PHYSICAL REVIEW E **110**, 034303 (2024)

Rosetta stone for the population dynamics of spiking neuron networks

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(Received 8 November 2021; accepted 30 July 2024; published 4 September 2024)

Populations of spiking neuron models have densities of their microscopic variables (e.g., single-cell membrane potentials) whose evolution fully capture the collective dynamics of biological networks, even outside equilibrium. Despite its general applicability, the Fokker-Planck equation governing such evolution is mainly studied within the borders of the linear response theory, although alternative spectral expansion approaches offer some advantages in the study of the out-of-equilibrium dynamics. This is mainly due to the difficulty in computing the state-dependent coefficients of the expanded system of differential equations. Here, we address this issue by deriving analytic expressions for such coefficients by pairing perturbative solutions of the Fokker-Planck approach with their counterparts from the spectral expansion. A tight relationship emerges between several of these coefficients and the Laplace transform of the interspike interval density (i.e., the distribution of first-passage times). "Coefficients" like the current-to-rate gain function, the eigenvalues of the Fokker-Planck operator and its eigenfunctions at the boundaries are derived without resorting to integral expressions. For the leaky integrate-and-fire neurons, the coupling terms between stationary and nonstationary modes are also worked out paving the way to accurately characterize the critical points and the relaxation timescales in networks of interacting populations.

DOI: 10.1103/PhysRevE.110.034303

I. INTRODUCTION

As in many other complex systems like macroscopic bodies composed of atoms and molecules [1], the collective dynamics of a network of neurons can be effectively described looking at the time evolution of the density function p of its microscopic state variables. This density changes in time according to the following continuity equation:

$$\partial_t p = -\vec{\nabla} \cdot \vec{S}_p, \tag{1}$$

where $\vec{S}_p$ is the net flux of particles, i.e., the probability current of neurons flowing out from an infinitesimal volume of the phase space. Neurons interact by exchanging action potentials, the "spikes," which are brief and stereotyped messages traveling along their axons. Given a ionic current I a neuron receives through its membrane, the timing of the spikes it emits can be faithfully reproduced by generalized integrate-and-fire (IF) neuron models [2,3]. In general, I depends also on the membrane potential as ionic conductances are voltage-gated [4,5]. The core state-variable of IF neurons is the somatic potential $V(t)$ integrating the input $I(V,t)$ as

$$\frac{dV}{dt} = F(V) + \frac{I(V,t)}{C_m}. \tag{2}$$

Here C_m is the membrane capacitance set to 1 by expressing I in units of voltage per time, and $F(V)$ is the drifting current determining the model-specific relaxation dynamics towards the equilibrium potential $V = 0$ [5]. $F(V)$ incorporates the decay time τ of the free membrane potential. When $V(t)$ crosses the threshold value v_{thr}, a spike is emitted and the membrane potential is reset to $V = v_{\text{res}}$ for a refractory period τ_0 past which the subthreshold dynamics (2) is restored.

Additional state variables such as synaptic conductances or activity-dependent ionic currents can be in principle incorporated to make more realistic the single-neuron spiking activity [4,5]. However, one-dimensional IF neurons preserve without loss of generality, all the key features of the network dynamics of interest here. In this framework the synaptic current is given by the combination $I(V,t) = \sum_{i=1}^{K} J_i(V) \sum_k \delta(t - t_{i,k} - d_i)$, where K is the number of presynaptic neurons and $J_i(V)$ is the synaptic efficacy, i.e., the instantaneous change of $V(t)$ each spike emitted at time $t_{i,k}$ by the presynaptic neuron i induces after the axonal delay d_i.

For mammalian cortical networks it is reasonable to assume a large number of presynaptic contacts ($K \to \infty$) and relatively small excitatory and inhibitory synaptic efficacies ($J_i \to 0$) [6,7]. In this limit, $I(V,t)$ can be linearized ($\partial_V J_i \simeq 0$) [5,8,9] making it independent from V, and the diffusion limit holds provided that the excitatory and inhibitory J_i are properly balanced [4,5]. The current is then well approximated by a (in general nonstationary) Gaussian noise [10,11]

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with infinitesimal mean $\mu(t)$ and variance $\sigma^2(t)$

$$\begin{aligned}\mu(\nu) &= KJ\nu(t) + \mu_{\mathrm{ext}}(t)\\ \sigma^2(\nu) &= KJ^2(1+\Delta^2)\nu(t) + \sigma^2_{\mathrm{ext}}(t).\end{aligned} \tag{3}$$

For the sake of simplicity, here we considered a homogeneous population of neurons with firing rate $\nu(t) = \lim_{K\to\infty} 1/K \sum_{i=1}^{K} \sum_k \delta(t - t_{i,k} - d_i)$ with $d_i = 0$ and synaptic efficacies randomly distributed with mean $J = \mathbb{E}(J_i)$ and standard deviation $\Delta J = \mathbb{E}[(J_i - J)^2]^{1/2}$. The recurrent synaptic input linearly depends on the activity $\nu(t)$ of the homogeneous population which can be either excitatory ($J > 0$) or inhibitory ($J < 0$). The nonrecurrent synaptic input contributes to the excitation-inhibition balance needed for the diffusion limit. It is assumed to originate from other excitatory and inhibitory networks, and it is incorporated as an additional mean $\mu_{\mathrm{ext}}(t)$ and variance $\sigma^2_{\mathrm{ext}}(t)$. In what follows we will refer to the more general case of voltage-gated conductances, such that both μ and σ^2 depend also on V as $J = J(V)$, thus making use of the linearized Eq. (3) only when explicitly specified.

By incorporating the above stochastic current in Eq. (2), a Langevin equation for the membrane potential of a single neuron results:

$$dV = [F(V) + \mu]dt + \sigma dW. \tag{4}$$

Here $W(t)$ is the standard Wiener process with 0 mean and $\langle dW(t)dW(t')\rangle = \delta(t - t')dt$. Note that, as the infinitesimal moments in Eq. (3) depend on time via the firing rate $\nu(t)$, $V(t)$ is in general a inhomogeneous stochastic process [12,13] leading to a faithful description of the out-of-equilibrium population dynamics. In homogeneous populations of N neurons with similar single-neuron parameters like v_{thr}, v_{res}, and τ, and constant connection likelihood $\epsilon = K/N$, the membrane potentials of different cells can be seen as independent stochastic realizations of the same Eq. (4). In the cortical network limit such independence is granted by having $J \to 0$, while the central limit theorem with $K \to \infty$ leads to have input currents with the same μ and σ^2. This implies that the presynaptic firing rate $\nu(t)$ is the same for all the neurons, and it is equivalent to the instantaneous rate of spikes emitted by the whole population per neuron, i.e., the population firing rate. Thus, although two generic neurons are not directly influencing each other, they both have dynamics conditioned by the same collective activity of the network.

This "extended" mean-field approximation [14] including also the fluctuation size σ of the "field" (i.e., the synaptic current), is the foundation of the so-called population density approach [12,13,15–17]. In this framework, the continuity equation (1) reduces to the following Fokker-Planck equation:

$$\partial_t p = -\partial_v S_p = -\partial_v[(F+\mu)p] + \tfrac{1}{2}\partial_v^2(\sigma^2 p) \equiv \mathcal{L}\, p, \tag{5}$$

where $\mathcal{L} = -\partial_v A + \partial_v^2 B$ is the Fokker-Planck operator with drift (A) and diffusion (B) coefficients

$$\begin{aligned}A(v,t) &= F(v) + \mu(v,t)\\ B(v,t) &= \tfrac{1}{2}\sigma^2(v,t).\end{aligned} \tag{6}$$

The firing rate is the flux of realizations (i.e., neurons) crossing the emission threshold v_{thr}

$$\nu(t) = S_p(v_{\mathrm{thr}}) = -\tfrac{1}{2}\partial_v(\sigma^2 p)|_{v=v_{\mathrm{thr}}}, \tag{7}$$

resulting from Eq. (5) by setting $p(v_{\mathrm{thr}}, t) = 0$ as v_{thr} is an absorbing barrier for the diffusive process $V(t)$ [4].

Finding the general solutions of Eq. (5) is challenging, and this is due to two main reasons. First, the Fokker-Planck operator depends on ν via the moments μ and σ^2 as in Eq. (3). As the firing rate depends on $p(v,t)$ from Eq. (7), it makes $\mathcal{L} = \mathcal{L}(p)$. Eq. (5) is thus a nonlinear partial differential equation. Second, when a neuron emits a spike, it does not disappear even if it is "absorbed" in v_{thr}. Actually, its dynamics is restored after resetting the membrane potential to v_{res}. This guarantees that the number of neurons is conserved, i.e., $\int_{v_{\mathrm{min}}}^{v_{\mathrm{thr}}} p(v,t)dv = 1$ at any time t. Such reset is incorporated in Eq. (5) by reentering the exiting flux of realizations in v_{thr} as a pointlike source $\delta(v - v_{\mathrm{res}})\nu(t - \tau_0)$. This source gives rise to a peculiar boundary condition: $S_p({v_{\mathrm{res}}}^+) - S_p({v_{\mathrm{res}}}^-) = \nu(t - \tau_0)$. As a result, the flux $S_p(v)$ is nonvanishing even under stationary conditions [12,15,18,19], leading to a breaking of the so-called potential condition [20] usually holding in equilibrium statistical physics as a consequence of the principle of detailed balance.

In addition to the numerical integration of the partial differential equations (1) and (5) [16,21–23], their analytical characterization is mainly investigated via the linear response theory dealing with the small deviations from the equilibrium states [12,17–19,24–27]. Due to its derivation intricacy only few valuable attempts have been pursued investigating perturbatively nonlinear dynamical regimes like limit cycles [12,28].

An alternative approach is to expand the density p as a linear combination of the eigenfunctions $\phi_n(v)$ of the Fokker-Planck operator $\mathcal{L}$

$$\mathcal{L}\phi_n = \lambda_n \phi_n, \tag{8}$$

corresponding to the eigenvalues λ_n, i.e., the spectrum of $\mathcal{L}$. First adopted in Refs. [15,18] to study the population dynamics of neuronal networks, this is a standard approach in statistical physics [20,29]. It is reminiscent of the time-dependent Hartree-Fock theory in quantum mechanics [30] where the basis $\{\phi_n\}_{n\in\mathbb{Z}}$ moves in time following the system evolution. Indeed, $\mathcal{L}$—and hence ϕ_n—depends parametrically on the time-dependent firing rate [13,15]. Interestingly, the nonstationary modes ϕ_n associated to the nonvanishing eigenvalues λ_n of $\mathcal{L}$, display a hierarchy of timescales [13,15,31] such that only the slowest modes of the spectrum contribute to the firing rate dynamics making it low-dimensional [13,18,32].

This elegant "spectral expansion" approach is particularly well suited to describe the out-of-equilibrium dynamics of neuronal networks as it does not rely on the perturbations of equilibrium states. However, it comes at a price: The coefficients of such expansion taking into account recurrent and external synaptic couplings, involve integrals that only in simplified models can be analytically solved [13,17]. Not only, if the firing rate fluctuates due to a broadband input from upstream neurons—or endogenously expressed in finite-size networks (i.e., composed of a finite number of neurons)—are taken into account, the approach requires to manage series which are not easily summable. This is an issue typically arising when second-order statistics like the Fourier power-spectrum $P_\nu(\omega) = |\nu(\omega)|^2$ is studied under stationary conditions [13,33,34].

Starting from such remarks, here we address the following question: Is there any way to exploit the advantages of both the perturbative and the spectral expansion approach to overcome their intrinsic limitations? In what follows we aim at using the relaxation dynamics of an uncoupled set of neurons and the response to small perturbations of a coupled network as a "Rosetta stone." This will allow us to translate some key expressions with a closed form in both linear response and renewal theory into compact and manageable sum of series and state-dependent coefficients for the spectral expansion approach. The results of this effort pave the way to a further exploitation of the spectral expansion to investigate the out-of-equilibrium dynamics of spiking neuron networks.

II. MATCHING THE RELAXATION OF $\nu(t)$

Single-compartment IF neurons with Markovian dynamics (4) and fixed reset potential are renewal processes. If the moments of the stochastic input current do not change in time, then the well-established renewal theory for this kind of stochastic processes fully characterize the probability density of the interspike intervals (ISIs) as a first-passage time problem. Here we show that the approach of the spectral expansion of the Fokker-Planck operator for a set of independent IF neurons can be directly related to the ISI density derived from the renewal theory. Matching these two equivalent descriptions of uncoupled neurons, allows us to derive the exact sum of a family of series that relates to the eigenvalues of the Fokker-Planck operator. As a result, we solve some notable integral expressions and specific useful values of the eigenfunctions of the Fokker-Planck operator. Starting from this the moments of ISI are worked out leading for instance to a novel formula for the so-called current-to-rate gain function, i.e., the asymptotic firing rate of neurons.

A. Relaxation dynamics from the renewal theory

Under stationary condition and in presence of synaptic current fluctuations ($\sigma \neq 0$), the collective firing rate $\nu(t)$ of a set of uncoupled IF neurons always approaches an equilibrium point ν_0. Due to the reset mechanism following the emission of a spike, spike trains emitted by IF neurons are renewal point processes. As such, ISIs separating two consecutive spikes do not depend on the ISIs occurred before. Finding the probability $\rho(t)dt$ to have an ISI in the interval $[t, t+dt]$ is a first-passage time problem [4], since it requires to know when $V(t)$ crosses the threshold v_{thr} for the first time starting from $V(0) = v_{\mathrm{res}}$. With this initial condition, the ISI density can be interpreted as the probability of first-spike occurrence $\rho_1(t) \equiv \rho(t)$, leading to recursively define the density $\rho_k(t)$ of the time until the kth emitted spike as

$$\rho_k(t) = \int_0^t \rho(\tau)\rho_{k-1}(t-\tau)d\tau. \tag{9}$$

This "renewal equation" [4,5] allows to derive the "spike-triggered firing rate," i.e., the mean density of spikes emitted by an isolated IF neuron at time t

$$\nu(t) = \sum_{k=1}^{\infty} \rho_k(t), \tag{10}$$

which in turn is equivalent to the relaxation to equilibrium of the firing rate $\nu(t)$.

The firing rate in Eq. (10) has a straightforward Laplace trasform $\hat{\nu}(s) \equiv \int_0^\infty \nu(t)e^{-st}dt$. Indeed, being $\rho_k(t)$ a convolution, Eq. (9) reduces to

$$\hat{\rho}_k(s) = \hat{\rho}(s)\hat{\rho}_{k-1}(s) = \hat{\rho}(s)^k.$$

Introducing it in Eq. (10), $\hat{\nu}(s)$ results to be

$$\begin{aligned}\hat{\nu}(s) &= \sum_{k=1}^{\infty} \hat{\rho}_k(s) = \sum_{k=1}^{\infty} \hat{\rho}(s)^k = \frac{1}{1-\hat{\rho}(s)} - 1 \\ &= \frac{\hat{\rho}(s)}{1-\hat{\rho}(s)}.\end{aligned} \tag{11}$$

This equation establishes a direct nonlocal relationship between the firing rate of a homogeneous pool of independent neurons and the ISI density of a single cell [5,35].

B. Relaxation dynamics from the spectral expansion

The firing rate $\nu(t)$ of the mentioned set of independent neurons can be alternatively derived by expanding the density $p(v,t)$ in Eq. (5) as

$$p(v,t) = \sum_n a_n(t)\phi_n(v),$$

where $\phi_n(v)$ are the eigenfunctions defined in Eq. (8), and $a_n(t) = \langle\psi_n|p\rangle = \int_{v_{\min}}^{v_{\mathrm{thr}}} \psi_n(v)p(v,t)dv$ are the projections of p on the same modes (i.e., eigenfunctions). The infinite set $\{\psi_n(v), \phi_n(v)\}$ with $n \in \mathbb{Z}$, is an orthonormal basis such that $\langle\psi_n|\phi_m\rangle = \delta_{nm}$ [13,15]. Here $\psi_n(v)$ are the eigenfunctions of the adjoint operator $\mathcal{L}^\dagger = A\partial_v + B\partial_v^2$ defined as $\langle\mathcal{L}^\dagger\psi_n|\phi_n\rangle \equiv \langle\psi_n|\mathcal{L}\phi_n\rangle$, and having the same spectrum as in Eq. (8):

$$\mathcal{L}^\dagger\psi_n = \lambda_n\psi_n. \tag{12}$$

In the following we will refer to the solution of Eq. (12) for an arbitrary complex $\lambda_n = s$ value as $\psi(v,s)$. The "expanded" p in the Fokker-Planck equation leads to the following equivalent dynamics for the projections a_n:

$$\begin{aligned}\dot{\vec{a}} &= \mathbf{\Lambda}\vec{a} \\ \nu &= \Phi + \vec{f}\cdot\vec{a},\end{aligned} \tag{13}$$

where the contribution due to the stationary mode ($n = 0$ with $\lambda_0 = 0$ and $a_0 = 1$) has been isolated, and a matrix formalism has been adopted such that $\{\vec{a}\}_n = a_n$ and $\{\mathbf{\Lambda}\}_{nm} = \lambda_n\delta_{nm}$ with $m, n \neq 0$ [13,15]. The current-to-rate gain function

$$\Phi(\mu,\sigma) = S_{\phi_0}(v_{\mathrm{thr}}) = -\tfrac{1}{2}\partial_v^2(\sigma^2\phi_0)|_{v=v_{\mathrm{thr}}} \tag{14}$$

is the flux of realization crossing v_{thr} under stationary condition, i.e., the asymptotic firing rate ν_0. The flux due to the nonstationary modes (ϕ_n with $n \neq 0$) are instead the elements of the infinite vector $\vec{f}$, which can be conveniently set to $f_n = 1/\tau$ [36].

The linear system (13) has a straightforward solution having constant coefficients (μ and σ do not depend on time):

$$\begin{aligned}\vec{a}(t) &= e^{\mathbf{\Lambda} t}\vec{a}(0)\\ \nu(t) &= \Phi + \vec{f}\cdot\vec{a}.\end{aligned} \tag{15}$$

As all neurons have a starting membrane potential $V(0) = v_{\mathrm{res}}$, $p(v,0) = \delta(v - v_{\mathrm{res}})$ and the initial value of the projections result to be

$$a_n(0) = \langle \psi_n | p(v,0)\rangle = \psi_n(v_{\mathrm{res}}).$$

Written explicitly, Eq. (15) gives the relaxation dynamics

$$\nu(t) = \Phi + \frac{1}{\tau}\sum_{n=1}^{\infty}\psi_n(v_{\mathrm{res}})e^{\lambda_n t}. \tag{16}$$

C. ISI moments and sums in the spectral expansion

A first sum of coefficients from the spectral expansion results by setting $t = 0$ in the relaxation dynamics (15):

$$\Phi = -\vec{f}\cdot\vec{\psi}_{\mathrm{res}} \equiv -\frac{1}{\tau}\sum_{n\neq 0}\psi_n(v_{\mathrm{res}}), \tag{17}$$

where we took into account that $\nu(0) = 0$. To our knowledge, this is a novel expression to carry out the current-to-rate gain function $\Phi(\mu,\sigma)$ for any IF neuron model.

We anticipate that this is only a particular case of a more general result. Indeed, the Laplace transform $\hat{\nu}(s)$ from the renewal theory in Eq. (11) can be directly compared to the one resulting from the firing rate equation (13). In this case we have

$$\begin{aligned} s\,\hat{\vec{a}}(s) - \vec{a}(0) &= \mathbf{\Lambda}\,\hat{\vec{a}}(s)\\ \hat{\nu}(s) &= \frac{\Phi}{s} + \vec{f}\cdot\hat{\vec{a}}(s),\end{aligned}$$

leading to $\hat{\vec{a}}(s) = (s\mathbf{I} - \mathbf{\Lambda})^{-1}\vec{\psi}_{\mathrm{res}}$, and eventually to

$$\hat{\nu}(s) = \frac{\Phi}{s} + \vec{f}\cdot(s\mathbf{I} - \mathbf{\Lambda})^{-1}\vec{\psi}_{\mathrm{res}}. \tag{18}$$

Recalling Eq. (11) and comparing the two transform $\hat{\nu}(s)$ we obtain:

$$\frac{\hat{\rho}(s)}{1 - \hat{\rho}(s)} - \frac{\Phi}{s} = \vec{f}\cdot(s\mathbf{I} - \mathbf{\Lambda})^{-1}\vec{\psi}_{\mathrm{res}} \equiv h(s), \tag{19}$$

highlighting a tight relationship between the ISI density $\rho(t)$, the eigenvalues λ_n and $\vec{\psi}_{\mathrm{res}}$.

From Eq. (19) other sums can be worked out recalling that the ISI moments $\langle(-t)^k\rangle = \lim_{s\to 0}\frac{d^k\rho(s)}{ds^k}$. We then perform the same limit on both hand sides of the equation resorting to the l'Hôpital's rule and finding that

$$\lim_{s\to 0} h(s) = \frac{\Phi\langle t^2\rangle - 2\langle t\rangle}{2\langle t\rangle}.$$

Here, considering that the gain function $\Phi = 1/\langle t\rangle$ and that $h(0) = -\vec{f}\cdot\mathbf{\Lambda}^{-1}\vec{\psi}_{\mathrm{res}}$, we obtain

$$h(0) = \frac{c_v^2 - 1}{2} = -\frac{1}{\tau}\sum_{n\neq 0}\frac{\psi_n(v_{\mathrm{res}})}{\lambda_n}, \tag{20}$$

where $c_v = \sqrt{\langle t^2\rangle - \langle t\rangle^2}/\langle t\rangle$ is the coefficient of variation of the ISIs.

We remark that other sums can be worked out deriving by s both hand sides of Eq. (19) and taking the limit $s \to 0$. Indeed, in this limit the derivatives of $h(s)$ reduce to

$$\left.\frac{d^k h}{ds^k}\right|_{s\to 0} = -k!\vec{f}\cdot\mathbf{\Lambda}^{-(k+1)}\vec{\psi}_{\mathrm{res}} = -\frac{k!}{\tau}\sum_{n\neq 0}\frac{\psi_n(v_{\mathrm{res}})}{\lambda_n^{k+1}}$$

for any $k > 0$.

D. Eigenvalues λ_k and eigenfunction values $\psi_k(v_{\mathrm{res}})$

We can further exploit Eq. (19) by making use of the Cauchy's residue theorem. Indeed,

$$\mathrm{Res}_{s=\lambda_k} h(s) = \mathrm{Res}_{s=\lambda_k}\frac{\hat{\rho}(s)}{1 - \hat{\rho}(s)} = \psi_k(v_{\mathrm{res}}) \tag{21}$$

for $\lambda_k \neq 0$. This allows us to work out from the Laplace transform of the ISI probability density the value of the kth eigenfunction of $\mathcal{L}^\dagger$ at $v = v_{\mathrm{res}}$. In this way $\psi_k(v_{\mathrm{res}})$ can be found without explicitly knowing neither the analytic expression for $\psi(v,s)$ nor the exact value of the λ_k. As $s = \lambda_k$ are poles of $h(s)$, a generic line integral of $\hat{\rho}/(1 - \hat{\rho})$ around each eigenvalues will give $\psi_k(v_{\mathrm{res}})$.

Note that, being $h(0)$ in Eq. (20) a finite function of the ISI c_v, $h(s)$ has no poles in 0. Thus, the above residue of $h(s)$ in $s = \lambda_0 = 0$—the eigenvalue of the stationary mode—is 0. This allows to derive from Eqs. (19) and (21) an alternative expression for the current-to-rate gain function:

$$\Phi = \mathrm{Res}_{s=0}\frac{\hat{\rho}(s)}{1 - \hat{\rho}(s)} = \psi_0(v_{\mathrm{res}}). \tag{22}$$

In principle, this general result can lead to work out novel analytic expressions for the gain functions of specific neuron models, as we will show later.

Similarly, the eigenvalues λ_k can be obtained without resorting to a often complicated minimization procedure as

$$\frac{\mathrm{Res}_{s=\lambda_k} s\,h(s)}{\mathrm{Res}_{s=\lambda_k} h(s)} = \frac{\lambda_k\psi_k(v_{\mathrm{res}})}{\psi_k(v_{\mathrm{res}})} = \lambda_k. \tag{23}$$

Interestingly, from the Cauchy theorem the residues can be computed as contour integrals including the singularity λ_k. This provides an effective numerical way to compute eigenvalues starting from approximated guesses. We will exploit this approach in the following for the specific case of leaky integrate-and-fire neurons.

E. Spectral equation for λ_k from $\hat{\rho}(s)$

The link between the spectrum of $\mathcal{L}^\dagger$ and $\hat{\rho}(s)$ pointed out by Eq. (19) should not be surprising as $\rho(t)$ is the density of a first-passage time. As such, $\rho(t)$ conditioned to have $V(0) = v_{\mathrm{res}}$ and $V(t) = v_{\mathrm{thr}}$, solves the backward Kolmogorov equation [4,35]

$$\partial_t\rho = A(v_{\mathrm{res}})\partial_{v_{\mathrm{res}}}\rho + B(v_{\mathrm{res}})\partial^2_{v_{\mathrm{res}}}\rho = \mathcal{L}^\dagger_{v_{\mathrm{res}}}\rho, \tag{24}$$

with boundary condition $\rho(t)|_{v_{\mathrm{res}}=v_{\mathrm{thr}}} = \delta(t)$. Here the coefficients A and B in Eq. (6) are evaluated at $v = v_{\mathrm{res}}$ and do not explicitly depend on time t. For the sake of clarity, we write explicitly the dependence of the operator $\mathcal{L}^{\dagger}_{v_{\rm res}}$ on the initial value of the membrane potential.

Performing the Laplace transform of both hand sides of the above equation we obtain

$$-\rho(t)|_{t=0} + s\hat{\rho}(s) = \mathcal{L}^{\dagger}_{v_{\rm res}}\hat{\rho}(s)$$

with $\hat{\rho}(s)$ the Laplace transform of the ISI density implicitly depending on $v_{\rm thr}$. In the case of interest, $v_{\rm res} < v_{\rm thr}$ and no spikes are emitted at $t = 0$ such that $\rho(t)|_{t=0} = 0$ and the above equation reduces to

$$\big(\mathcal{L}^{\dagger}_{v_{\rm res}} - s\big)\hat{\rho}(v_{\rm res}, s) = 0,$$

where we made explicit the dependence of $\hat{\rho}$ on the initial potential $v_{\rm res}$. As pointed out in [37], this is exactly the same equation for the eigenfunctions $\psi_k(v) = \psi(v, \lambda_k)$ provided that $s = \lambda_k$ leading to the equivalence:

$$\hat{\rho}(v_{\rm res}, s) = a(s)\psi(v_{\rm res}, s).$$

The arbitrary function $a(s)$ can be derived taking into account the boundary condition $\rho(v_{\rm thr}, t) = \delta(t)$ leading to $\hat{\rho}(v_{\rm thr}, s) = 1$ and hence to $a(s) = 1/\psi(v_{\rm thr}, s)$, allowing to recover the known relationship [37]

$$\hat{\rho}(s) = \frac{\psi(v_{\rm res}, s)}{\psi(v_{\rm thr}, s)}. \tag{25}$$

Following Ref. [38], this equation allows to derive a spectral equation to determine the eigenvalues λ_k. Indeed, from the boundary condition associated to the conservation of flux of realizations exiting from $v_{\rm thr}$ and reentering in $v_{\rm res}$ after the emission of spike, we have $\psi(v_{\rm res}, \lambda_k) = \psi(v_{\rm thr}, \lambda_k)$ [13,15,17]. Incorporating this constraint into Eq. (25) we eventually have

$$\hat{\rho}(\lambda_k) = 1, \tag{26}$$

i.e., yet another way to compute the eigenvalues of the Fokker-Planck operator in Eq. (8) as previously derived in Ref. [38].

F. Normalization factor of eigenfunctions $\psi_k(v)$

As summarized at the beginning of this section, the spectral expansion of the population density relies on the assumption that the eigenfunctions $\psi_k(v)$ and $\phi_k(v)$ are orthonormal, i.e.,

$$\langle\psi_n|\phi_m\rangle = \int_{v_{\rm min}}^{v_{\rm thr}} \psi_n(v)\phi_m(v)dv = \delta_{nm}.$$

Such condition is guaranteed by normalizing the generic solution of the equation $(\mathcal{L}^{\dagger} - \lambda_k)\tilde{\psi}_k = 0$ by a factor Z_k in order to have $\psi_k \equiv \tilde{\psi}_k/Z_k$ and

$$Z_k = \langle\tilde{\psi}_k|\phi_k\rangle = \int_{v_{\rm min}}^{v_{\rm thr}} \tilde{\psi}_k(v)\phi_k(v)dv.$$

This integral expression requires to know explicitly the eigenfunctions of both $\mathcal{L}$ and $\mathcal{L}^{\dagger}$. Not only, even when they are available, a closed form of this integral is difficult to be obtained. Hence, its numerical evaluation is required even when the integration domain is infinite, as usually $v_{\rm min} \to -\infty$, eventually making the computation of Z_k demanding.

Even in this case, a way out to this issue is offered by the residue theorem starting from the knowledge of $\rho(s)$. Indeed, inserting Eq. (25) into Eq. (21) we have

$${\rm Res}_{s=\lambda_k} \frac{\tilde{\psi}(v_{\rm res}, s)}{\tilde{\psi}(v_{\rm thr}, s) - \tilde{\psi}(v_{\rm res}, s)} = \psi_k(v_{\rm res}) = \frac{\tilde{\psi}_k(v_{\rm res})}{Z_k},$$

where we took into account that the normalization factor does not depend on v and thus the equivalence $\psi(v_{\rm res}, s)/\psi(v_{\rm thr}, s) = \tilde{\psi}(v_{\rm res}, s)/\tilde{\psi}(v_{\rm thr}, s)$ holds. Putting out from the residue computation the numerator which becomes $\tilde{\psi}(v_{\rm res}, s) \to \tilde{\psi}_k(v_{\rm res})$, the following expression results

$${\rm Res}_{s=\lambda_k} \frac{1}{\tilde{\psi}(v_{\rm thr}, s) - \tilde{\psi}(v_{\rm res}, s)} = \frac{1}{Z_k}, \tag{27}$$

giving the normalization factor as a limit expression without computing any integral or knowing $\phi_k(v)$. This equation can be further developed, as the limit underlying the residue can be solved resorting to the l'Hôpital's rule eventually leading to have

$$Z_k = \tilde{\psi}_k^{(1)}(v_{\rm thr}) - \tilde{\psi}_k^{(1)}(v_{\rm res}), \tag{28}$$

with $\tilde{\psi}_k^{(1)}(v) = \partial_s\tilde{\psi}(v, s)|_{s=\lambda_k}$. The above integral expression of Z_k thus reduces to a combination of derivatives of the eigenfunction $\tilde{\psi}(v, s)$. Given this integral-free normalization factor, from Eq. (22) a novel analytic expression for the current-to-rate gain function results:

$$\Phi = \frac{\tilde{\psi}_0(v_{\rm res})}{\tilde{\psi}_0^{(1)}(v_{\rm thr}) - \tilde{\psi}_0^{(1)}(v_{\rm res})}. \tag{29}$$

Note that dividing both hand sides of Eq. (28) by Z_k leads to have for any k

$$\psi_k^{(1)}(v_{\rm thr}) - \psi_k^{(1)}(v_{\rm res}) = 1. \tag{30}$$

Using this equivalence in Eq. (29), we close the loop recovering the gain function Φ expressed in Eq. (22).

G. Some remarks on eigenfunctions $\phi_k(v)$ and $\psi_k(v)$

Due to the important role played by $\psi_k(v)$ in the first-passage time problem and, as we will see later, in determining the network response to small perturbations, here we briefly derive its general expression.

The spectral equation $(\mathcal{L} - \lambda_n)\phi_n = 0$ is a second-order differential equation which can be recast into the general form

$$k_2(v)\frac{d^2\phi_n}{dv^2} + k_1(v)\frac{d\phi_n}{dv} + k_0(v, \lambda_n)\phi_n = 0, \tag{31}$$

where $k_1(v) = B(v)$, $k_2(v) = 2B'(v) - A(v)$ and $k_0(v, \lambda_n) = B''(v) - A'(v) - \lambda_n$, assuming that the coefficients in Eq. (6) do not depend on t. The solutions ϕ_n are in general a linear combination of two fundamental (i.e., independent) solutions $f_1(v, \lambda_n)$ and $f_2(v, \lambda_n)$ of the same equation [39]. The coefficients a, b, and d of the combination are determined by solving a linear system constrained by the boundary conditions of the problem (see for instance [36]):

$$\phi_n(v) = \begin{cases} a\, f_1(v, \lambda_n) + b\, f_2(v, \lambda_n) & v_{\rm res} \leqslant v \leqslant v_{\rm thr} \\ d\, f_2(v, \lambda_n) & v_{\rm min} < v \leqslant v_{\rm res} \end{cases},$$

where we arbitrarily choose $f_2(v, \lambda_n)$ to be the only solution in the domain $v \leqslant v_{\rm res}$ by imposing the proper limit at $v = v_{\rm min}$ (see below).

The eigenfunctions $\psi_n(v) = \psi(v, \lambda_n)$ of the adjoint Fokker-Planck operator $\mathcal{L}^\dagger$ can be derived resorting to the potential function $U(v)$ [20]

$$e^{U(v)} \equiv B(v) e^{-\int \frac{A(v)}{B(v)} dv}, \tag{32}$$

such that $\psi_n = e^U \phi_n$. In doing so the boundary conditions for $p(v, t)$ must be taken into account leading to request that (i) $\psi_n(v)$ and its derivative are continuous function; (ii) $\psi_n'(v_{\mathrm{min}}) = 0$ in the case $v = v_{\mathrm{min}}$ is a reflecting barrier, alternatively to consider $v_{\mathrm{min}} \to -\infty$ and $\phi_n(v_{\mathrm{min}}) \to 0$; and (iii) $\psi_n(v_{\mathrm{res}}) = \psi_n(v_{\mathrm{thr}})$ [13,15,17]. Given these conditions and the above expression for $\phi_n(v)$ the adjoint eigenfunctions are in general

$$\begin{aligned} \psi_n(v) &= \frac{f_2(v, \lambda_n)}{Z_n} e^{U(v)} \\ &= \frac{f_2(v, \lambda_n)}{Z_n B(v) \mathcal{W}(v)}, \end{aligned} \tag{33}$$

Here we make use of the known expression for the Wronskian $\mathcal{W}(v) = f_1'(v) f_2(v) - f_1(v) f_2'(v)$ which can be in general expressed as [39]

$$\mathcal{W}(v) = c\, e^{-\int \frac{k_1(v)}{k_2(v)} dv} = \frac{c}{B(v)^2} e^{\int \frac{A(v)}{B(v)} dv}. \tag{34}$$

The arbitrary constant c here can be set to 1 as it is taken into account in the normalization factor Z_n given by Eq. (27).

H. Density $\hat{\rho}(s)$ and gain $\Phi(\mu, \sigma)$ for notable neurons

The simplest model is the perfect IF (PIF) neuron introduced in Ref. [40] in which the membrane potential $V(t)$ is a diffusion Wiener process with drift, i.e., $F(V) = \mu$. In this model ISI moments are finite only if $\mu > 0$, and the ISI density $\hat{\rho}(s)$ is an inverse Gaussian whose Laplace transform is [4,35,41]

$$\hat{\rho}_{\mathrm{PIF}}(s) = \exp\left[\frac{v_{\mathrm{thr}} - v_{\mathrm{res}}}{\sigma^2}\left(\mu - \sqrt{\mu^2 + 2\sigma^2 s}\right)\right]. \tag{35}$$

From this, the first and second moments of the ISI result to be $\langle t \rangle = 1/\Phi = (v_{\mathrm{thr}} - v_{\mathrm{res}})/\mu$ and $\langle t^2 \rangle = \sigma^2/(\mu^2 \Phi)$ [4].

A generalization of the PIF neuron model is the one in which a reflecting barrier at $v_{\mathrm{min}} = 0$ is incorporated, allowing to have finite moments of the ISI also for $\mu \leqslant 0$. The model was introduced as a former "neuromorphic" implementation in VLSI circuits of an IF neuron [42]. This VLSI IF (VIF) neuron has a closed form of $\hat{\rho}(s)$ [19]:

$$\hat{\rho}_{\mathrm{VIF}}(s) = \frac{\zeta(s) e^{\xi}}{\zeta(s) \cosh[\zeta(s)] + \xi \sinh[\zeta(s)]} \tag{36}$$

with $\xi = v_{\mathrm{thr}} \mu / \sigma^2$ and $\zeta(s) = \sqrt{\xi^2 + 2 s v_{\mathrm{thr}}/\sigma^2}$, fixing the reset potential at the reflecting barrier $v_{\mathrm{res}} = v_{\mathrm{min}} = 0$.

The standard, and widely used, leaky integrate-and-fire (LIF) neuron with $F(V) = -V/\tau$ has also a closed form for the Laplace transform of the ISI density [37,43]:

$$\hat{\rho}_{\mathrm{LIF}}(s) = \frac{\sqrt{e^{x_r{}^2}} \mathcal{D}_{-s}(-\sqrt{2} x_r)}{\sqrt{e^{x_t{}^2}} \mathcal{D}_{-s}(-\sqrt{2} x_t)} \tag{37}$$

with $x_t = (v_{\mathrm{thr}} - \mu\tau)/\sigma\sqrt{\tau}$ and $x_r = (v_{\mathrm{res}} - \mu\tau)/\sigma\sqrt{\tau}$. $\mathcal{D}_\nu(z)$ is the parabolic cylinder function solution of the Weber differential equation [39].

From Eq. (25) we can rewrite $\hat{\rho}(s) = \tilde{\psi}(x_r, s)/\tilde{\psi}(x_t, s)$ simplifying the normalization factor, thus allowing to derive the eigenfunctions $\tilde{\psi}(x, s)$ for the mentioned IF neurons. For the specific case of the LIF neuron we have

$$\tilde{\psi}_{\mathrm{LIF}}(x, s) = e^{\frac{x^2}{2}} \mathcal{D}_{-s}(-\sqrt{2} x), \tag{38}$$

which for the stationary mode $s = 0$ reduces to $\tilde{\psi}_{\mathrm{LIF}}(x, 0) = 1$ [39]. The same expression can be directly derived from Eq. (33). Indeed, for the LIF neuron $A(x) = -x$ and $B = 1/2$ such that $e^{U(x)} = e^{x^2}/2$, thus to have $f_2(x, s) = e^{-x^2/2} \mathcal{D}_{-s}(-\sqrt{2} x)$ which is a fundamental solution of the related Eq. (31). Note that an alternative and equivalent expression for $\tilde{\psi}_{\mathrm{LIF}}(x, s)$ exists and it relies on confluent hypergeometric functions [43,44].

By using the above expression for $\tilde{\psi}_{\mathrm{LIF}}$ in Eq. (29) we can compute the current-to-rate gain function Φ_{LIF}:

$$\Phi_{\mathrm{LIF}}(x_r, x_t) = \frac{1}{\tilde{\psi}^{(1)}_{0,\mathrm{LIF}}(x_t) - \tilde{\psi}^{(1)}_{0,\mathrm{LIF}}(x_r)}, \tag{39}$$

with

$$\begin{aligned} \tilde{\psi}^{(1)}_{0,\mathrm{LIF}}(x) &= \partial_s \tilde{\psi}_{\mathrm{LIF}}(x, s)|_{s=0} \\ &= -e^{\frac{x^2}{2}} \mathcal{D}_0^{(1,0)}(-\sqrt{2} x) \\ &= \frac{\pi}{2} \mathrm{Erfi}(x) + x^2 \, {}_2F_2\left(\begin{matrix} 1, 1 \\ \frac{3}{2}, 2 \end{matrix}; x^2\right). \end{aligned} \tag{40}$$

Here $\mathcal{D}_0^{(1,0)}(z) = \partial_\nu \mathcal{D}_\nu(z)|_{\nu=0}$, $\mathrm{Erfi}(x)$ is the imaginary error function and ${}_2F_2(\mathbf{a}, \mathbf{b}, x)$ is the generalized hypergeometric function defined in Ref. [39]. To derive such expression we used the explicit formula for $\mathcal{D}_\nu^{(1,0)}(z)$ in Ref. [45] valid in the limit $\nu \to 0$. Note that expanding ${}_2F_2$ in series, the mean output frequency previously derived in Refs. [43,44] is recovered.

In Fig. 1 we compare this new expression and the standard current-to-rate gain function from [47,48]

$$\Phi_{\mathrm{LIF}}(x_r, x_t) = \frac{1}{\sqrt{\pi} \int_{x_r}^{x_t} \mathrm{e}^{u^2} [1 + \mathrm{erf}(u)] du}. \tag{41}$$

As expected the two Φ_{LIF} perfectly overlap. However, we remark that the numerical computation of Eq. (39) is more demanding and its stability weakens for relatively small variances σ^2.

I. Eigenvalues and relaxation $\nu(t)$ of LIF neurons

Given for these example neurons the eigenfunctions $\psi(v, s)$, we can directly test the validity of some the general equations derived in this section. To do that we first compute the eigenvalues λ_k. From Eq. (26), for the PIF neuron they result to be [38]

$$\lambda_n = -2\pi^2 \frac{\sigma^2}{(v_{\mathrm{thr}} - v_{\mathrm{res}})^2} n^2 + i 2\pi \Phi n. \tag{42}$$

As under strongly drift-dominated regime [$\mu \gg F(v_{\mathrm{thr}})$] both LIF and VIF neurons are well approximated by a PIF model, it is not surprising to see that the above expression has been

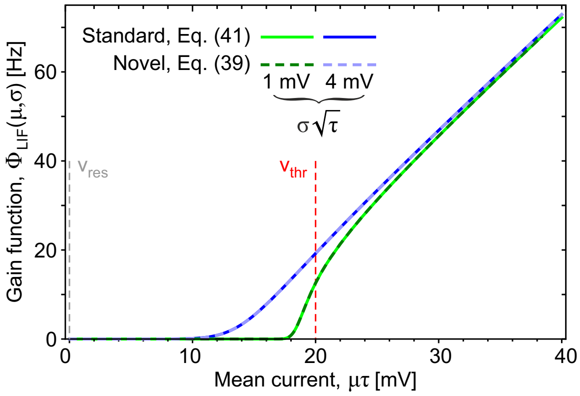

FIG. 1. Comparison of the current-to-rate gain function Φ_{LIF} from the standard Eq. (41) (solid) and the novel Eq. (39) (dashed) for two example synaptic-current variance $\sigma^2\tau = 1$ mV and 4 mV (green and blue, respectively). Φ_{LIF} is function of the current moments as $x_t = x_t(\mu, \sigma)$ and $x_r = x_r(\mu, \sigma)$ (see main text). Neuron parameters are $\tau = 20$ ms, $v_{\mathrm{thr}} = 20$ mV, and $v_{\mathrm{res}} = 0$. The code to produce this and the other figures can be found in Ref. [46].

previously worked out in both References [15,17,18] and Reference [13], respectively. Equation (42) can then be exploited as an initial guess of λ_n in order to identify a suited line integral to work out the actual eigenvalues from Eq. (23). Note that, in the regimes dominated by the current fluctuations σ, λ_n are no more well approximated by Eq. (42) as they are real [13,49]. Besides, for LIF and VIF neurons with $v_{\min} < v_{\mathrm{res}}$, an additional set of real λ_k exists [31,49,50]. These λ_k can be found and computed by searching along the real axis ($\mathrm{Im}\, s = 0$) the nonzero residues in Eq. (23).

In Fig. 2(a) the eigenvalues (circles) computed for an example set of uncoupled and identical LIF neurons is shown. As remarked, we have both complex conjugate couples and real λ_k. The eigenvalues are found at the intersection of the solution of both the real and imaginary part of the spectral equation $\rho_{\mathrm{LIF}}(s) = 1$ (red and blue curves, respectively). This confirms the reliability of the approach we introduced. Note that, also the eigenvalue $\lambda_0 = 0$ of the stationary mode is shown. In Fig. 2(b) a wider set of λ_k ($M = 100$) computed in the same way is plotted. On the one hand the complex conjugate eigenvalues are distributed along a rotated parabola, as expected from Eq. (42). On the other hand, the real λ_k display a nonuniform distribution.

With the availability of such a large number of eigenvalues for the LIF neuron, we can test the rate of convergence of some of the series derived in this section. First we look at the relaxation dynamics of $\nu(t)$ given by Eq. (16). As previously described, and not surprisingly [13,32,38], by increasing the number M of summed modes the accuracy in reproducing $\nu(t)$ at shorter timescales improves [Fig. 2(c)]. The modes included are sorted by $-\mathrm{Re}\, \lambda_k$ covering decreasing timescales ($-1/\mathrm{Re}\, \lambda_k$). For instance, as the second couple of complex conjugate λ_k in Figs. 2(a) and 2(b) is $\mathrm{Re}\, \lambda_k \tau \simeq -5$, the case $M = 4$ accurately reproduces $\nu(t)$ as $t \gg \tau/5 \simeq 4$ ms (compare light-red and black curves).

Note that, at $t < -1/\mathrm{Re}\, \lambda_M$ the estimated $\nu(t)$ from the corresponding sum of M terms in Eq. (16) blows up. This means that in the limit $t \to 0$ we need a rapidly increasing number of modes to have an accurate estimate of $\nu(t) \to 0$. This is the limit when Eq. (16) reduces to Eq. (17), meaning that the latter does not appear to be a convenient way to compute $\Phi_{\mathrm{LIF}}(\mu, \sigma)$. To make this argument clearer, in Fig. 3(a), for different $\Delta t \ll 1/\Phi_{\mathrm{LIF}}$, such that $\nu(\Delta t) \simeq 0$, we show how slowly the sum in Eq. (16) approximate Φ_{LIF} (red-dashed line). For the cases plotted ($\Delta t = \{8, 4, 2\}$ ms), M rapidly diverges in order to well approximate the asynmptotic firing rate (red dashed line, $M = \{6, 13, 31\}$, respectively). A limited rate of convergence is also apparent in Fig. 3(b), where the coefficient of variation c_v of the ISI for the same LIF neurons computed from Eq. (20) is shown by varying the number M of summed modes.

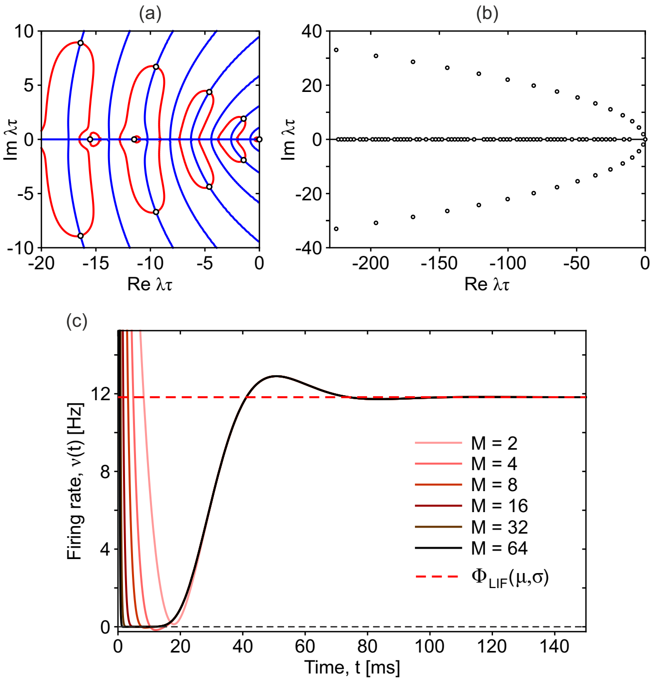

FIG. 2. Eigenvalues λ_k and relaxation dynamics of the firing rate $\nu(t)$ of an uncoupled set of LIF neurons. (a) Distribution of λ_k, roots of the spectral equation $\rho_{\mathrm{LIF}}(s) = 1$ (circles). Red and blue curves, separate solutions of $\mathrm{Re}\, \rho_{\mathrm{LIF}}(s) = 1$ and $\mathrm{Im}\, \rho_{\mathrm{LIF}}(s) = 0$, respectively. (b) Same as (a) for a wider set ($M = 100$) of λ_k computed as the ratio of residues in Eq. (23) with line integrals around the approximated guesses of the eigenvalues (see text). (c) Relaxation dynamics of $\nu(t)$ as in Eq. (16) including a finite number M of eigenmodes (those with greatest $\mathrm{Re}\, \lambda_k$). Only the real part of the sum is taken, as with $M = \{2, 4, 8, 16, 32, 64\}$ not all the complete pairs of complex conjugate λ_k are necessarily selected. Red dashed line, stationary firing rate $\Phi_{\mathrm{LIF}}(\mu, \sigma) = 11.8$ Hz. Neuron parameters: $\tau = 20$ ms, $v_{\mathrm{thr}} = 20$ mV, $v_{\mathrm{res}} = 0$ mV, $\mu\tau = 17$ mV, and $\sigma\sqrt{\tau} = 4.5$ mV.

III. LINEAR RESPONSE AS A “ROSETTA STONE”

Since now, we focused on a set of uncoupled spiking neurons. In other words, the expressions we derived pertain to the single-neuron domain. However, a similar approach facing the spectral expansion and the perturbative description of the population dynamics can be further extended. In this section we focus on this aspect, complementing our “Rosetta stone” approach to the case of the linear response theory of

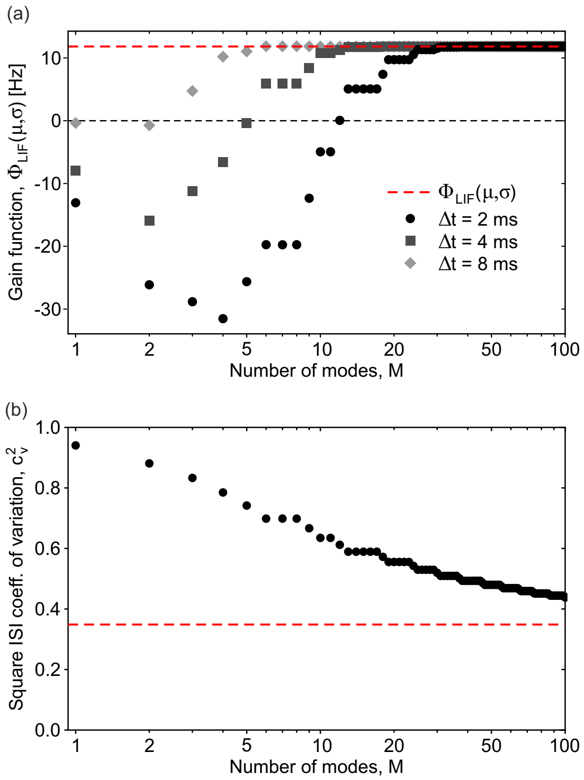

FIG. 3. Rate of convergence of the series giving the gain function Φ and coefficient of variation c_v of the ISI for LIF neurons. (a) $\Phi_{\rm LIF}$ estimated from Eq. (16) considering $\nu(\Delta t) \simeq 0$ for $\Delta t \ll 1/\Phi_{\rm LIF} \simeq 85$ ms. The sum $\tau^{-1}\sum_{n=1}^{M}\psi_{n,{\rm LIF}}(v_{\rm res})e^{\lambda_n \Delta t}$ is computed by varying the number of modes M sorted by $-\mathrm{Re}\,\lambda_k$. Different Δt are tested: 2 ms, circles; 4 ms, squares; 8 ms, diamonds. Dashed red line, $\Phi_{\rm LIF}$ as in Fig. 2(c). (b) c_v^2 computed from Eq. (20): $1 - 2\tau^{-1}\sum_{n=1}^{M}\psi_{n,{\rm LIF}}(v_{\rm res})\lambda_n$. The sum is computed as in (a). Dashed red line, $c_v^2 = 0.35$ resulting from the ISI moments computed from the derivatives of the Laplace transform $\rho_{\rm LIF}(s)$. Neuron parameters as in Fig. 2.

networks of spiking neurons. The aim is to derive a closed formula for the integrals giving the coupling coefficients appearing in the spectral expansion when neurons in the network are synaptically coupled.

A. Linear response from spectral expansion

Under the "extended" mean-field approximation [14], the drift and diffusion coefficients of the Fokker-Planck equation for a network of coupled spiking neurons are function of the firing rate ν. This because both the infinitesimal mean and variance of the synaptic current depend on the network activity: $\mu = \mu(\nu)$ and $\sigma^2 = \sigma^2(\nu)$. In this general framework the dynamics of the projection coefficients $a_n(t)$ and of $\nu(t)$ result to be [13,15]

$$\dot{\vec{a}} = (\mathbf{\Lambda} + \mathbf{C}\dot{\nu})\vec{a} + \vec{c}\,\dot{\nu}$$
$$\nu = \Phi + \vec{f}\cdot\vec{a}, \qquad (43)$$

where in addition to the coefficients found in Eq. (13), we have now the coupling terms between modes defined as $\{\mathbf{C}\}_{nm} = c_{nm}$ and $\{\vec{c}\}_n = c_{n0}$ for any $m, n \neq 0$ with $c_{nm} = \langle \partial_\nu \psi_n | \phi_m \rangle$.

The couplings can in general affect both current moments μ and σ^2 independently as in the case of a nonstationary external input. For this reason in order to compute the linear response we take into account a small and arbitrary perturbations $\epsilon(t)$ with different amplification in the drift and diffusion coefficients (6)

$$A(v,t) = A_0(v) + A_1(v)\,\epsilon(t)$$
$$B(v,t) = B_0(v) + B_1(v)\,\epsilon(t),$$

where only the input changes up to the first order are taken into account (i.e., $o(\epsilon^2) \simeq 0$). Here the time dependence of A and B is fully embedded in $\epsilon(t)$, and the above expression results from a Taylor expansion with $A_0(v) = A|_{\epsilon=0}$ and $A_1(v) = \partial_\epsilon A|_{\epsilon=0}$ and the same for $B(v,\epsilon)$. As an example, considering a perturbation due to a small deterministic current $\delta I(t) = \epsilon(t)$, the above amplification terms reduce to $A_1(v) = 1$ and $B_1(v) = 0$.

The coupling terms can then be generalized as $c_{nm}^{(\epsilon)} = \langle \partial_\epsilon \psi_n | \phi_m \rangle$. Deriving by ∂_ϵ and applying the ket $|\phi_m\rangle$ to both hand sides of the spectral equation (12) an expression for $c_{nm}^{(\epsilon)}$ results:

$$\begin{aligned}
&\langle \psi_n | \phi_m \rangle \partial_\epsilon \lambda_n + \lambda_n c_{nm}^{(\epsilon)} \\
&\quad = \delta_{nm}\partial_\epsilon \lambda_n + \lambda_n c_{nm}^{(\epsilon)} \\
&\quad = \langle \mathcal{L}^\dagger \partial_\epsilon \psi_n | \phi_m \rangle + A_1 \langle \psi_n' | \phi_m \rangle + B_1 \langle \psi_n'' | \phi_m \rangle \\
&\quad = \langle \partial_\epsilon \psi_n | \mathcal{L} \phi_m \rangle + A_1 \langle \psi_n' | \phi_m \rangle + B_1 \langle \psi_n'' | \phi_m \rangle \\
&\quad = \lambda_m c_{nm}^{(\epsilon)} + A_1 \langle \psi_n' | \phi_m \rangle + B_1 \langle \psi_n'' | \phi_m \rangle,
\end{aligned}$$

where $\psi_n' = \partial_v \psi_n$ and $\psi_n'' = \partial_v^2 \psi_n$. Indeed, from this we have

$$c_{nm}^{(\epsilon)} = \frac{A_1 \langle \psi_n' | \phi_m \rangle + B_1 \langle \psi_n'' | \phi_m \rangle}{\lambda_n - \lambda_m} \qquad \forall n \neq m \qquad (44)$$

and

$$\partial_\epsilon \lambda_n = A_1 \langle \psi_n' | \phi_n \rangle + B_1 \langle \psi_n'' | \phi_n \rangle. \qquad (45)$$

Under the linear response approximation, the Fourier transform of Eq. (43) leads to the transfer function $H_\epsilon(\omega)$ of the firing rate [13,33]

$$H_\epsilon(\omega) \equiv \frac{\hat{\nu}_1(\omega)}{\hat{\epsilon}(\omega)} = \partial_\epsilon \Phi + i\omega \vec{f}(i\omega \mathbf{I} - \mathbf{\Lambda})^{-1}\vec{c}_\epsilon, \qquad (46)$$

where $\hat{\nu}_1(\omega) = \int_{-\infty}^{\infty}(\nu(t) - \nu_0)e^{-i\omega t}dt$ is the Fourier transform of the firing rate fluctuating around $\nu_0 = \Phi(\mu_0, \sigma_0)$, $\hat{\epsilon}(\omega)$ is the same transform for $\epsilon(t)$ and $\{\vec{c}_\epsilon\}_n = c_{n0}^{(\epsilon)}$ are those from Eq. (44).

B. Linear response from Fokker-Planck equation

The same transfer function $H_\epsilon(\omega)$ can be worked out directly from the Fokker-Planck Eq. (5) [51]. Here we follow the perturbative approach introduced in Refs. [12,26] to the study of IF neuron networks. In this framework Eq. (5) can be decomposed by taking into account only the first-order perturbations of the probability density

$$p(v,t) = \phi_0(v) + p_1(v,t) + \mathcal{O}(\epsilon^2),$$

i.e., considering $p_1(v,t) = \mathcal{O}(\epsilon)$ and neglecting higher-order terms of the perturbation $\epsilon(t)$. The eigenfunction ϕ_0 is the stationary probability density when the input current has constant moments μ_0 and σ_0 (i.e., with $A = A_0$ and $B = B_0$). As a consequence, the firing rate is $\nu(t) = \nu_0 + \nu_1(t) + \mathcal{O}(\epsilon^2)$ with $\nu_0 \equiv \Phi(\mu_0, \sigma_0)$ (the unperturbed firing rate) and

$$\nu_1(t) = -\,\partial_v (B_1 \phi_0)|_{v=v_{\mathrm{thr}}}\,\epsilon(t) - (B_0\,\partial_v p_1)|_{v=v_{\mathrm{thr}}}.$$

From the Fourier transform of this perturbed firing rate the transfer function results to be

$$\begin{aligned} H_\epsilon^{(P)}(\omega) &\equiv \frac{\hat{\nu}_1(\omega)}{\hat{\epsilon}(\omega)} \\ &= -\,\partial_v(B_1\phi_0)|_{v=v_{\mathrm{thr}}} - (B_0 \hat{q}_1')|_{v=v_{\mathrm{thr}}}. \end{aligned} \tag{47}$$

Here $\hat{q}_1'(v,\omega) \equiv \partial_v \hat{q}_1(v,\omega)$ with $\hat{q}_1 = \hat{p}_1/\hat{\epsilon}$ the Fourier transform of the Green function determining the linear relationship between the input ϵ and the first-order perturbation p_1: $p_1(v,t) \equiv \int_0^\infty q_1(v,\tau)\epsilon(t-\tau)d\tau$.

Considering that also the operator $\mathcal{L}$ depends on ϵ, we can write it as $\mathcal{L} = \mathcal{L}_0 + \epsilon(t)\mathcal{L}_1 + \mathcal{O}(\epsilon^2)$ leading to

$$\begin{aligned} \dot{p}_1 &= \mathcal{L}_0\phi_0 + \mathcal{L}_0 p_1 + \epsilon\mathcal{L}_1\phi_0 + \mathcal{O}(\epsilon^2) \\ &\simeq \mathcal{L}_0 p_1 + \epsilon \mathcal{L}_1 \phi_0. \end{aligned}$$

Applying the bilateral Laplace transform to both hand sides of this equation we eventually obtain

$$s\,\hat{q}_1(v,s) = \mathcal{L}_0 \hat{q}_1(v,s) + F_0(v) \tag{48}$$

with $F_0(v) = \mathcal{L}_1\phi_0(v) = -\partial_v(A_1\phi_0) + \partial_v^2(B_1\phi_0)$, whose solution used in Eq. (47) with $s = i\omega$ gives the searched transfer function.

As in Ref. [12], the $\hat{q}_1$ solving Eq. (48) can be derived as the sum of two functions: the solution of the homogeneous equation $(\mathcal{L}_0 - s)\hat{q}_1 = 0$ [i.e., the spectral equation (31) with $s = \lambda_n$ having fundamental solutions f_1 and f_2], and the particular solution $Q(v,s)$ to be determined:

$$\hat{q}_1(v) = \begin{cases} a\,f_1(v) + b\,f_2(v) + Q(v) & v_{\mathrm{res}} < v < v_{\mathrm{thr}} \\ d\,f_2(v) + Q(v) & v_{\mathrm{min}} < v < v_{\mathrm{res}} \end{cases}.$$

For the sake of clarity, the dependency on s in all functions is implicit. As in the above derivation, the usual boundary conditions lead to a system of linear equations in a, b, and d to be solved. After some algebra and referring to Eq. (33) (see Appendix A for details), we find that:

$$\hat{q}_1'(v_{\mathrm{thr}}) = \frac{\frac{\mathcal{W}_{Q,f_2}(v_{\mathrm{thr}})}{\mathcal{W}(v_{\mathrm{thr}})Z} - \frac{\mathcal{W}_{\Delta Q,f_2}(v_{\mathrm{res}})}{\mathcal{W}(v_{\mathrm{res}})Z}}{B_0(v_{\mathrm{thr}})[\psi(v_{\mathrm{thr}}) - \psi(v_{\mathrm{res}})]}, \tag{49}$$

where the Wronskian $\mathcal{W}(v)$ is from Eq. (34), $\Delta Q(v) \equiv \lim_{\delta\to 0} Q(v+|\delta|) - Q(v-|\delta|)$ and $\mathcal{W}_{f,g}(v) \equiv f'(v)g(v) - f(v)g'(v)$. We remark that this formula is valid in general for any IF neuron model. Besides, it depends only on the particular solution $Q(v)$ and on the eigenfunction ψ, as from Eq. (33) $f_2(v) = \psi(v)\,Z\,B_0(v)\mathcal{W}(v)$ with $Z(s) = Z_n|_{\lambda_n = s}$.

The above expression for $\hat{q}_1'(v_{\mathrm{thr}})$ can be further simplified resorting to the method of variation of parameters [39], which allows to write the particular solution as a combination of the fundamental ones:

$$Q(v) = \alpha_1(v) f_1(v) + \alpha_2(v) f_2(v), \tag{50}$$

with

$$\begin{aligned} \alpha_1(v) &\equiv \int_{v_{\mathrm{min}}}^{v} \frac{f_2(y)F_0(y)}{B_0(y)\mathcal{W}(y)}dy \\ &= Z\int_{v_{\mathrm{min}}}^{v} \psi(y)F_0(y)dy \\ \alpha_2(v) &\equiv -\int_{v_{\mathrm{min}}}^{v} \frac{f_1(y)F_0(y)}{B_0(y)\mathcal{W}(y)}dy. \end{aligned}$$

As f_1 and f_2 are continuous functions, $\Delta Q(v) = 0$ leading to have $\mathcal{W}_{\Delta Q, f_2}(v_{\mathrm{res}}) = 0$ in Eq. (49). In the same equation, the other addendum of the numerator simplifies as follows:

$$\begin{aligned} \mathcal{W}_{Q,f_2} &= Q' f_2 - Q f_2' \\ &= (\alpha_1' f_1 + \alpha_2' f_2) f_2 + \alpha_1 \mathcal{W} \\ &= \alpha_1 \mathcal{W}, \end{aligned}$$

considering that from Eq. (50) $\alpha_1' f_1 + \alpha_2' f_2 = 0$. Inserting here the expression for α_1, we obtain

$$\frac{\mathcal{W}_{Q,f_2}(v)}{\mathcal{W}(v)Z} = \int_{v_{\mathrm{min}}}^{v} \psi(y)F_0(y)dy.$$

All these simplifications eventually lead to the final expression for $\hat{q}_1'(v_{\mathrm{thr}})$:

$$\hat{q}_1'(v_{\mathrm{thr}}) = \frac{\int_{v_{\mathrm{min}}}^{v_{\mathrm{thr}}} \psi(y)F_0(y)dy}{B_0(v_{\mathrm{thr}})[\psi(v_{\mathrm{thr}}) - \psi(v_{\mathrm{res}})]}. \tag{51}$$

It is interesting to note that from this general result arises the deep relationship between the linear response of a network (H_ϵ), its stationary state ($F_0 = \mathcal{L}_1\phi_0$) and the statistics of the single-neuron first-passage time (ψ_k).

C. Transfer function of LIF neurons

For the specific example of networks of LIF neurons analytic results can be carried out for the transfer function. In this case the linearized synaptic current Eq. (3) holds and perturbations can be directly taken into account in the mean and the variance of the input

$$\begin{aligned} \mu(t) &= \mu_0 + \mu_1\,\epsilon(t) \\ \sigma^2(t) &= \sigma_0^2 + \sigma_1^2\,\epsilon(t). \end{aligned}$$

Here μ_0 and σ_0 do not depend on time and set the fixed point around which perturbations are studied.

As in Sec. II H, it is also convenient to change variable in $x = v - \mu_0)/\sigma_0$ leading to simplify the Fokker-Planck equation (5) into:

$$\partial_t p(x,t) = \partial_x(xp) + \tfrac{1}{2}\partial_x^2 p \equiv \mathcal{L}_x p,$$

where for the sake of simplicity we set $\tau = 1$. A different unit time can be adopted simply multiplying by τ all the variables like μ_0, σ_0^2, $\nu(t)$, and λ_n. Unperturbed drift and diffusion coefficients thus reduce to $A_0(x) = -x$ and $B_0 = 1/2$, while the perturbation-related ones are $A_1 = \mu_1$ and $B_1 = \sigma_1^2$.

The general expressions (49) can be now worked out for LIF neurons:

$$\hat{q}_1'(x_t) = \frac{2}{\sigma_0[\psi(x_t) - \psi(x_r)]}\left[\frac{\mathcal{W}_{Q,f_2}(x_t)}{Z\mathcal{W}(x_t)} - \frac{\mathcal{W}_{\Delta Q,f_2}(x_r)}{Z\mathcal{W}(x_r)}\right],$$

where we have taken into account that $\partial_v = \sigma_0^{-1}\partial_x$ leading to rescale the normalization factor as $Z \to \sigma_0 Z$. This with Eq. (47) allows eventually to write the transfer function

$$H_\epsilon^{(P)} = \frac{\sigma_1^2}{\sigma_0^2}\nu_0 - \frac{\sigma_0}{2}\hat{q}_1'(x_t). \tag{52}$$

Focusing now on the specific case of an input change affecting only the drift μ, we have $F_0(x) = -\phi_0'(x)/\sigma_0$ by setting $\mu_1 = 1$ and $\sigma_1^2 = 0$. The related particular solution of Eq. (48) can be verified to be [12]

$$Q_\mu(x, s) = -\frac{\phi_0'(x)}{(s+1)\sigma_0}.$$

Recalling that $\nu_0 = \Phi = -\phi_0'(x_t)/2$, we remark that $Q_\mu(x_t, s) = 2\nu_0/[(s+1)\sigma_0]$ highlighting the direct link between $Q(x)$ and the flux of realizations $S_{\phi_0}(x)$ under stationary condition. Making use of all this information in the above expression for $\hat{q}_1'(x_t)$ (see Appendix B for details), from Eq. (52) we can derive the transfer function of the modulated drift $\mu(t)$ of the input current

$$H_\mu^{(P)}(s) = \frac{\nu_0}{(s+1)\sigma_0}\,\frac{\psi'(x_t, s) - \psi'(x_r, s)}{\psi(x_t, s) - \psi(x_r, s)}, \tag{53}$$

where $\psi' = \partial_x\psi$. With a similar derivation detailed in Appendix B, the transfer function of the perturbations to the variance $\sigma^2(t)$ ($\mu_1 = 0$ and $\sigma_1^2 = 1$) results to be

$$H_\sigma^{(P)}(s) = \frac{\nu_0}{(s+2)\sigma_0^2}\left[s + \frac{x_t\psi'(x_t, s) - x_r\psi'(x_r, s)}{\psi(x_t, s) - \psi(x_r, s)}\right], \tag{54}$$

where the related particular solution of Eq. (48)

$$Q_\sigma(x, s) = \frac{\phi_0''(x)}{2(s+1)\sigma_0^2}$$

has been used [12].

Equations (53) and (54) are due to Ref. [12] for the modulation of μ and to Ref. [52] for the modulation of σ^2. In Ref. [52] the explicit expression of $\partial_x\psi$ was incorporated, although a further simplification was previously given in Ref. [53] such that:

$$\begin{aligned}\psi'(x, s) &= \sqrt{2}\,\psi(x, s-1) + 2x\,\psi(x, s)\\ &= \sqrt{2}\,s\,\psi(x, s+1).\end{aligned} \tag{55}$$

With this no derivatives in the above transfer functions have to be computed.

Recalling Eq. (3), we remark that under mean-field approximation the mean and the variance of the input current depend on the firing rate, and the rate-to-rate transfer function $H_\nu(s)$ can be eventually carried:

$$H_\nu(s) = H_\mu(s)\frac{d\mu}{d\nu} + H_\sigma(s)\frac{d\sigma^2}{d\nu}.$$

D. Matching the transfer functions to derive c_{n0}

Starting from these old and new results we now derive an expression for the coupling coefficients between nonstationary and stationary modes $c_{n0}^{(\epsilon)} = \{\vec{c}_\epsilon\}_n$ found in Eqs. (43) and (46). To this purpose we note that the transfer function $H_\epsilon(s)$ (where $s = i\omega$) derived with the spectral expansion approach, can give

$$\mathrm{Res}_{s=\lambda_n} H_\epsilon(s) = \lambda_n\, c_{n0}^{(\epsilon)}.$$

Due to the equivalence between this $H_\epsilon(s)$ and $H_\epsilon^{(P)}(s)$ from the perturbative approach for LIF neurons, we can carry out an explicit expression for the coupling coefficients as

$$c_{n0}^{(\epsilon)} = \frac{1}{\lambda_n}\mathrm{Res}_{s=\lambda_n} H_\epsilon^{(P)}(s).$$

To compute the residues from Eqs. (53) and (54), we point out that the spectral equation Eq. (26) can be expressed directly in terms of adjoint eigenfunctions: $\psi(x_r, \lambda_n) = \psi(x_t, \lambda_n)$. From this we have

$$\mathrm{Res}_{s=\lambda_n}\frac{1}{\psi(x_t, s) - \psi(x_r, s)} = 1,$$

which straightforwardly leads to

$$c_{n0}^{(\mu)} = \frac{\nu_0}{\sigma_0\lambda_n(\lambda_n+1)}[\psi_n'(x_t) - \psi_n'(x_r)] \tag{56}$$

and to

$$c_{n0}^{(\sigma)} = -\frac{\nu_0}{2\sigma_0^2\lambda_n(\lambda_n+2)}(x_t\psi_n'(x_t) - x_r\psi_n'(x_r)). \tag{57}$$

Here we can eventually make use of Eq. (55) allowing to explicitly write $\psi_n'(x) = \sqrt{2}\,\lambda_n\psi(x, \lambda_n + 1)$. Remarkably, as for the LIF neuron $\psi_n(x)$ is given by Eqs. (38) and (28), once we known the eigenvalues λ_n, the expressions for both $c_{n0}^{(\mu)}$ and $c_{n0}^{(\sigma)}$ are closed formulas, not requiring any integral on the x domain. Finally, recalling the dependence on ν of the moments of synaptic current in Eq. (3), the coupling coefficients in the firing rate Eq. (43) are

$$\begin{aligned}c_{n0} &= \langle\partial_\nu\psi_n|\phi_0\rangle\\ &= \frac{d\mu}{d\nu}c_{n0}^{(\mu)} + \frac{d\sigma^2}{d\nu}c_{n0}^{(\sigma)}\\ &= \tau KJ\big(c_{n0}^{(\mu)} + J(1+\Delta^2)c_{n0}^{(\sigma)}\big),\end{aligned} \tag{58}$$

where we reintroduced explicitly τ.

Figure 4(a) shows an example distribution of coupling coefficients $c_{n0}^{(\mu)}$ due to a μ-perturbation. They appear to be mainly real and their size scales as $|\lambda_n\tau|^{-3/2}$ [Fig. 4(b)]. Increasing the number M of eigenmodes the match between Eq. (46) from the spectral expansion and the exact Eq. (53) widen at higher Fourier frequencies ω both in the absolute value [Fig. 4(c)] and in the phase [Fig. 4(d)], confirming the correctness of the derived expressions. It is interesting to note that a relatively small number M of eigenmodes has to be taken into account in order to have a good match of the linear response theory in the physiological range $\omega/2\pi < 200$ Hz.

Similar results are found for the case of a σ modulation of the input current (Fig. 5). In this example case it is interesting to note a different scaling of the size $|c_{n0}^{(\sigma)}|$ following two different slopes, -1 and -2, depending on the real or complex nature of the eigenvalues, respectively [Fig. 5(b)].

We conclude coming back to the general case of arbitrary spiking neurons. Applying the residue approach by making use of Eq. (51) we eventually obtain the general integral

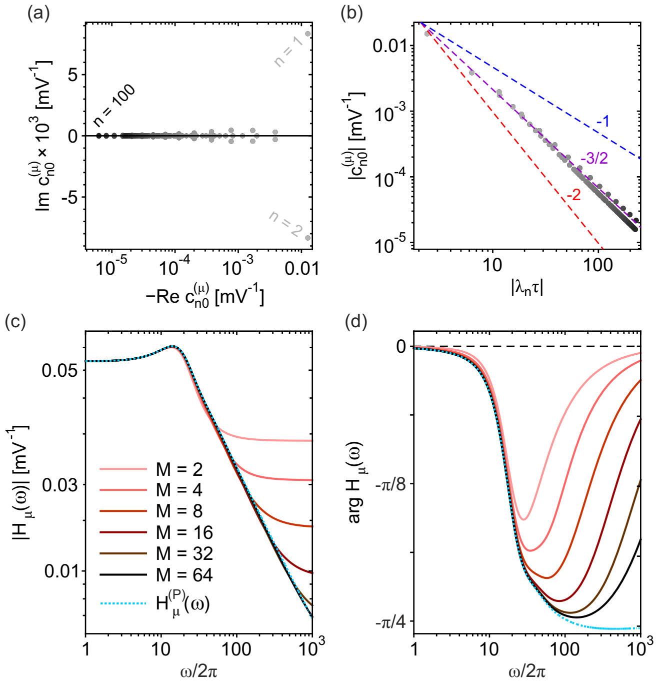

FIG. 4. Coupling coefficients $c_{n0}^{(\mu)}$ from Eq. (56) in the linear response to a perturbation of the mean input current μ for LIF neurons. (a) Coupling coefficients of the first 100 eigenmodes n (sorted by Re λ_n). (b) Scaling of the magnitude $|c_{n0}^{(\mu)}|$ with the size $|\lambda_n\tau|$ of the related eigenvalues. Blue, purple, and red dashed lines correspond to -1, $-3/2$, and -2 slopes, respectively. (c) Transfer function H_μ from Eq. (46) varying the number M of eigenmodes incorporated (reddish curves) and $H_\mu^{(P)}$ from Eq. (53) (cyan dotted curve): absolute values. (d) Phase of the transfer functions as in (c). Neuron parameters as in Fig. 2.

expression

$$c_{n0}^{(\epsilon)} = -\frac{1}{\lambda_n}\int_{v_{\min}}^{v_{\text{thr}}} \psi_n(y)F_0(y)dy = -\frac{\langle\psi_n|F_0\rangle}{\lambda_n}.$$

Note that such expression is the same as Eq. (44) with $m = 0$. This because $F_0 = -\partial_v(A_1\phi_0) + \partial_v^2(B_1\phi_0)$ and, given the usual boundary conditions, partial derivatives can be moved to be applied directly to $\psi_n(v)$.

IV. CONCLUSION

Here, by carrying out and pairing the dynamics of the firing rate $\nu(t)$ derived from two different approaches, we found novel analytic expressions for the coefficients underlying the spectral expansion of the population density $p(v, t)$. In the case of an uncoupled set of spiking neurons, we used the renewal theory in combination with the spectral expansion approach by pairing the relaxation dynamics of $\nu(t)$—part of our "Rosetta stone"—eventually obtaining sums of series in closed form. More specifically, we uncovered a new expression of the current-to-rate gain function $\Phi(\mu, \sigma)$ in Eq. (17) as series of the adjoint eigenfunctions evaluated at the reset potential $\psi_n(v_{\text{res}})$. We also found a tight relationship between the moments of the ISI distribution and a suited combination of the $\psi_n(v_{\text{res}})$ and the eigenvalues λ_n of the Fokker-Planck operator. We remark that all these findings are model-independent highlighting the descriptive power of the spectral expansion and further extending recent results reported in Ref. [38].

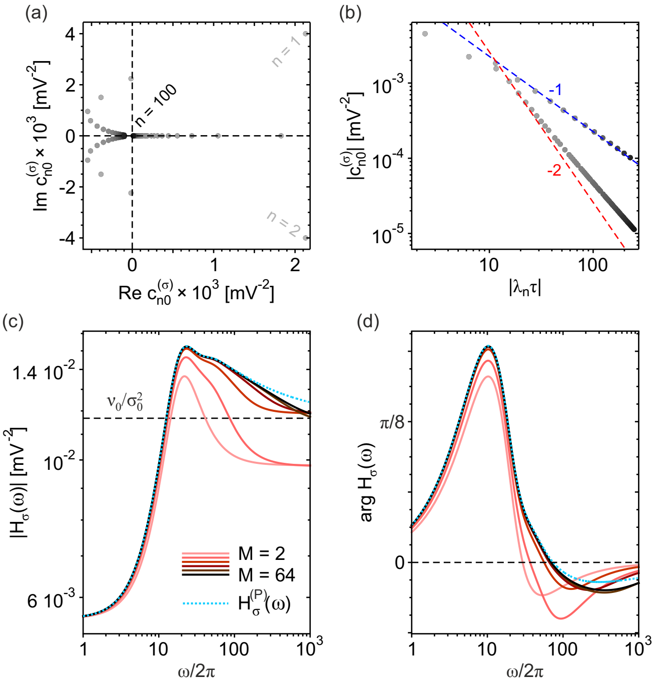

FIG. 5. Coupling coefficients $c_{n0}^{(\sigma)}$ from Eq. (57) in the linear response to a perturbation of the input current fluctuations σ for LIF neurons. (a) $c_{n0}^{(\sigma)}$ of the first 100 eigenmodes n. (b) Magnitude $|c_{n0}^{(\mu)}|$ versus $|\lambda_n\tau|$. [(c) and (d)] Amplitude and phase of the transfer function H_σ from Eq. (46) varying M and $H_\sigma^{(P)}$ from Eq. (54). Other details as in Fig. 4. Neuron parameters as in Fig. 2.

From the same side of our Rosetta stone, we found an alternative way to compute both $\psi_n(v_{\text{res}})$ and λ_n. Indeed, relying on the residue theorem, Eqs. (21) and (23) show how to obtain from the Laplace transform $\rho(s)$ of the ISI density both these coefficients. Notably, these equations provide a great advantage in practical terms to estimate numerically the eigenvalues λ_n even when their analytic expressions are not available. This is due to the fact that usually eigenvalues results from the numerical search of the roots of the spectral equation (26) [13,38], or of the zeros of numerically derived functions [31,54]. Evaluating residues instead requires computation of a limit or of a line integral around the border of a domain centered around some rough guess for λ_n. The expected computational advantages resulting from this residue-based approach can pave the way to effective implementations of the spectral expansion formalism in the numerical integration of the network dynamics of spiking neurons.

For the specific case of LIF neurons, we also derived additional analytic expressions for the coupling coefficients c_{n0} involved in the evaluation of both the out-of-equilibrium dynamics and the critical points of coupled networks via the firing rate equation (43). Here we resorted to the linear response to a small perturbation of the input as the other side of our Rosetta stone. Pairing the perturbative response carried out from the spectral expansion approach and directly from the Fokker-Planck equation, we finally obtained Eqs. (56) and (57). These expressions for c_{n0} result to involve only the eigenfunctions at the reset potential $\psi_n(v_{\rm res})$ and the eigenvalues λ_n. These coefficients in turn appear to be tightly linked in Eq. (19) to the ISI density $\rho(t)$ of isolated cells. In other words the coupling coefficients are the expression of a single-neuron feature valid under stationary condition, rather than being a direct function of the synaptic efficacy J. Although this may appear as a contradiction, we remark that in Eq. (58) these single-neuron features in $c_{n0}^{(\epsilon)}$ mainly play a modulatory role of the synaptic coupling KJ, which is fully taken into account in the mean-field expressions for the current moments $\mu(\nu)$ and $\sigma^2(\nu)$.

In the framework of the spectral expansion of $p(v,t)$, approximated expressions for $c_{n0}^{(\mu)}$ has been previously derived in Ref. [15], finding

$$c_{n0}^{(\mu)} \simeq \frac{\nu_0}{\lambda_n + 1} C(\mu)$$

for networks of LIF neurons working in drift-dominated regime ($\mu\tau > v_{\rm thr}$) and with small synaptic noise ($x_t \gg 1$). This is perfectly compatible with what we derived here and reported in Eq. (56), provided that $C(\mu) = 1/\lambda_n$ with $\lambda_n = \lambda_n(\mu, \sigma_0)$. Note that our result has a more general applicability being valid also under subthreshold noise-dominated regime ($\mu\tau < v_{\rm thr}$). Another expression for $c_{n0}^{(\mu)}$ has been recently presented also in Ref. [38]. In this case the spectral expansion approach targeted the refractory density, leading to obtain for the case of a Poisson model with a refractory period τ_0, the following expression:

$$c_{n0}^{(\mu)} = \frac{\partial_\mu \Phi}{\lambda_n + (1 - \tau_0 \lambda_n)\nu_0} \xrightarrow[\tau_0 \to 0]{} \frac{\partial_\mu \Phi}{\lambda_n + \nu_0}.$$

This equation appears to be qualitatively different from our Eq. (56) and does not match the evidence shown in Fig. 4 for an example network where $|c_{n0}^{(\mu)}| \sim |\lambda_n|^{-3/2}$. A possible explanation of such disagreement on one hand may reside in the fact that LIF neurons are not Poissonian processes. On the other hand, this might highlight a qualitative difference in the population dynamics described by the refractory density approach compared to the classical one focused on the evolution of the membrane potential density. To further clarify, we note that, aside from the case of an uncoupled population—where a strong relationship exists between the two formalisms through the stationary ISI distribution—there is currently no method to derive an exact hazard function in the time-dependent or coupled scenarios. Furthermore, there are no guarantees that such an expression can be formulated self-consistently as a function solely of the time elapsed since the last spike, thereby bridging the gap with the fully determined Fokker-Planck equation.

Note that our derivation of the coupling terms c_{n0} for LIF neurons can in principle be applied to other IF neuron models. We expect in this case qualitatively similar results, confirming that the ISI density-based coefficients $c_{n0}^{(\epsilon)}$ eventually modulate the system response with strength proportional to KJ. We also draw the reader attention to the fact that here we did not report any expression for the coupling coefficients C_{nm} between nonstationary modes ($n, m \neq 0$). They are involved in the nonlinear response of the neuronal network playing a role when the time derivative $\dot{\nu}$ of the firing rate is relatively large and the density $p(v,t)$ is significantly different from the stationary one (ϕ_0) [13]. Provided that such constraints are not violated, the network dynamics can be fully described by taking into account the only coefficients of the spectral expansion we studied, even when the firing rate is driven outside equilibrium [31,50].

Regarding the applicability to the out-of-equilibrium dynamics, we further point out that all the mentioned coefficients depend on the infinitesimal moments μ and σ of the synaptic current. This means that under the extended mean-field approximation that leads to Eq. (3), all the coefficients depend from time to time on the activity $\nu(t)$ of the network. Here μ and σ must be interpreted as parameters. Indeed, it is true that our Rosetta stone approach allowed us to carry out these spectral expansion coefficients from the quasiequilibrium dynamics (linear response and relaxation in uncoupled sets), i.e., considering μ and σ as fixed. Nonetheless, for a given μ and σ they contribute to faithful represent a snapshot of the moving basis $\{|\phi_n\rangle\}_{n\in\mathbb{Z}}$ onto which the density $p(v,t)$ is projected. The basis moves as the drift and diffusion terms in the Fokker-Planck equation (5) vary describing a sequence of stochastic processes (i.e., the membrane potentials of the neurons) locally homogeneous in time. We believe this is an important point to stress. Starting from the linearizable (quasiequilibrium) dynamics of spiking neuron networks, the spectral expansion coefficients can be derived paving the way to describe the same system outside equilibrium.

ACKNOWLEDGMENTS

We thank L. Falorsi and L. Buffa for helpful comments on an earlier version of the paper. The code used to produce all the figures is freely available [46]. This research has received funding from the European Union's Horizon 2020 Framework Programme for Research and Innovation under the Specific Grant Agreement No. 945539 (Human Brain Project SGA3) and from the Italian National Recovery and Resilience Plan (PNRR), M4C2, funded by the European Union–NextGenerationEU (Project IR0000011, CUP B51E22000150006, "EBRAINS-Italy"), to MM.

APPENDIX A: DERIVATION OF EQS. (49) AND (50)

To derive the Laplace transform of the Green function $q_1(x_t)$ in Eq. (49), we recall that it is given by the following linear combination:

$$\hat{q}_1(v) = \begin{cases} a\, f_1(v) + b\, f_2(v) + Q(v) & v_{\rm res} < v < v_{\rm thr} \\ d\, f_2(v) + Q(v) & v_{\rm min} < v < v_{\rm res} \end{cases},$$

for which holds the same boundary conditions in the v domain for $p(v,t)$. This because $\hat{q}_1$ is a linear transform in the t domain of the first-order perturbation p_1. Such boundary conditions [13,15,17], allows to set the linear system to find the coefficients a, b, and d [12,36]:

$$a\,f_1(v_{\text{thr}}) + b\,f_2(v_{\text{thr}}) = -Q(v_{\text{thr}})$$

$$a\,f_1(v_{\text{res}}) + (b-d)f_2(v_{\text{res}}) = -\Delta Q(v_{\text{res}})$$

$$B_0(v_{\text{thr}})[a\,f_1'(v_{\text{thr}}) + b\,f_2'(v_{\text{thr}})] - B_0(v_{\text{res}})[a\,f_1'(v_{\text{res}}) + (b-d)f_2'(v_{\text{res}})] = B_0(v_{\text{res}})\Delta Q'(v_{\text{res}}) - B_0(v_{\text{thr}})Q'(v_{\text{thr}}).$$

These equations correspond respectively to the conditions about (i) the absorbing barrier in $v = v_{\text{thr}}$; (ii) the fact that A, B, their derivatives with respect to v and p_1 are continuous functions; and (iii) the reentering flux in $v = v_{\text{res}}$.

Solving the above system we have

$$a = \frac{B_0(v_{\text{thr}})\mathcal{W}_{Q,f_2}(v_{\text{thr}})f_2(v_{\text{res}}) - B_0(v_{\text{res}})\mathcal{W}_{\Delta Q,f_2}(v_{\text{res}})f_2(v_{\text{thr}})}{B_0(v_{\text{res}})\mathcal{W}(v_{\text{res}})f_2(v_{\text{thr}}) - B_0(v_{\text{thr}})\mathcal{W}(v_{\text{thr}})f_2(v_{\text{res}})}$$

and

$$b = \frac{B_0(v_{\text{res}})\big[\mathcal{W}_{\Delta Q,f_2}(v_{\text{res}})f_1(v_{\text{thr}}) - \mathcal{W}(v_{\text{res}})Q(v_{\text{thr}})\big] - B_0(v_{\text{thr}})\mathcal{W}_{Q,f_1}(v_{\text{thr}})f_2(v_{\text{res}})}{B_0(v_{\text{res}})\mathcal{W}(v_{\text{res}})f_2(v_{\text{thr}}) - B_0(v_{\text{thr}})\mathcal{W}(v_{\text{thr}})f_2(v_{\text{res}})}.$$

Note that we do not report the expression for d as we aim at deriving $\hat{q}_1'(v_{\text{thr}})$ for which the domain of interest is $v > v_{\text{res}}$. Finally, using Eq. (33) for $\psi(v)$, the denominator of these fractions can be further simplified in $B_0(v_{\text{res}})\mathcal{W}(v_{\text{res}})B_0(v_{\text{thr}})\mathcal{W}(v_{\text{thr}})[\psi(v_{\text{thr}}) - \psi(v_{\text{res}})]$, eventually leading with some algebra to Eq. (49).

The method of variation of parameters [39] requires to express the second-order differential equation (48) in canonical form:

$$\begin{aligned}
(\mathcal{L}_0 - s)\hat{q}_1 &= -F_0 \Rightarrow\\
-\partial_v(A_0\hat{q}_1) + \partial_v^2(B_0\hat{q}_1) - s\hat{q}_1 &= -F_0 \Rightarrow\\
-A_0\hat{q}_1' + B_0''\hat{q}_1 + 2B_0'\hat{q}_1' + B_0\hat{q}_1'' - (s + A_0')\hat{q}_1 &= -F_0 \Rightarrow\\
B_0\hat{q}_1'' + (2B_0' - A_0)\hat{q}_1' + (B_0'' - A_0' - s)\hat{q}_1 &= -F_0 \Rightarrow\\
\hat{q}_1'' + \frac{2B_0' - A_0}{B_0}\hat{q}_1' + \frac{B_0'' - A_0' - s}{B_0}\hat{q}_1 &= -\frac{F_0}{B_0}.
\end{aligned}$$

This gives the inhomogeneous term $-F_0/B_0$ to take into account in computing the coefficients $\alpha_1(v)$ and $\alpha_2(v)$ in Eq. (50).

APPENDIX B: DERIVATION OF $H_\epsilon^{(P)}$ FOR LIF NEURONS

From Eq. (47) we know that the generic transfer function $H_\epsilon^{(P)}$ is proportional to $\hat{q}_1'(v_{\text{thr}})$ given by Eq. (49), whose derivation has been detailed in the previous Appendix. Starting from this, and adopting the same change of variable of the main text, here we provide the key steps needed to obtain the explicit expressions for $H_\epsilon^{(P)}$ reported in Eqs. (53) and (54) for the specific case of the standard LIF neuron model. If the input modulation involves only the mean μ, then $Q_\mu(x) = K\,\phi_0'(x)$, where both $Q_\mu(x)$ and K are implicitly dependent on s, and from Ref. [12] $K(s) = -1/[(s+1)\sigma_0]$. Remembering that $\mathcal{L}_{x0}\phi_0 = \partial_x(x\phi_0) + \frac{1}{2}\partial_x^2\phi_0 = 0$ we can write

$$\begin{aligned}
Q_\mu'(x) &= -2xQ_\mu(x) - 2K\phi_0(x)\\
&= \frac{\mathcal{W}'(x)}{\mathcal{W}(x)}Q_\mu(x) - 2K\phi_0(x),
\end{aligned}$$

where we taken into account that from Eq. (34) the Wronskian for the LIF neuron reduces to the differential equation $\mathcal{W}'(x) = -2x\,\mathcal{W}(x)$. The first term of the numerator in Eq. (49) for the LIF neuron then reduces to

$$\begin{aligned}
\frac{\mathcal{W}_{Q,f_2}(x_t)}{\mathcal{W}(x_t)Z} &= \frac{Q_\mu'f_2 - Q_\mu f_2'}{\mathcal{W}Z}\bigg|_{x=x_t}\\
&= -\frac{Q_\mu}{Z}\left(-\frac{\mathcal{W}'f_2}{\mathcal{W}^2} + \frac{f_2'}{\mathcal{W}}\right) - 2K\phi_0\frac{f_2}{\mathcal{W}Z}\bigg|_{x=x_t}\\
&= -(Q_\mu + 2K\phi_0)\psi'|_{x=x_t}\\
&= -Q_\mu(x_t)\psi'(x_t),
\end{aligned}$$

where we used Eq. (33) replacing λ_n with s and defining $Z(s) = Z_n|_{\lambda_n=s}$, and we took into account the boundary condition $\phi_0(x_t) = 0$. The same can be done with the other term $\mathcal{W}_{\Delta Q,f_2}(x_r)/\mathcal{W}(x_r)Z$ by taking into account the other boundary condition about the flux conservation, $Q(x_t) = \Delta Q(x_r)$, eventually leading to rewrite Eq. (49) as

$$\hat{q}_1'(x_t) = -\frac{2}{\sigma_0}Q_\mu(x_t)\frac{\psi'(x_t) - \psi'(x_r)}{\psi(x_t) - \psi(x_r)}.$$

Analogous results hold whenever the particular solution is proportional to the derivative of the stationary eigenfunction.

In the case of a changing variance σ^2 of the input current, the particular solution is $Q_\sigma(x) = K\phi_0''(x)$ with $K(s) = 1/[2(s+2)\sigma_0^2]$ [12]. As above, to compute $\mathcal{W}_{Q,f_2}$ and $\mathcal{W}_{\Delta Q,f_2}$ in Eq. (49) we need the derivative Q_σ' which results to be

$$Q_\sigma' = K\phi_0''' = -K(2x\phi_0'' + 4\phi_0') = K(4x^2 - 4)\phi_0' + 4Kx\phi_0.$$

by using the stationary equation $\mathcal{L}_{x0}\phi_0 = 0$. As $\phi_0(x_t) = 0$ and $\Delta\phi_0(x_r) = 0$, the term $4Kx\phi_0$ does not give any contribution and can be neglected leading to

$$\begin{aligned}
\frac{\mathcal{W}_{Q,f_2}}{\mathcal{W}Z} &= \frac{K\phi_0'}{\mathcal{W}Z}(-4f_2 + 2x(2xf_2 + f_2'))\\
&= K\phi_0'\left[-4\frac{f_2}{\mathcal{W}Z} + 2x\left(-\frac{\mathcal{W}'f_2}{\mathcal{W}^2Z} + f_2'\right)\right]\\
&= K(s)\phi_0'(x)[-4\psi(x,s) + 2x\psi'(x,s)].
\end{aligned}$$

With this, the two terms in the numerator of Eq. (49) can be derived, and substituting the resulting $\hat{q}'(x_t)$ in Eq. (52) we eventually obtain Eq. (54).

[1] L. D. Landau and E. M. Lifshits, *Statistical Physics*, 2nd ed. (Pergamon Press, Oxford, 1969).

[2] C. Pozzorini, S. Mensi, O. Hagens, R. Naud, C. Koch, and W. Gerstner, PLoS Comput. Biol. **11**, e1004275 (2015).

[3] C. Teeter, R. Iyer, V. Menon, N. Gouwens, D. Feng, J. Berg, A. Szafer, N. Cain, H. Zeng, M. Hawrylycz *et al.*, Nat. Commun. **9**, 709 (2018).

[4] H. C. Tuckwell, *Introduction to Theoretical Neurobiology: Volume 2*, Cambridge Studies in Mathematical Biology (Cambridge University Press, Cambridge, UK, 1988).

[5] W. Gerstner, W. M. Kistler, R. Naud, and L. Paninski, *Neuronal Dynamics: From Single Neurons to Networks and Models of cognition* (Cambridge University Press, Cambridge, UK, 2014).

[6] J. DeFelipe, L. Alonso-Nanclares, and J. I. Arellano, J. Neurocytol. **31**, 299 (2002).

[7] H. Markram, E. Muller, S. Ramaswamy, M. W. Reimann, M. Abdellah *et al.*, Cell **163**, 456 (2015).

[8] D. J. Amit and M. Tsodyks, Network: Comput. Neural Syst. **3**, 121 (1992).

[9] M. J. E. Richardson, Phys. Rev. E **69**, 051918 (2004).

[10] B. Grigelionis, Theory Probab. Appl. **8**, 177 (1963).

[11] G. V. Vinci, R. Benzi, and M. Mattia, Phys. Rev. Lett. **130**, 097402 (2023).

[12] N. Brunel and V. Hakim, Neural Comput. **11**, 1621 (1999).

[13] M. Mattia and P. Del Giudice, Phys. Rev. E **66**, 051917 (2002).

[14] D. J. Amit and N. Brunel, Cereb. Cortex **7**, 237 (1997).

[15] B. W. Knight, D. Manin, and L. Sirovich, in *Symposium on Robotics and Cybernetics: Computational Engineering in Systems Applications*, edited by E. Gerf (Cite Scientifique, Lille, France, 1996), pp. 1–5.

[16] D. Q. Nykamp and D. Tranchina, J. Comput. Neurosci. **8**, 19 (2000).

[17] B. W. Knight, Neural Comput. **12**, 473 (2000).

[18] L. F. Abbott and C. van Vreeswijk, Phys. Rev. E **48**, 1483 (1993).

[19] S. Fusi and M. Mattia, Neural Comput. **11**, 633 (1999).

[20] H. Risken, *The Fokker-Planck Equation* (Springer, Berlin, 1984).

[21] A. Omurtag, B. W. Knight, and L. Sirovich, J. Comput. Neurosci. **8**, 51 (2000).

[22] M. de Kamps, Neural Comput. **15**, 2129 (2003).

[23] D. Cai, L. Tao, M. Shelley, and D. W. McLaughlin, Proc. Natl. Acad. Sci. USA **101**, 7757 (2004).

[24] A. Treves, Network: Comput. Neural Syst. **4**, 259 (1993).

[25] N. Brunel, F. S. Chance, N. Fourcaud, and L. F. Abbott, Phys. Rev. Lett. **86**, 2186 (2001).

[26] M. J. E. Richardson, Phys. Rev. E **76**, 021919 (2007).

[27] M. J. E. Richardson and R. Swarbrick, Phys. Rev. Lett. **105**, 178102 (2010).

[28] N. Brunel, J. Comput. Neurosci. **8**, 183 (2000).

[29] R. F. Fox, Phys. Rev. A **39**, 4148 (1989).

[30] A. D. McLachlan and M. A. Ball, Rev. Mod. Phys. **36**, 844 (1964).

[31] M. Augustin, J. Ladenbauer, F. Baumann, and K. Obermayer, PLoS Comput. Biol. **13**, e1005545 (2017).

[32] E. S. Schaffer, S. Ostojic, and L. F. Abbott, PLoS Comput. Biol. **9**, e1003301 (2013).

[33] M. Mattia and P. Del Giudice, Phys. Rev. E **70**, 052903 (2004).

[34] M. Mattia, M. Biggio, A. Galluzzi, and M. Storace, PLoS Comput. Biol. **15**, e1007404 (2019).

[35] D. R. Cox and H. D. Miller, *The Theory of Stochastic Processes* (Chapman & Hall/CRC, Boca Raton, FL, 1977).

[36] T. Deniz and S. Rotter, Phys. Rev. E **95**, 012412 (2017).

[37] A. Siegert, Phys. Rev. **81**, 617 (1951).

[38] B. Pietras, N. Gallice, and T. Schwalger, Phys. Rev. E **102**, 022407 (2020).

[39] F. W. J. Olver, D. W. Lozier, R. F. Boisvert, and C. W. Clark, *NIST Handbook of Mathematical Functions* (Cambridge University Press, New York, 2010).

[40] G. L. Gerstein and B. Mandelbrot, Biophys. J. **4**, 41 (1964).

[41] D. A. Darling and A. Siegert, Ann. Math. Stat. **24**, 624 (1953).

[42] C. Mead, *Analog VLSI and Neural System* (Addison-Wesley, Reading, MA, 1989).

[43] R. M. Capocelli and L. M. Ricciardi, Kybernetik **8**, 214 (1971).

[44] B. K. Roy and D. R. Smith, Bull. Math. Biophys. **31**, 341 (1969).

[45] Y. A. Brychkov, *Handbook of Special Functions: Derivatives, Integrals, Series and Other Formulas* (CRC Press, Boca Raton, FL, 2008).

[46] M. Mattia (2024), https://github.com/mauriziomattia/RosettaStoneForSNNdynamics.

[47] P. I. M. Johannesma, in *Neural Networks*, edited by E. R. Caianiello (Springer, Berlin, 1968), pp. 116–144.

[48] L. M. Ricciardi and L. Sacerdote, Biol. Cybern. **35**, 1 (1979).

[49] G. V. Vinci, L. Fasano, and M. Mattia, Zenodo (2021), https://zenodo.org/doi/10.5281/zenodo.5646221.

[50] M. Mattia and G. V. Vinci, Zenodo (2021), https://zenodo.org/doi/10.5281/zenodo.5518214.

[51] L. Gammaitoni, P. Hänggi, P. Jung, and F. Marchesoni, Rev. Mod. Phys. **70**, 223 (1998).

[52] B. Lindner and L. Schimansky-Geier, Phys. Rev. Lett. **86**, 2934 (2001).

[53] L. M. Ricciardi and S. Sato, J. Appl. Probab. **25**, 43 (1988).

[54] S. Ostojic, J. Neurophysiol. **106**, 361 (2011).