_2 \rangle), \quad (\text{C4})$$

$$\tau_e \dot{x}_2 = -x_2 + \sqrt{2\sigma_{x_2}^2} \tau_e \xi_e', \quad (\text{C5})$$

$$\tau_i \dot{y}_2 = -y_2 + \sqrt{2\sigma_{y_2}^2} \tau_i \xi_i', \quad (\text{C6})$$

where the subscripts 1,2 indicate the neuron number, and we have omitted external inputs for simplicity. We assume that correlations exist between excitatory and inhibitory inputs to the two neurons, i.e., $\langle \xi_\alpha(t) \xi_\beta'(t') \rangle = c_{\alpha\beta}(t) \delta(t - t')$ for $\alpha = e, i$.

1. Joint firing rate

We are interested in the probability that a pair of neurons described by (C1)–(C6) cross their firing thresholds simultaneously. This is given by the total probability current flowing through the region of the hyperplane $\{v_1 = v_{\vartheta_1}, v_2 = v_{\vartheta_2}\}$ defined by the upward crossing condition $\dot{v}_1, \dot{v}_2 > 0$. Thus,

$$r_{12} = \int_0^\infty \int_0^\infty \dot{v}_1 \dot{v}_2 p(v_{\vartheta_1}, v_{\vartheta_2}, \dot{v}_1, \dot{v}_2) d\dot{v}_1 d\dot{v}_2,$$

where $p(v_{\vartheta_1}, v_{\vartheta_2}, \dot{v}_1, \dot{v}_2)$ is the probability density that the two neurons are found at their respective firing thresholds, with velocities equal to \dot{v}_1 and \dot{v}_2 . As in the single-neuron case, we expand this probability as $p_\vartheta p(v_1, \dot{v}_2 | v_{\vartheta_1}, v_{\vartheta_2})$, where

$$p_\vartheta = \iint p(v_{\vartheta_1}, v_{\vartheta_2}, \dot{v}_1, \dot{v}_2) d\dot{v}_1 d\dot{v}_2$$

is the marginal probability density of the two neurons being at their firing threshold. This is given by a two-dimensional Gaussian

$$p_\theta = \frac{\exp\left[-\frac{1}{2(1-\rho^2)}\left(\frac{\bar{v}_{\vartheta_1}^2}{\sigma_{v_1}^2} + \frac{\bar{v}_{\vartheta_2}^2}{\sigma_{v_2}^2} - 2\rho\frac{\bar{v}_{\vartheta_1}\bar{v}_{\vartheta_2}}{\sigma_{v_1}\sigma_{v_2}}\right)\right]}{2\pi\sigma_{v_1}\sigma_{v_2}\sqrt{1-\rho^2}},$$

where $\bar{v}_{\vartheta_i} = v_{\vartheta_i} - \langle v_i \rangle$, and the correlation coefficient ρ is defined by

$$\rho = \frac{\text{cov}(v_1, v_2)}{\sigma_{v_1}\sigma_{v_2}}.$$

Similarly, the conditional density $p(\dot{v}_1, \dot{v}_2 | v_{\vartheta_1}, v_{\vartheta_2})$ is given by a two-dimensional Gaussian, the mean and covariance of which remain to be determined. The joint firing rate can then be written

$$\frac{r_{12}}{p_\vartheta} = \int_0^\infty \int_0^\infty \dot{v}_1 \dot{v}_2 p(\dot{v}_1, \dot{v}_2 | v_{\vartheta_1}, v_{\vartheta_2}) d\dot{v}_1 d\dot{v}_2. \quad (\text{C7})$$

The integral on the right-hand side is best performed by using two independent variables a and b defined as

$$\dot{v}_1 = [\sigma_{v_1}^2]_\theta \left(\sqrt{\frac{1+\dot{\rho}_\theta}{2}} a + \sqrt{\frac{1-\dot{\rho}_\theta}{2}} b \right),$$

$$\dot{v}_2 = [\sigma_{v_2}^2]_\theta \left(\sqrt{\frac{1+\dot{\rho}_\theta}{2}} a - \sqrt{\frac{1-\dot{\rho}_\theta}{2}} b \right),$$

where

$$\dot{\rho}_\theta = \frac{\text{cov}(\dot{v}_1, \dot{v}_2)_\theta}{[\sigma_{v_1}^2]_\theta [\sigma_{v_2}^2]_\theta}$$

is the correlation coefficient of \dot{v}_1 and \dot{v}_2 conditional on both neurons being at their firing thresholds simultaneously. These new variables are scaled ($\sigma_a^2 = \sigma_b^2 = 1$) and independent [$\text{cov}(a, b) = 0$] over the range of the integral. Equation (C7) then simplifies as

$$\frac{4\pi r_{12}}{[\sigma_{v_1}^2]_\theta [\sigma_{v_2}^2]_\theta p_\vartheta} = I[\langle a \rangle, \langle b \rangle] \quad (\text{C8})$$

with

$$I[\langle a \rangle, \langle b \rangle] = \int_0^\infty da \int_{-\lambda a}^{\lambda a} db [(a^2 - b^2) + \dot{\rho}_\theta(a^2 + b^2)] e^{-(a-(a))^2/2} e^{-(b-(b))^2/2},$$

where $\lambda = \sqrt{\frac{1+\dot{\rho}_\theta}{1-\dot{\rho}_\theta}}$. In general, the variables a and b do not have zero mean and the above integral does not admit a closed form solution. A Taylor expansion for $\langle a \rangle, \langle b \rangle \ll 1$ can be made, which yields to lowest order

$$\begin{aligned} I[0,0] &= \int_0^\infty da \int_{-\lambda a}^{\lambda a} db [(a^2 - b^2) + \dot{\rho}_\theta(a^2 + b^2)] e^{-(a^2+b^2)/2} \\ &= \int_0^\infty dr \int_{-\arctan(\lambda)}^{\arctan(\lambda)} d\theta r^3 [\dot{\rho}_\theta + \cos^2(\theta) - \sin^2(\theta)] e^{-r^2/2} \\ &= \frac{4\lambda}{1+\lambda^2} + 4\dot{\rho}_\theta \arctan(\lambda) \\ &= 2\sqrt{1-\dot{\rho}_\theta^2} + 4\dot{\rho}_\theta \arctan\sqrt{\frac{1+\dot{\rho}_\theta}{1-\dot{\rho}_\theta}}. \end{aligned} \quad (\text{C9})$$

Similarly, we find for the first- and second-order terms

$$\begin{aligned} \vec{\nabla} I[0,0] \begin{pmatrix} \langle a \rangle \\ \langle b \rangle \end{pmatrix} &= 2\sqrt{\pi}(1+\dot{\rho}_\theta)^{3/2} \langle a \rangle \\ &= 2\sqrt{\pi}(1+\dot{\rho}_\theta)(\beta_1 + \beta_2), \end{aligned} \quad (\text{C10})$$

where $\beta_i = \langle \dot{v}_i \rangle_\theta / (\sqrt{2}[\sigma_{v_i}^2]_\theta)$, and

$$\begin{aligned} &\frac{1}{2} \begin{pmatrix} \langle a \rangle \\ \langle b \rangle \end{pmatrix}^T \left[\frac{\partial^2 I[0,0]}{\partial x_i \partial x_j} \right] \begin{pmatrix} \langle a \rangle \\ \langle b \rangle \end{pmatrix} \\ &= [(1+\dot{\rho}_\theta)\langle a \rangle^2 + (1-\dot{\rho}_\theta)\langle b \rangle^2](1-\dot{\rho}_\theta)\lambda \\ &\quad + 2\arctan\lambda[(1+\dot{\rho}_\theta)\langle a \rangle^2 - (1-\dot{\rho}_\theta)\langle b \rangle^2] \\ &= 2\sqrt{1-\dot{\rho}_\theta^2}(\beta_1^2 + \beta_2^2) + 8\beta_1\beta_2 \arctan\sqrt{\frac{1+\dot{\rho}_\theta}{1-\dot{\rho}_\theta}}. \end{aligned}$$

Summing the above expression with (C9) and (C10) and replacing into (C8) yields expression (8) for the joint firing rate.

2. Conditional moments

Evaluating expression (8) requires the statistics of \dot{v}_1 and \dot{v}_2 given that both neurons are at their firing threshold. To determine these statistics, we proceed as in the single-neuron case by defining new variables z_1 and z_2 , defined by $z_i = \dot{v}_i + \alpha_i v_1 + \beta_i v_2$, and request that these be independent of both v_1 and v_2 :

$$\langle z_i v_j \rangle = \langle z_i \rangle \langle v_j \rangle$$

$$\langle \dot{v}_i \rangle_\theta = \langle \dot{v}_i \rangle + \alpha_i (\langle v_1 \rangle - v_{\theta 1}) + \beta_i (\langle v_2 \rangle - v_{\theta 2}),$$

$$\begin{aligned} \text{cov}(\dot{v}_i, \dot{v}_j)_\theta &= \text{cov}(\dot{v}_i, \dot{v}_j) + \frac{1}{1 - \rho^2} \left[\rho^2 \left(\frac{\text{cov}(\dot{v}_i, v_1) \text{cov}(\dot{v}_j, v_2) + \text{cov}(\dot{v}_j, v_1) \text{cov}(\dot{v}_i, v_2)}{\text{cov}(v_1, v_2)} \right) \right. \\ &\quad \left. - \frac{\text{cov}(\dot{v}_i, v_1) \text{cov}(\dot{v}_j, v_1)}{\sigma_{v_1}^2} - \frac{\text{cov}(\dot{v}_i, v_2) \text{cov}(\dot{v}_j, v_2)}{\sigma_{v_2}^2} \right]. \end{aligned}$$

For the stationary case, it can be seen by a direct calculation that if the two neurons have identical membrane time constants ($\tau_1 = \tau_2$), then $\text{cov}(\dot{v}_i, v_j) = 0$. It follows that $\beta_1 = \beta_2 = 0$, so that the expression of the joint firing rate simplifies as

$$r_{12}^{\text{stat}} = p_\theta \frac{\sigma_{\dot{v}_1} \sigma_{\dot{v}_2}}{2\pi} \left[\sqrt{1 - \rho^2} + 2\rho \arctan \sqrt{\frac{1 + \rho}{1 - \rho}} \right].$$

3. Example of correlated populations

To illustrate possible applications of these results, we consider here in more detail the example given in the main text. We consider two populations of P neurons. Each population consists of unconnected, identical neurons, but the neurons in population 1 may differ from those of population 2. Each population receives excitatory and inhibitory inputs from an external source. The excitatory input to population 1 consists of a background input, with rate R_{e1}^{bg} , which is independent across neurons, and a shared input with rate R_{e1}^{sh} that is identical for all neurons within this population. The presence of the shared input implies that the excitatory inputs to any two neurons in population 1 are positively correlated; the strength of this correlation can be described by the correlation coefficient

$$c_{ee}^{11} = \frac{\langle N_1^p N_1^q \rangle - \langle N_1^p \rangle \langle N_1^q \rangle}{\sigma_{N_1^p} \sigma_{N_1^q}}, \quad (\text{C11})$$

where N_1^p and N_1^q represent the number of excitatory spikes received by two neurons labeled p and q in population 1 during a small time interval. Furthermore, it is assumed that the shared inputs to population 1 are cross correlated with the shared input to population 2; the strength of this correlation is described by a second correlation coefficient c_{ee}^{12} defined in a

for $i, j = 1, 2$. This gives

$$\begin{bmatrix} \sigma_{v_1}^2 & \text{cov}(v_1, v_2) \\ \text{cov}(v_1, v_2) & \sigma_{v_2}^2 \end{bmatrix} \begin{bmatrix} \alpha_i \\ \beta_i \end{bmatrix} = - \begin{bmatrix} \text{cov}(\dot{v}_i, v_1) \\ \text{cov}(\dot{v}_i, v_2) \end{bmatrix},$$

which is solved by

$$\begin{aligned} \alpha_i &= \frac{1}{1 - \rho^2} \left[\rho^2 \frac{\text{cov}(\dot{v}_i, v_2)}{\text{cov}(v_1, v_2)} - \frac{\text{cov}(\dot{v}_i, v_1)}{\sigma_{v_1}^2} \right], \\ \beta_i &= \frac{1}{1 - \rho^2} \left[\rho^2 \frac{\text{cov}(\dot{v}_i, v_1)}{\text{cov}(v_1, v_2)} - \frac{\text{cov}(\dot{v}_i, v_2)}{\sigma_{v_2}^2} \right]. \end{aligned}$$

The conditional statistics can then be calculated by taking advantage of the independence property (11), which yields

similar way,

$$c_{ee}^{12} = \frac{\langle N_1^p N_2^q \rangle - \langle N_1^p \rangle \langle N_2^q \rangle}{\sigma_{N_1^p} \sigma_{N_2^q}}, \quad (\text{C12})$$

where N_2^q is the number of excitatory spikes received by neuron q in population 2. Similar definitions are also assumed for the inhibitory inputs, as well for the inputs to the second population.

Consider now the pooled output spikes of population 1: during a small time interval Δt , the number of output spikes is a random variable N_1 defined by

$$N_1 = \sum_{p=1}^P N_1^p,$$

where N_1^p is the number of spikes produced by the neuron labeled p during this time interval, and the sum runs over all neurons in population 1. The mean and variance of N_1 are therefore given by

$$\begin{aligned} \langle N_1 \rangle &= \sum_{p=1}^P \langle N_1^p \rangle = P r_1 \Delta t, \\ \sigma_{N_1}^2 &= \sum_{p,q=1}^P (\langle N_1^p N_1^q \rangle - \langle N_1^p \rangle \langle N_1^q \rangle) \\ &= \sum_{p=1}^P \sigma_{N_1^p}^2 + \sum_{\substack{p,q=1 \\ p \neq q}}^P \text{cov}(N_1^p, N_1^q) \quad (\text{C13}) \end{aligned}$$

$$= P r_1 \Delta t + P(P-1)(r_{11} - r_1^2) \Delta t^2, \quad (\text{C14})$$

where r_1 is the firing rate of a single neuron [calculated with Eq. (5)], and r_{11} is the joint firing rate for a pair of neurons in population 1 [calculated with Eq. (8)]. In deriving (C14), we have assumed that the time step Δt is sufficiently small so that the number of action potentials emitted by a single neuron N_1^p can be approximated by a Bernoulli random variable (i.e., $r_1 \Delta t \ll 1$). The covariance of the number of spikes of the two populations is given by

$$\text{cov}(N_1, N_2) = \sum_{p,q=1}^P (\langle N_1^p N_2^q \rangle - \langle N_1^p \rangle \langle N_2^q \rangle) = P^2(r_{12} - r_1 r_2) \Delta t^2, \quad (\text{C15})$$

where N_2 refers to the spikes of population 2. The correlation coefficient of N_1 and N_2 is thus given by

$$c_{\text{out}} = \frac{\left(\frac{P}{P-1}\right)(r_{12} - r_1 r_2)}{\sqrt{\left[r_{11} - r_1^2 + \frac{r_1}{(P-1)\Delta t}\right] \left[r_{22} - r_2^2 + \frac{r_2}{(P-1)\Delta t}\right]}}, \quad (\text{C16})$$

where the terms dependent on the time step are of the order of P^{-1} . For sufficiently large populations,

$$c_{\text{out}} \rightarrow \frac{r_{12} - r_1 r_2}{\left[r_{11} - r_1^2\right]^{1/2} \left[r_{22} - r_2^2\right]^{1/2}} \quad (P \rightarrow \infty)$$

becomes independent of the time interval considered.

The Gaussian approximation for this model is constructed as follows. As in the single-neuron case, we write the system (C1)–(C6) as

$$\frac{d\vec{z}}{dt} = A\vec{z} + \vec{\mu} + B\vec{\xi}(t),$$

where $\vec{\xi}$ is a multidimensional white noise, and

$$\begin{aligned} \vec{z} &= (v_\alpha(t), x_\alpha(t), y_\alpha(t), v_\beta(t), x_\beta(t), y_\beta(t))^T, \\ A &= \begin{pmatrix} -1/\tau_\alpha(t) & E_e - \langle v_\alpha(t) \rangle & E_i - \langle v_\alpha(t) \rangle & 0 & 0 & 0 \\ 0 & -1/\tau_e & 0 & 0 & 0 & 0 \\ 0 & 0 & -1/\tau_i & 0 & 0 & 0 \\ 0 & 0 & 0 & -1/\tau_\beta(t) & E_e - \langle v_\beta(t) \rangle & E_i - \langle v_\beta(t) \rangle \\ 0 & 0 & 0 & 0 & -1/\tau_e & 0 \\ 0 & 0 & 0 & 0 & 0 & -1/\tau_i \end{pmatrix}, \\ B(t) &= \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \sigma_{x_\alpha}(t) \sqrt{2(1 - c_{ee}^{\alpha\beta}(t)^2)/\tau_e} & 0 & 0 & \sigma_{x_\alpha}(t) c_{ee}^{\alpha\beta}(t) \sqrt{2/\tau_e} & 0 \\ 0 & 0 & \sigma_{y_\alpha}(t) \sqrt{2(1 - c_{ii}^{\alpha\beta}(t)^2)/\tau_i} & 0 & 0 & \sigma_{y_\alpha}(t) c_{ii}^{\alpha\beta}(t) \sqrt{2/\tau_i} \\ 0 & 0 & 0 & 0 & \sigma_{x_\beta} \sqrt{2/\tau_e} & 0 \\ 0 & 0 & 0 & 0 & 0 & \sigma_{y_\beta} \sqrt{2/\tau_i} \end{pmatrix}, \\ \vec{\mu}(t) &= (E_\alpha(t)/\tau_\alpha(t), 0, 0, E_\beta(t)/\tau_\beta(t), 0, 0)^T. \end{aligned}$$

The noise amplitudes are defined by $\sigma_{x_\alpha}^2 = J_\alpha^2 \tau_e (R_{e\alpha}^{\text{bg}} + R_{e\alpha}^{\text{sh}})/2$, where J_e denotes the size of the jump in excitatory conductance after an excitatory spike is received, and with a similar definition for the inhibitory noise terms σ_{y_α} . The statistics of the velocities \dot{v}_α and \dot{v}_β can be obtained from the covariance matrix C using $\sigma_{v_\alpha}^2 = (ACA^T)_{11}$, $\sigma_{v_\beta}^2 = (ACA^T)_{44}$, and $\text{cov}(\dot{v}_\alpha, \dot{v}_\beta) = (ACA^T)_{14}$. The equations for the mean $\langle z \rangle$ and covariance matrix C ,

$$\frac{d}{dt} \langle z \rangle = A \langle z \rangle + \vec{\mu}, \quad \frac{d}{dt} C = AC + CA^T + BB^T,$$

are integrated twice with $(\alpha, \beta) = (1, 1)$ and $(2, 2)$, which yields the firing rates r_1, r_2 and the joint firing rates r_{11}, r_{22} , and a third time with $(\alpha, \beta) = (1, 2)$ to obtain the joint firing rate r_{12} . The correlation coefficient c_{out} between the pooled outputs of the two populations is then calculated using Eq. (C16).

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