

## Maximum-Entropy Closures for Kinetic Theories of Neuronal Network Dynamics

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We analyze (1 + 1)D kinetic equations for neuronal network dynamics, which are derived via an intuitive closure from a Boltzmann-like equation governing the evolution of a one-particle (i.e., one-neuron) probability density function. We demonstrate that this intuitive closure is a generalization of moment closures based on the maximum-entropy principle. By invoking maximum-entropy closures, we show how to systematically extend this kinetic theory to obtain higher-order, (1 + 1)D kinetic equations and to include coupled networks of both excitatory and inhibitory neurons.

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How do networks of neurons in the brain store and process information? Fascinating as this question may be, the vast hierarchy of the multiple spatial and temporal scales in the cortical dynamics presents a significant challenge to theoretical and computational endeavors. For simulating and understanding the dynamics of large networks, an important approach is to derive effective dynamics, in which the issue naturally arises of what is an efficient representation of network dynamics. For example, the cat or monkey primary visual cortex exhibits laminar structures, in which many cellular properties such as orientation preference are arranged in regular patterns or maps across the cortex [1]. This suggests an important coarse-grained theoretical construction: some neuronal subpopulations may now be effectively represented by coarse-grained patches which are sufficiently large to contain many neurons, yet sufficiently small that regular response properties of the individual neurons within each patch are approximately the same for each neuron. Here, as a first step, we further develop theoretical frameworks for studying these homogenized, coarse-grained patches, i.e., networks of neurons with homogeneous couplings, for which applications of theoretical concepts and tools from nonequilibrium statistical physics to the network dynamics have been shown to be rather fruitful [2]. Recently, starting with such “microscopic” networks of homogeneously coupled, conductance-based integrate-and-fire (I&F) neurons, without introduction of any new parameters, kinetic equations have been derived via moment closures from a Boltzmann-like equation that governs the evolution of a one-particle (i.e., one-neuron) probability density function (PDF) [3]. This is very much reminiscent of derivations of hydrodynamic equations from the Boltzmann equation for molecular motion in fluids [4]. As shown previously [3], this kinetic theory captures the effects of large fluctuations in neuronal networks, with numerical efficiency and surprising accuracy. In this Letter, we analyze this kinetic theory approach and demonstrate that the postulated moment closures [3] are indeed a simple extension of closures based on the maximum-entropy principle (MEP).

We begin with a brief description of conductance-based I&F neuronal networks [5]. In an all-to-all coupled network of  $N_E$  excitatory neurons and  $N_I$  inhibitory neurons, the I&F dynamics of the  $i$ th neuron’s membrane potential,  $V_i^\lambda$ , of  $\lambda$  type is governed by

$$\begin{aligned} \frac{dV_i^\lambda}{dt} &= -\frac{V_i^\lambda - \varepsilon_r}{\tau} - \frac{G_i^{\lambda E}}{\tau}(V_i^\lambda - \varepsilon_E) - \frac{G_i^{\lambda I}}{\tau}(V_i^\lambda - \varepsilon_I), \\ \frac{dG_i^{\lambda E}}{dt} &= -\frac{G_i^{\lambda E}}{\sigma_E} + \sum_\mu \frac{f_E}{\sigma_E} \delta(t - t_\mu^{i,E}) + \frac{1}{\sigma_E} F_{\lambda E}^i, \\ \frac{dG_i^{\lambda I}}{dt} &= -\frac{G_i^{\lambda I}}{\sigma_I} + \sum_\mu \frac{f_I}{\sigma_I} \delta(t - t_\mu^{i,I}) + \frac{1}{\sigma_I} F_{\lambda I}^i, \end{aligned} \quad (1)$$

with  $\lambda = E, I$  labeling excitation and inhibition. Whenever  $V_i^\lambda(t)$  crosses the firing (spiking) threshold  $V_T$ , a spike is recorded with the spike time  $t_{sp}$  such that  $V_i^\lambda(t_{sp}^-) = V_T$  and  $V_i^\lambda(t_{sp}^+) = \varepsilon_r$ , where  $\varepsilon_r$  is the reset voltage [6]. Here,  $G_i^{\lambda E}(t)$  and  $G_i^{\lambda I}(t)$  are the excitatory and inhibitory conductances of the  $i$ th neuron of  $\lambda$  type, with corresponding reversal potentials  $\varepsilon_E$  and  $\varepsilon_I$ , respectively. Note that, from physiology, we have  $\varepsilon_I \leq \varepsilon_r < V_T < \varepsilon_E = 0$  mV. (Typical values are  $\varepsilon_I = -80$  mV,  $\varepsilon_r = -70$  mV,  $V_T = -55$  mV, and  $\varepsilon_E = 0$  mV.)  $\tau$  is the membrane time constant of the membrane potential, whereas  $\sigma_E$  and  $\sigma_I$  are the decay time constants of excitatory and inhibitory conductances, respectively. For external inputs, we assume that the  $i$ th neuron of the excitatory [inhibitory] population receives external spikes,  $\{t_\mu^{i,E}\}$  [ $\{t_\mu^{i,I}\}$ ], each of which is an independent realization of a Poisson process with rate  $\nu_{0E}(t)$  [ $\nu_{0I}(t)$ ].  $f_E$  ( $f_I$ ) describes the strength of the excitatory (inhibitory) input.  $F_{\lambda E}^i = (S_{\lambda E}/N_E) \sum_{j \in \mathcal{P}_E} \times \sum_\mu \delta(t - t_{j\mu}^E)$ , and  $F_{\lambda I}^i = (S_{\lambda I}/N_I) \sum_{j \in \mathcal{P}_I} \sum_\mu \delta(t - t_{j\mu}^I)$  describe the interactions between neurons in the network.  $t_{j\mu}^E$  ( $t_{j\mu}^I$ ) is the spike time of the  $\mu$ th spike of the  $j$ th excitatory (inhibitory) neuron. The parameters  $S_{\lambda E}$  ( $S_{\lambda I}$ ) describe the strength of network couplings from the excitatory (inhibitory) population to the  $\lambda$  population of neurons.  $\mathcal{P}_E$  ( $\mathcal{P}_I$ ) denotes the set of excitatory (inhibitory) neurons. The factor  $1/N_{E,I}$  ensures that there is a well-

defined network coupling in the limit of  $N_{E,I} \rightarrow \infty$ . We note in passing that, for certain statistical properties, I&F neurons have been shown experimentally to be a reasonably good model of real neurons [7].

First, for conceptual simplicity, we discuss the kinetic theory for an all-to-all coupled network consisting of  $N$  excitatory I&F neurons, whose dynamics is governed by

$$\begin{aligned} \tau \frac{dV_i}{dt} &= -(V_i - \varepsilon_r) - G_i(t)(V_i - \varepsilon_E), \\ \sigma \frac{dG_i}{dt} &= -G_i + f \sum_{\mu} \delta(t - t_{\mu}^i) + \frac{S}{N} \sum_j \sum_{\mu} \delta(t - t_{j\mu}), \end{aligned} \quad (2)$$

[i.e., Eq. (1) without any inhibitory neurons,  $N_I \equiv 0$ ] where  $V_i$  is the membrane potential of the  $i$ th neuron in the network and  $\sigma$  is the decay time scale of the excitatory conductance time course [6].  $S$  is the strength of coupling between neurons in the network.

To capture the statistical behavior of the network, we study the evolution of the PDF,  $\rho(v, g, t) = \mathbb{E}[\frac{1}{N} \times \sum_{i=1}^N \delta(v - V_i(t)) \delta(g - G_i(t))]$ , where  $\mathbb{E}(\cdot)$  is the expectation with respect to all possible sets of  $N$  independent realizations of the input Poisson spike train with rate  $\nu_0(t)$  for given initial data (further average over an ensemble of initial conditions can be performed if necessary). If the input spike train summed from all other neurons to the  $i$ th neuron is approximated [8] by a Poisson process, a (2 + 1)D Boltzmann-like equation can be derived for  $\rho = \rho(v, g, t)$  [3]:

$$\begin{aligned} \partial_t \rho &= \partial_v \left\{ \left[ \left( \frac{v - \varepsilon_r}{\tau} \right) + g \left( \frac{v - \varepsilon_E}{\tau} \right) \right] \rho \right\} + \partial_g \left( \frac{g}{\sigma} \rho \right) \\ &+ \nu_0(t) \left[ \rho \left( v, g - \frac{f}{\sigma}, t \right) - \rho(v, g, t) \right] \\ &+ m(t) N \left[ \rho \left( v, g - \frac{S}{N\sigma}, t \right) - \rho(v, g, t) \right] \end{aligned} \quad (3)$$

for  $N \gg 1$ , where  $m(t)$  is the population-averaged firing rate per neuron. Note that, from Eq. (2), the jump in conductance of a neuron, induced by a single spike from the external input, is  $f/\sigma$ , whereas the jump, induced by a single spike from another neuron in the network, is  $S/(N\sigma)$ . Assuming that these jumps are small, a diffusion approximation of Eq. (3) yields

$$\begin{aligned} \partial_t \rho &= \partial_v \left\{ \left[ \left( \frac{v - \varepsilon_r}{\tau} \right) + g \left( \frac{v - \varepsilon_E}{\tau} \right) \right] \rho \right\} \\ &+ \partial_g \left\{ \left[ \frac{1}{\sigma} [g - \bar{g}(t)] \rho + \frac{\sigma_g^2(t)}{\sigma} \partial_g \rho \right] \right\} \end{aligned} \quad (4)$$

with

$$\bar{g}(t) \equiv f \nu_0(t) + S m(t), \quad (5a)$$

$$\sigma_g^2(t) \equiv \frac{1}{2\sigma} \left[ f^2 \nu_0(t) + \frac{S^2}{N} m(t) \right]. \quad (5b)$$

Equation (4) expresses the conservation of probability with  $J_V(v, g) = -\left[ (v - \varepsilon_r) + g(v - \varepsilon_E) \right] \rho(v, g) / \tau$  as its flux along the  $v$  direction, which satisfies  $J_V(V_T, g) =$

$J_V(\varepsilon_r, g)$ , reflecting that the neurons that just fired all enter through the reset voltage. Firing rate is one of the most important quantities measured in physiological experiments to describe neuronal network properties. The dynamics of the network (2) is characterized by  $m(t)$  as determined by the total probability flux across the threshold  $V_T$  regardless of the values of conductance, i.e.,  $m(t) = \int J_V(V_T, g, t) dg$ . Thus, for a given  $\rho(v, g, t)$ , we can determine the firing rate. However, Eq. (4) is specified with the parameters  $\bar{g}(t)$  and  $\sigma_g^2(t)$ , which are functions of  $m(t)$ , which, in turn, is solved via the boundary value of  $\rho(V_T, g, t)$  through  $J_V(V_T, g)$ . In this sense, therefore, Eq. (4) is a nonlinear (2 + 1)D equation.

Clearly, analytical insights and computational advantage can be achieved if the (2 + 1)D dynamics [Eq. (4)] can be reduced to a (1 + 1)D effective dynamics. We now turn to this reduction. Equation (4) can be projected to  $g$  space to yield

$$\partial_t \rho^{(g)}(g) = \partial_g \left\{ \frac{1}{\sigma} \left[ (g - \bar{g}) + \sigma_g^2 \partial_g \right] \rho^{(g)}(g) \right\} \quad (6)$$

with  $\rho^{(g)}(g) = \int_{\varepsilon_r}^{V_T} \rho(v, g) dv$ . Defining the conditional moments  $\mu_n(v) = \int g^n \rho(g|v) dg$ , where  $\rho(v, g) = \rho(g|v) \rho^{(v)}(v)$ , and  $\rho^{(v)}(v) = \int \rho(v, g) dg$ , integrating Eq. (4) over  $g$  yields

$$\partial_t \rho^{(v)}(v) = \partial_v [U(\mu_1, v) \rho^{(v)}(v)], \quad (7)$$

and multiplying Eq. (4) by  $g^n$ , then integrating over  $g$ , generates an infinite hierarchy of equations governing the evolution of  $\mu_n(v)$ :

$$\begin{aligned} \partial_t \mu_n &= \frac{1}{\tau \rho^{(v)}} \partial_v \left\{ [\mu_{n+1} - \mu_n \mu_1] (v - \varepsilon_E) \rho^{(v)} \right\} \\ &- \frac{n}{\sigma} (\mu_n - \bar{g} \mu_{n-1}) + \frac{n(n-1) \sigma_g^2}{\sigma} \mu_{n-2} \\ &+ U(\mu_1, v) \partial_v \mu_n \end{aligned} \quad (8)$$

with  $U(\mu_1, v) \equiv [(v - \varepsilon_r) + \mu_1(v)(v - \varepsilon_E)] / \tau$  and  $\mu_0(v) = 1$ . Note that, for example, the evolution of  $\mu_1$  depends on the evolution of  $\mu_2$  in Eq. (8) for  $n = 1$ . Thus, the closure issue naturally arises, i.e., how to truncate this hierarchy to close the equations to lower order moments such that the truncated dynamics can still capture the essential dynamics of the system.

We postulate a closure based on MEP. Here, we illustrate the procedure for closing Eq. (8) at  $\mu_2$ . First, the entropy

$$S[\rho] \equiv - \int \rho(g|v) \log \frac{\rho(g|v)}{\rho_{\text{eq}}(g)} dg$$

is maximized subject to the constraints that (i)  $\int \rho(g|v) dg = 1$ , (ii)  $\int g \rho(g|v) dg = \mu_1(v)$ , where  $\rho_{\text{eq}}(g)$  is the equilibrium solution of Eq. (6); i.e.,  $\rho_{\text{eq}}(g) \equiv (1/\sqrt{2\pi\sigma_g^2}) \exp[-(g - \bar{g})^2 / 2\sigma_g^2]$  if  $\bar{g}, \sigma_g^2$  are constants. The maximization yields the solution  $\hat{\rho}(g|v) = \rho_{\text{eq}}(g) \times \exp[-\lambda_0(v) - \lambda_1(v)g]$ , where  $\lambda_0, \lambda_1$  are Lagrange multi-

pliers. Solving the constraints (i) and (ii) leads to the result that the entropy attains its maximum at  $\hat{\rho}(g|v) = (1/\sqrt{2\pi}\sigma_g) \exp\{-[g - \mu_1(v)]^2/2\sigma_g^2\}$  with  $\mu_1(v) = \bar{g} - \lambda_1(v)\sigma_g^2$ . Next, this entropy-maximizing  $\hat{\rho}(g|v)$  is used to evaluate  $\mu_2(v) = \int g^2 \hat{\rho}(g|v) dg$  to express the 2nd moment in terms of the 1st moment, i.e., a *closure* condition:

$$\mu_2(v) = \mu_1^2(v) + \sigma_g^2. \quad (9)$$

Under the closure (9), Eq. (8), for  $n = 1$ , becomes closed; i.e.,  $\mu_2$  is replaced by  $\mu_1^2 + \sigma_g^2$ . Thus, we arrive at the (1 + 1)D kinetic equations governing the coupled excitatory neuronal networks:

$$\partial_t \rho^{(v)}(v) = \partial_v [U(\mu_1, v) \rho^{(v)}(v)], \quad (10a)$$

$$\begin{aligned} \partial_t \mu_1(v) = & -\frac{1}{\sigma} [\mu_1(v) - \bar{g}] + U(\mu_1, v) \partial_v \mu_1(v) \\ & + \frac{\sigma_g^2}{\tau \rho^{(v)}(v)} \partial_v [(v - \varepsilon_E) \rho^{(v)}(v)], \end{aligned} \quad (10b)$$

which are closed with respect to  $\mu_1(v)$  and  $\rho^{(v)}(v)$ . Mathematically, a closure issue is often a coarse-graining issue, i.e., whether there exists a scale below which the dynamics either by itself is sufficiently smooth (without much structure) or can be averaged out. In Ref. [3], a moment closure is intuited from this coarse-graining viewpoint; i.e., the conditional variance  $\Sigma^2(v) \equiv \mu_2 - \mu_1^2$  is a sufficiently slowly varying function of  $v$ . Hence, it is postulated in Ref. [3] that

$$\Sigma^2(v) = \sigma_g^2(t), \quad (11)$$

as a closure to derive Eq. (10). Conceptually, it is surprising to note that the closure condition (9) derived under MEP precisely coincides with closure (11) if  $\bar{g}$ ,  $\sigma_g^2$  are constants. Therefore, the closure (11) can be viewed as a generalization of the maximum-entropy closure to a time-dependent case. The kinetic Eqs. (10) derived under the closure (11) is dynamically very accurate as shown in Fig. 1 [3] in capturing the statistical properties of the original microscopic I&F neuronal network dynamics by comparing the prediction of the kinetic theory (10) with the full simulation of the I&F neuronal networks under a time-dependent input [9]. Figure 1 also shows the failure of a mean-field closure; i.e.,  $\mu_2(v) = \mu_1(v)^2$  in capturing statistical properties of the system.

The advantage of the MEP approach is to enable one to systematically go beyond the low order kinetic Eq. (10). For example, to include, in the kinetic theory, the dynamics of  $\mu_2$ , which is governed by Eq. (8) with  $n = 2$ , which depends on  $\mu_3(v)$ , an additional constraint  $\int g^2 \rho(g|v) dg = \mu_2(v)$  should be added to the entropy maximization. This yields the closure condition  $\mu_3 =$

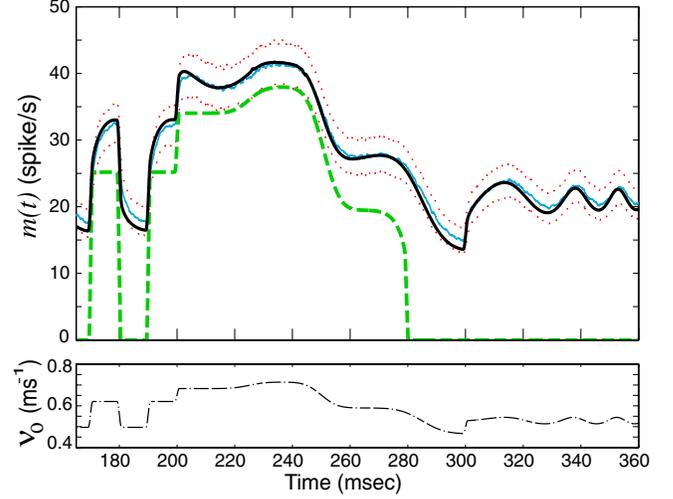


FIG. 1 (color online). Dynamical accuracy of kinetic theory (10)— $m(t)$  (upper panel) as a function of input rate  $\nu_0(t)$  (dot-dashed line in the lower panel).  $m(t)$  computed using Eq. (10) (thick solid line) is compared with that measured from the full simulation of the original I&F dynamics (2) with the dotted lines indicating 1 standard deviation away from the population mean (thin solid line); The thick dashed line is  $m(t)$  computed via a mean-field approximation [3,10] obtained using the closure  $\mu_2(v) = \mu_1(v)^2$ . Parameters:  $\tau = 20$  ms,  $\sigma = 0.1$  ms,  $f = 0.48$  ms,  $S = 0.1$ ,  $N = 100$ .

$3\mu_2\mu_1 - 2\mu_1^3$ , under which Eq. (8) with  $n = 2$  is closed to become

$$\begin{aligned} \partial_t \mu_2 = & -\frac{2}{\sigma} [\mu_2 - \bar{g}\mu_1] + \frac{2\sigma_g^2}{\sigma} + U(\mu_1, v) \partial_v \mu_2 \\ & + \frac{2}{\tau \rho^{(v)}} \partial_v \{ \mu_1 [\mu_2 - \mu_1^2] (v - \varepsilon_E) \rho^{(v)} \}. \end{aligned} \quad (12)$$

Equations (7), (12), and (8) for  $n = 1$ , constitute higher-order (1 + 1)D kinetic equations that are closed with respect to  $\mu_1(v)$ ,  $\mu_2(v)$  and  $\rho^{(v)}(v)$ .

We now turn to a brief description of how to extend the maximum-entropy argument to the coupled I&F dynamics (1) with *both* excitatory and inhibitory neurons. The PDF is now defined by  $\rho_\lambda(v, g_E, g_I, t) = \mathbb{E}[\frac{1}{N_\lambda} \sum_{i=1}^{N_\lambda} \delta(v - V_i^\lambda(t)) \times \delta(g_E - G_i^{\lambda E}(t)) \delta(g_I - G_i^{\lambda I}(t))]$  for the  $\lambda$  population,  $\lambda = E, I$ , where  $\mathbb{E}(\cdot)$  is the expectation with respect to all possible sets of independent realizations of the input Poisson spike process in an ensemble of identically structured networks. Assuming (i)  $N_E, N_I \gg 1$ , and (ii) the Poisson property for summed spike trains from all other neurons in the network, a diffusion approximation to the Boltzmann-like equation similar to Equation (3) yields

$$\begin{aligned} \partial_t \rho_\lambda = & \partial_{g_E} \left\{ \frac{1}{\sigma_E} \{ [g_E - \bar{g}_{\lambda E}(t)] \rho_\lambda + \sigma_{\lambda E}^2 \partial_{g_E} \rho_\lambda \} \right\} + \partial_{g_I} \left\{ \frac{1}{\sigma_I} \{ [g_I - \bar{g}_{\lambda I}(t)] \rho_\lambda + \sigma_{\lambda I}^2 \partial_{g_I} \rho_\lambda \} \right\} \\ & + \partial_v \left\{ \frac{1}{\tau} [(v - \varepsilon_r) + g_E(v - \varepsilon_E) + g_I(v - \varepsilon_I)] \rho_\lambda \right\} \end{aligned} \quad (13)$$

with  $\bar{g}_{\lambda\lambda'}(t) = f_{\lambda'}\nu_{0\lambda'}(t) + S_{\lambda\lambda'}m_{\lambda'}(t)$ , and  $\sigma_{\lambda\lambda'}^2 = [f_{\lambda'}^2\nu_{0\lambda'}(t) + S_{\lambda\lambda'}^2m_{\lambda'}(t)/N_{\lambda'}]/2\sigma_{\lambda'}$  with  $\lambda' = E, I$ . Marginalization of Eq. (13) to  $g_E, g_I$  leads to

$$\partial_t \rho_{\lambda}^{(\lambda')}(g_{\lambda'}) = \partial_{g_{\lambda'}} \left\{ \left[ \frac{g_{\lambda'} - \bar{g}_{\lambda\lambda'}}{\sigma_{\lambda'}} + \frac{\sigma_{\lambda\lambda'}^2}{\sigma_{\lambda'}} \partial_{g_{\lambda'}} \right] \rho_{\lambda}^{(\lambda')}(g_{\lambda'}) \right\}, \quad (14)$$

where, e.g.,  $\rho_{\lambda}^{(E)}(g_E) = \int_{\varepsilon_I}^{V_T} dv \int dg_I \rho_{\lambda}(v, g_E, g_I, t)$ . Similar to Eq. (6), Eq. (14) has a Gaussian equilibrium solution:  $\rho_{\text{eq}}(g_{\lambda'}) \equiv (1/\sqrt{2\pi}\sigma_{\lambda\lambda'}) \exp[-(g_{\lambda'} - \bar{g}_{\lambda\lambda'})^2/2\sigma_{\lambda\lambda'}^2]$  for  $\lambda' = E, I$ . We again invoke MEP by maximizing the entropy

$$S[\rho_{\lambda}] = - \int \rho_{\lambda}(g_E, g_I|v) \log \frac{\rho_{\lambda}(g_E, g_I|v)}{\rho_{\text{eq}}(g_E)\rho_{\text{eq}}(g_I)} dg_E dg_I$$

subject to the constraints that  $\int \rho_{\lambda}(g_E, g_I|v) dg_E dg_I = 1$ ,  $\int g_{\lambda'} \rho_{\lambda}(g_E, g_I|v) dg_E dg_I = \mu_{\lambda\lambda'}(v)$ . For  $\mu_{\lambda\lambda'}^{(2)}(v) \equiv \int g_{\lambda'}^2 \rho_{\lambda}(g_E, g_I|v) dg_E dg_I$ , and  $\mu_{\lambda EI}^{(2)}(v) \equiv \int g_E g_I \rho_{\lambda}(g_E, g_I|v) dg_E dg_I$ , the closure thus obtained consists of *Closure Condition I*:

$$\mu_{\lambda E}^{(2)}(v) = \mu_{\lambda E}^2(v) + \sigma_{\lambda E}^2, \quad \mu_{\lambda I}^{(2)}(v) = \mu_{\lambda I}^2(v) + \sigma_{\lambda I}^2,$$

which are similar to the closure above for a purely excitatory neuronal network, and *Closure Condition II*:

$$\mu_{\lambda EI}^{(2)}(v) = \mu_{\lambda E}(v)\mu_{\lambda I}(v);$$

i.e., the conditional correlation between the excitatory and inhibitory conductances vanishes. Under these closure conditions, Eq. (13) gives rise to the following (1 + 1)D kinetic equations:

$$\partial_t \rho_{\lambda}^{(v)} = \partial_v [U_{\lambda}(\mu_{\lambda E}, \mu_{\lambda I}, v) \rho_{\lambda}^{(v)}], \quad (15a)$$

$$\begin{aligned} \partial_t \mu_{\lambda\lambda'} = & -\frac{1}{\sigma_{\lambda'}} [\mu_{\lambda\lambda'} - \bar{g}_{\lambda\lambda'}] + U_{\lambda}(\mu_{\lambda E}, \mu_{\lambda I}, v) \partial_v \mu_{\lambda\lambda'} \\ & + \frac{\sigma_{\lambda\lambda'}^2}{\tau \rho_{\lambda}^{(v)}} \partial_v [(v - \varepsilon_{\lambda'}) \rho_{\lambda}^{(v)}], \end{aligned} \quad (15b)$$

which are closed with respect to  $\mu_{\lambda\lambda'}(v)$  and  $\rho_{\lambda}^{(v)}(v)$  for  $\lambda, \lambda' = E, I$ . Here,  $U_{\lambda}(\mu_{\lambda E}, \mu_{\lambda I}, v) \equiv [(v - \varepsilon_r) + \mu_{\lambda E}(v)(v - \varepsilon_E) + \mu_{\lambda I}(v)(v - \varepsilon_I)]/\tau$ . Equations (15) constitute the kinetic equations for dynamics of coupled excitatory and inhibitory networks. Clearly, the maximum-entropy approach allows one to systematically extend the kinetic theory to higher orders in the hierarchy for the general neuronal network (1).

In summary, we have shown that the closures used in the derivation of kinetic theories [3] are a generalization of moment closures based on MEP. We have presented a systematic way of deriving higher-order kinetic equations

via maximum-entropy closures from the Boltzmann-like equation governing the evolution of a one-particle (one-neuron) PDF for the neuronal network dynamics. Finally, we point out that the order  $n$  of the hierarchy (8) to be closed can be consistently determined by the order used in the Taylor expansion of Eq. (3).

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- [1] T. Bonhoeffer and A. Grinvald, *Nature (London)* **353**, 429 (1991); G. Blasdel, *J. Neurosci.* **12**, 3115 (1992); **12**, 3139 (1992); R. Everson *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **95**, 8334 (1998); P. Maldonado *et al.*, *Science* **276**, 1551 (1997).
  - [2] B. Knight, *J. Gen. Physiol.* **59**, 734 (1972); W. Wilbur and J. Rinzel, *J. Theor. Biol.* **105**, 345 (1983); L. F. Abbott and C. van Vreeswijk, *Phys. Rev. E* **48**, 1483 (1993); A. Treves, *Network* **4**, 259 (1993); T. Chawanya *et al.*, *Biol. Cybern.* **68**, 483 (1993); G. Barna *et al.*, *Biol. Cybern.* **79**, 309 (1998); J. Pham *et al.*, *Neural Networks* **11**, 415 (1998); N. Brunel and V. Hakim, *Neural Comput.* **11**, 1621 (1999); N. Fourcaud and N. Brunel, *Neural Comput.* **14**, 2057 (2002); W. Gerstner, *Neural Comput.* **12**, 43 (2000); A. Omurtag *et al.*, *J. Comput. Neurosci.* **8**, 51 (2000); A. Omurtag *et al.*, *Network: Comput. Neural Syst.* **11**, 247 (2000); D. Nykamp and D. Tranchina, *J. Comput. Neurosci.* **8**, 19 (2000); *Neural Comput.* **13**, 511 (2001); E. Haskell *et al.*, *Network: Comput. Neural Syst.* **12**, 141 (2001); H. Hasegawa, *Phys. Rev. E* **67**, 041903 (2003); **70**, 066107 (2004).
  - [3] D. Cai *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **101**, 7757 (2004); D. Cai *et al.*, *Commun. Math. Sci.* **4**, 97 (2006).
  - [4] H. Grad, *Commun. Pure Appl. Math.* **2**, 331 (1949); C. D. Levermore, *J. Stat. Phys.* **83**, 1021 (1996).
  - [5] C. Koch, *Biophysics of Computation* (Oxford University Press, Oxford, 1999).
  - [6] Note that kinetic theories described here can be extended to include more complicated time courses of conductances, such as an  $\alpha$  function, and even more realistic neuronal models [5] with a finite refractory period (Note that no refractory period is assumed here).
  - [7] M. Carandini *et al.*, *J. Neurophysiol.* **76**, 3425 (1996); A. Rauch *et al.*, *ibid.* **90**, 1598 (2003).
  - [8] E. Cinlar, in *Stochastic Point Processes: Statistical Analysis, Theory, and Applications*, edited by P. Lewis (Wiley, New York, 1972), pp. 549–606.
  - [9] Note that it is  $10^{4-5}$  times faster using kinetic theory (10) than using the I&F dynamics simulation to obtain the firing rate computationally.
  - [10] A. Treves, *Network* **4**, 259 (1993); M. Shelley and D. McLaughlin, *J. Comput. Neurosci.* **12**, 97 (2002).