A Generalized Rate Model for Neuronal Ensembles

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Abstract

There has been a long-standing controversy whether information in neuronal networks is carried by the firing rate code or by the firing temporal code. The current status of the rivalry between the two codes is briefly reviewed with the recent studies such as the brain-machine interface (BMI). Then we have proposed a generalized rate model based on the finite $N$-unit Langevin model subjected to additive and/or multiplicative noises, in order to understand the firing property of a cluster containing $N$ neurons. The stationary property of the rate model has been studied with the use of the Fokker-Planck equation (FPE) method. Our rate model is shown to yield various kinds of stationary distributions such as the interspike-interval distribution expressed by non-Gaussians including gamma, inverse-Gaussian-like and log-normal-like distributions.

The dynamical property of the generalized rate model has been studied with the use of the augmented moment method (AMM) which was developed by the author [H. Hasegawa, J. Phys. Soc. Jpn. 75 (2006) 033001]. From the macroscopic point of view in the AMM, the property of the $N$-unit neuron cluster is expressed in terms of three quantities: $\mu$, the mean of spiking rates of $R = (1/N) \sum_i r_i$ where $r_i$ denotes the firing rate of a neuron $i$ in the cluster; $\gamma$, averaged fluctuations in local variables ($r_i$); $\rho$, fluctuations in global variable ($R$). We get equations of motions of the three quantities, which show $\rho \sim \gamma/N$ for weak couplings. This implies that the population rate code is generally more reliable than the single-neuron rate code. Dynamical responses of the neuron cluster to pulse and sinusoidal inputs calculated by the AMM are in good agreement with those by direct simulations (DSs).

Our rate model is extended and applied to an ensemble containing multiple neuron clusters. In particular, we have studied the property of a generalized Wilson-Cowan model for an ensemble consisting of two kinds of excitatory and inhibitory clusters.

Keywords: neuron ensemble, rate code, temporal code, rate model, Wilson-Cowan model
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**Abbreviations**

AMM: augmented moment method
BCI: brain-computer interface
BMI: brain-machine interface
DS: direct simulation
FPE: Fokker-Planck equation
1 Introduction

Human brain contains more than $10^{10}$ neurons [1]. Neurons communicate information, emitting short voltage pulses called spikes, which propagate through axons and dendrites to neurons at the next stage. It has been a long-standing controversy how neurons communicate information by firings or spikes [2]-[6]. The issue on the neural code is whether information is encoded in the rate of firings of neurons (rate code) or in the more precise firing times (temporal code). The rate code was first recognized by Adrian [7] who noted that the neural firing was increased with increasing the stimulus intensity. The firing rate $r(t)$ of a neuron is defined by

$$r(t) = \frac{n(t, t + t_w)}{t_w} = \frac{1}{t_w} \int_t^{t+t_w} \sum_k \delta(t' - t_k) \, dt',$$

where $t_w$ denotes the time window, $n(t, t + t_w)$ the number of firings between $t$ and $t + t_w$, and $t_k$ the $k$th firing time. It has been widely reported that firing activities of motor and sensory neurons vary in response to applied stimuli. In the temporal code, on the contrary, the temporal information like the inter-spike interval (ISI) defined by

$$T_k = t_{k+1} - t_k,$$

and its distribution $\pi(T)$, ISI histogram (ISIH), are considered to play the important role in the neural activity. More sophisticated methods such as the auto- and cross-correlograms and joint peri-stimulus time histogram (JPSTH) have been also employed for an analysis of correlated firings based on the temporal-code hypothesis. There have been accumulated experimental evidences, which seem to indicate a use of the temporal code in brain [2][8]-[11]. A fly can react to new stimuli and the change the direction of flight within 30-40 ms [2]. In primary visual cortices of mouse and cat, repetitions of spikes with the millisecond accuracy have been observed [8]. Humans can recognize visual scenes within tens of milliseconds, even though recognition is involved several processing steps [9]-[11].

The other issue on the neural code is whether information is encoded in the activity of a single (or very few) neuron or that of large number of neurons (population code) [12][13]. The classical population code is employed in a number of systems such as motor neurons [14], the place cell in hippocampus [15] and neurons in middle temporal (MT) areas [16]. Neurons in motor cortex of the monkey, for example, encode the direction of reaching movement of the arm. Information on the direction of the arm movement is decoded from a set of neuronal firing rates by summing the preferred direction vector weighted by the firing rate of each neuron in the neural population [13]. It has been considered that the rate code needs the time window of a few hundred milliseconds to accumulate information on firing rate, and then its information capacity and speed are limited compared to the temporal code. It is, however, not true when the rate is averaged over the ensembles (population rate code). The population average promotes the response, suppressing the effects of neuronal variability [17][18]. The population rate code is expected to be a useful coding method in many areas in the brain. Indeed, in recent brain-machine interface (BMI) or brain-computer interface
(BCI) [19][20][21], the information on hand position and velocity etc. at time $t$ is modeled as a weighted linear combination of neuronal firing rates collected by multi-electrodes as given by [20]

$$\mathbf{y}(t) = \sum_{u} \mathbf{a}(u) \mathbf{r}(t-u). \quad (3)$$

Here $\mathbf{y}(t)$ denotes a vector expressing position, velocity etc., $\mathbf{r}(t-u)$ expresses a vector of firing rates at time $t$ and timelag $u$, and $\mathbf{a}(u)$ stands for a vector of weight at the timelag $u$. Equation (3) is transformed to a matrix form, from which a vector $\mathbf{a}(u)$ is obtained by the linear filter method [22][23] with training data of $\mathbf{y}(t)$ and $\mathbf{r}(t-u)$. The predictor of a new, unobserved stimulus $\hat{\mathbf{y}}(t)$ for a observed $\hat{\mathbf{r}}(t-u)$ is then given by

$$\hat{\mathbf{y}}(t) = \sum_{u} \mathbf{a}(u) \hat{\mathbf{r}}(t-u). \quad (4)$$

Visual and sensory feedback signals like the pressure on animal’s skin may be sent back to the brain. It has been reported that an artificial hand is successfully manipulated by such decoding method for observed firing-rate signals of $\hat{\mathbf{r}}(t-u)$ [19][20]. A success in BMI strongly suggests that the population rate code is employed in sensory and motor neurons while it is still not clear which code is adopted in higher-level cortical neurons.

The microscopic, conductance-based mechanism of firings of neurons is fairly well understood. The dynamics of the membrane potential $V_i$ of the neuron $i$ in the neuron cluster is expressed by the Hodgkin-Huxley-type model given by [24]

$$C \frac{dV_i}{dt} = \sum_n g_n(V_i, \alpha_n)(V_r - V_i) + I_i. \quad (5)$$

Here $C$ expresses the capacitance of a cell: $V_r$ is the recovery voltage: $g_n(V_i, \alpha_n)$ denotes the conductance for $n$ ion channel ($n =$Na, K etc.) which depends on $V_i$ and $\alpha_n$, the gate function for the channel $n$: $I_i$ is the input arising from couplings with other neurons and an external input. The dynamics of $\alpha_n$ is expressed by the first-order differential equation. Since it is difficult to solve nonlinear differential equations given by Eq. (5), the reduced, simplified neuron models such as the integrate-and-fire (IF), the FitzHugh-Nagumo (FN) and Hindmarsh-Rose (HR) models have been employed. In the simplest IF model with a constant conductance, Eq. (5) reduces to the linear differential equation, which requires an artificial reset of $V_i$ at the threshold $\theta$.

It is not easy to analytically obtain the rate $r(t)$ or ISI $T(t)$ from spiking neuron model given by Eq. (5). There are two approaches in extracting the rate from spiking neuron model. In the first approach, Fokker-Planck equation (FPE) is applied to the IF model to calculate the probability $p(V,t)$, from which the rate $r(t)$ is obtainable. In order to avoid the difficulty of the range of variable: $-\infty < V \leq \theta$ in the original IF model, sophisticate quadratic and exponential IF models, in which the range of variable is $-\infty < V \leq \infty$, have been proposed [25]. In the second approach, the rate model is derived from the conductance-based model with synapses by using the $f-I$ relation between the applied dc current $I$ and the frequency $f$ of autonomous firings [26][27][28]. It has been shown that the conductance-
based model may lead to the rate model if the network state does not possess a high degree of synchrony [28].

In the rate-code hypothesis, a neuron is regarded as a black box receiving and emitting signals expressed by the firing rate. The dynamics of the rate \( r_i(t) \) of the neuron \( i \) in a cluster is expressed by

\[
\tau \frac{dr_i}{dt} = -r_i + K \left( \sum_j w_{ij}r_j + I_i \right),
\]

where \( \tau \) denotes the relaxation time, \( w_{ij} \) the coupling between neurons \( i \) and \( j \), and \( I_i \) an external input. The gain function \( K(x) \) is usually given by the sigmoid function or by the \( f - I \) relation mentioned above. One of disadvantages of the rate model is that the mechanism is not well biologically supported. Nevertheless, the rate model has been adopted for a study on many subjects of the brain. The typical rate model is the Wilson-Cowan (WC) model, with which the stability of a cluster consisting of excitatory and inhibitory neurons is investigated [29] [30]. The rate model given by Eq. (6) with \( K(x) = x \) is the Hopfield model [31], which has been extensively employed for a study on the memory in the brain with incorporating the plasticity of synapses into \( w_{ij} \).

It is well known that neurons in brains are subjected to various kinds of noises, though their precise origins are not well understood. The response of neurons to stimuli is modified by noises in various ways. Although firings of a single in vitro neuron are reported to be precise and reliable [32], those of in vivo neurons are quite unreliable, which is expected to be due to noisy environment. The strong criticism against the temporal code is that it is not vulnerable to noises, while the rate code is robust against them.

Noises may be, however, beneficial for the signal transmission in the brain against our wisdom. The most famous phenomenon is the stochastic resonance [33], in which the signal-to-noise ratio of subthreshold signals is improved by noises. It has been shown that the noise is essential for the rate-code signal to propagate through multilayers described by the IF model: otherwise firings tend to synchronize, by which the rate-code signal is deteriorated [34] [35]. Recent study using HH model has shown that firing-rate signals propagate through the multiplexer with the synchrony [36].

It is theoretically supposed that there are two types of noises: additive and multiplicative noises. The magnitude of the former is independent of the state of variable while that of the latter depends on its state. Interesting phenomena caused by the two noises have been investigated [37]. It has been realized that the property of multiplicative noises is different from that of additive noises in some respects. (1) Multiplicative noises induce the phase transition, creating an ordered state, while additive noises are against the ordering [38] [39]. (2) Although the probability distribution in stochastic systems subjected to additive Gaussian noise follows the Gaussian, it is not the case for multiplicative Gaussian noises which generally yield non-Gaussian distribution [40] [45]. (3) The scaling relation of the effective strength for additive noise given by \( \beta(N) = \beta(1)/\sqrt{N} \) is not applicable to that for multiplicative noise: \( \alpha(N) \neq \alpha(1)/\sqrt{N} \), where \( \alpha(N) \) and \( \beta(N) \) denote effective
strengths of multiplicative and additive noises, respectively, in the $N$-unit system [46]. A naive approximation of the scaling relation for multiplicative noise: $\alpha(N) = \alpha(1)/\sqrt{N}$ as adopted in Ref. [38], yields the result which does not agree with that of direct simulation (DS) [46].

Formally, noise can be introduced to the spiking and rate models, by adding a fluctuating noise term on the right-hand side of Eqs. (5) and (6), respectively. ISI data obtained from neuronal systems have been analyzed by using various population rate methods (for a recent review, see Refs. [47-48]). Experimental ISI data cannot always be described in terms of a single probability distribution. They are fitted by a superposition of some known probability densities such as the gamma, inverse-Gaussian and log-normal distributions. The gamma distribution with parameters $\lambda$ and $\mu$ is given by

$$P_{\text{gam}}(x) = \frac{\mu^{-\lambda}}{\Gamma(\lambda)} x^{\lambda-1} \exp\left(-\frac{x}{\mu}\right),$$

which is derived from a simple stochastic integrate-and-fire (IF) model with additive noises for Poisson inputs [49], $\Gamma(x)$ being the gamma function. For $\lambda = 1$ in Eq. (7), we get the exponential distribution relevant to a simple Poisson process. The inverse Gaussian distribution with parameters $\lambda$ and $\mu$ given by

$$P_{\text{IG}}(x) = \left(\frac{\lambda}{2\pi x^3}\right)^{1/2} \exp\left[-\frac{\lambda(x - \mu)^2}{2\mu^2 x}\right],$$

is obtained from a stochastic IF model in which the membrane potential is represented as a random walk with drift [50]. The log-normal distribution with parameters $\mu$ and $\sigma$ given by

$$P_{\text{LN}}(x) = \frac{1}{\sqrt{2\pi\sigma^2}} x \exp\left[-\frac{(\log x - \mu)^2}{2\sigma^2}\right],$$

is adopted when the log of ISI is assumed to follow the Gaussian [51]. Fittings of experimental ISI data to a superposition of these probability densities have been extensively discussed in the literature [47-51].

Much study has been made on the spiking neuron model for coupled ensembles with the use of two approaches: direct simulations (DSs) and analytical approaches such as FPE and moment method. DSs have been performed for large-scale networks mostly consisting of IF neurons. Since the time to simulate networks by conventional methods grows as $N^2$ with $N$, the size of the network, it is rather difficult to simulate realistic neuron clusters. In the FPE, dynamics of neuron ensembles is described by the population activity. Although the FPE is powerful method which is formally applicable to the arbitrary $N$, actual calculations have been made for $N = \infty$ with the mean-field and diffusion approximations. Quite recently, the population density method has been developed as a tool modeling large-scale neuronal clusters [52, 53]. As a useful semi-analytical method for stochastic neural models, the moment method was proposed [54]. For example, when the moment method is applied to $N$-unit FN model, original $2N$-dimensional stochastic equations are transformed to $N(2N + 3)$-dimensional deterministic equations. This figure becomes 230, 20300 and 2 003 000 for $N = 10, 100$ and 100, respectively.
In many areas of the brain, neurons are organized into groups of cells such as column in the visual cortex [55]. Experimental findings have shown that within small clusters consisting of finite number of neurons (∼10 − 1000), there exist many cells with very nearly identical responses to identical stimuli [55]. Analytical, statistical methods having been developed so far are mean-field-type theories which may deal with infinite-size systems, but not with finite-size ones. Based on a macroscopic point of view, Hasegawa [56] has proposed the augmented moment method (AMM), which emphasizes not the property of individual neurons but rather that of ensemble neurons. In the AMM, the state of finite $N$-unit stochastic ensembles is described by a fairly small number of variables: averages and fluctuations of local and global variables. For $N$-unit FN neuron ensembles, for example, the number of deterministic equation in the AMM becomes eight independent of $N$. This figure of eight is much smaller that those in the moment method mentioned above. The AMM has been successfully applied to a study on the dynamics of the Langevin model and stochastic spiking models such as FN and HH models, with global, local or small-world couplings (with and without transmission delays) [57]–[61].

The AMM in Ref. [56] was originally developed by expanding variables around their stable mean values in order to obtain the second-order moments both for local and global variables in stochastic systems. In recent papers [46]–[62], we have reformulated the AMM with the use of FPE to discuss stochastic systems subjected to multiplicative noise: the FPE is adopted to avoid the difficulty due to the Ito versus Stratonovich calculus inherent to multiplicative noise [63].

An example of calculations with the use of the AMM for a FN neuron cluster subjected to additive and multiplicative noises is presented in Figs. 1(a)–(e) [64]. When input pulses shown in Fig. 1(a) are applied to the 10-unit FN neuron cluster, the membrane potential $v_i(t)$ of a given neuron depicted in Fig. 1(b) is obtained by DS with a single trial. It has the much irregularity because of added noises. When we get the ensemble-averaged potential given by $V(t) = (1/N) \sum_i v_i(t)$, the irregularity is reduced as shown in Fig. 1(c). This is one of the advantages of the population code [17]. The results shown in Figs. 1(b) and 1(c) are obtained by a single trial. When we have repeated DS and taken the average over 100 trials, the irregularity in $V(t)$ is furthermore reduced as shown in Fig. 1(d). The result of the AMM, $\mu(t)$, plotted in Fig. 1(e) is in good agreement with that of DS in Fig. 1(d).

The purpose of the present paper is two fold: to propose a generalized rate model for neuron ensembles and to study its property with the use of FPE and the AMM. The paper is organized as follows. In Sec. 2, we discuss the generalized rate model for a single cluster containing $N$ neurons, investigating its stationary and dynamical properties. In Sec. 3, our rate model is extended and applied to an ensemble containing multiple neuron clusters. In particular, we study the two-cluster ensemble consisting of excitatory and inhibitory clusters. The final Sec. 4 is devoted to discussion and conclusion.
2 Single neuron clusters

2.1 Generalized rate model

We have adopted a neuronal cluster consisting of $N$ neurons. The dynamics of firing rate $r_i \geq 0$ of a neuron $i$ is assumed to be described by the Langevin model given by

$$\frac{dr_i}{dt} = F(r_i) + H(u_i) + \alpha G(r_i)\eta_i(t) + \beta \xi_i(t), \quad (i = 1 - N)$$ (10)

with

$$u_i(t) = \left( \frac{w}{Z} \right) \sum_{k(\neq i)} r_k(t) + I_i(t),$$ (11)

where $F(x)$, $G(x)$ and $H(x)$ are arbitrary functions of $x$; $Z = (N - 1)$ denotes the coordination number; $w$ is the coupling strength; $I_i(t)$ expresses an input from external sources; $\alpha$ and $\beta$ are the strengths of additive and multiplicative noises, respectively, given by $\eta_i(t)$ and $\xi_i(t)$ expressing zero-mean Gaussian white noises with correlations given by

$$< \eta_i(t) \eta_j(t') > = \delta_{ij} \delta(t - t'),$$ (12)

$$< \xi_i(t) \xi_j(t') > = \delta_{ij} \delta(t - t'),$$ (13)

$$< \eta_i(t) \xi_j(t') > = 0.$$ (14)

The rate models proposed so far have employed $F(x) = -\lambda x$ and $G(x) = 0$ (no multiplicative noises). In this paper, we will adopt several functional forms for $F(x)$ and $G(x)$. As for the gain function $H(x)$, two types of expressions have been adopted. In the first category, the sigmoid function such as $H(x) = \tanh(x)$, $1/(1 + e^{-x})$, $\text{atan}(x)$, etc. have been adopted. In the second category, $H(x)$ is given by the $f-I$ function as $H(x) = (x - x_c)\Theta(x - x_c)$ which expresses the frequency $f$ of autonomous oscillation of a neuron for the applied dc current $I$, $x_c$ denoting the critical value and $\Theta(x)$ the Heaviside function: $\Theta(x) = 1$ for $x \geq 0$ and 0 otherwise. It has been theoretically shown in Ref. [65] that when spike inputs with the mean ISI ($T_i$) are applied to an HH neuron, the mean ISI of output signals ($T_o$) is $T_o = T_i$ for $T_i \approx 15 \text{ ms}$ and $T_o \sim 15 \text{ ms}$ for $T_i > 15 \text{ ms}$. This is consistent with the recent calculation for HH neuron multilayers, which shows a nearly linear relationship between the input ($r_i$) and output rates ($r_o$) for $r_i < 60 \text{ Hz}$ [36]. It is interesting that the $r_i - r_o$ relation is continuous despite the fact that the HH neuron has the discontinuous first-type $f-I$ relation. We will adopt, in this paper, a simple expression given by [66]

$$H(x) = \frac{x}{\sqrt{x^2 + 1}},$$ (15)

although our result is valid for an arbitrary form for $H(x)$. The nonlinear, saturating behavior in $H(x)$ arises from the property of the refractory period ($\tau_r$) where spike outputs are prevented for $t_f < t < t_f + \tau_r$ after firing at $t = t_f$. 

8
2.2 Stationary property

2.2.1 Distribution of \( r \)

The Fokker-Planck equation for the distribution of \( p(r_i,t) \) is given by [67]

\[
\frac{\partial}{\partial t} p(r_i,t) = -\sum_k \frac{\partial}{\partial r_k} \left\{ \left[ F(r_k) + \frac{\phi \alpha^2}{2} G'(r_k)G(r_k) + H(u_k) \right] p(r_i,t) \right\} + \frac{1}{2} \sum_k \frac{\partial^2}{\partial r_k^2} \left\{ \left[ \alpha^2 G(r_k)^2 + \beta^2 \right] p(r_i,t) \right\},
\]

(16)

where \( G'(x) = dG(x)/dx \), and \( \phi = 1 \) and 0 in the Stratonovich and Ito representations, respectively.

The stationary distribution \( p(r) \) for \( w = 0 \) and \( I_i(t) = I \) is given by

\[
\ln p(r) \propto X(r) + Y(r) - \left( 1 - \frac{\phi}{2} \right) \ln \left[ \frac{\alpha^2 G(r)^2}{2} + \frac{\beta^2}{2} \right],
\]

(17)

with

\[
X(r) = 2 \int dr \left\{ \frac{F(r)}{\alpha^2 G(r)^2 + \beta^2} \right\},
\]

(18)

\[
Y(r) = 2 \int dr \left\{ \frac{H(I)}{\alpha^2 G(r)^2 + \beta^2} \right\}.
\]

(19)

Hereafter we mainly adopt the Stratonovich representation.

**Case I** \( F(x) = -\lambda x \) and \( G(x) = x \)

For the linear Langevin model, we get

\[
p(r) \propto \left[ \frac{\alpha^2 r^2}{\beta^2} \right]^{-\left( \frac{\lambda/\alpha^2 + 1/2}{\lambda/\alpha^2} \right)} e^{Y(r)},
\]

(20)

with

\[
Y(r) = \left( \frac{2H}{\alpha \beta} \right) \arctan \left( \frac{\alpha r}{\beta} \right),
\]

(21)

where \( H = H(I) \). In the case of \( H = Y(r) = 0 \), we get the \( q \)-Gaussian given by [43, 44]

\[
p(r) \propto \left[ 1 - (1-q)\gamma r^2 \right]^{-\frac{1}{1-q}},
\]

(22)

with

\[
\gamma = \frac{2\lambda + \alpha^2}{2\beta^2},
\]

(23)

\[
q = \frac{2\lambda + 3\alpha^2}{2\lambda + \alpha^2}.
\]

(24)

We examine the some limiting cases of Eq. (20) as follows.

(A) For \( \alpha = 0 \) and \( \beta \neq 0 \), Eq. (20) becomes

\[
p(r) \propto e^{-\frac{\alpha^2}{\beta^2} (r-H/\lambda)^2}.
\]

(25)

(B) For \( \beta = 0 \) and \( \alpha \neq 0 \), Eq. (20) becomes

\[
p(r) \propto r^{-(2\lambda/\alpha^2 + 1)} e^{-(2H/\alpha^2)/r}.
\]

(26)
Distributions $p(r)$ calculated with the use of Eqs. (22)-(26) are plotted in Figs. 2(a)-2(c). The distribution $p(r)$ for $\alpha = 0.0$ (without multiplicative noises) in Fig. 2(a) shows the Gaussian distribution which is shifted by an applied input $I = 0.1$. When multiplicative noises are added ($\alpha \neq 0$), the form of $p(r)$ is changed to the $q$-Gaussian given by Eq. (22). Figure 2(b) shows that when the magnitude of additive noises $\beta$ is increased, the width of $p(r)$ is increased. Figure 2(c) shows that when the magnitude of external input $I$ is increased, $p(r)$ is much shifted and widely spread. Note that for $\alpha = 0.0$ (no multiplicative noises), $p(r)$ is simply shifted without a change in its shape when increasing $I$.

**Case II** $F(x) = -\lambda x^a$ and $G(x) = x^b$ ($a, b \geq 0$)

The special case of $a = 1$ and $b = 1$ has been discussed in the preceding case I [Eqs. (22)-(26)]. For arbitrary $a \geq 0$ and $b \geq 0$, the probability distribution $p(r)$ given from Eqs. (17)-(19) becomes

$$p(r) \propto \left[1 + \left( \frac{a^2}{\beta^2} \right) r^{2b} \right]^{-1/2} \exp[X(r) + Y(r)],$$

with

$$X(r) = -\left( \frac{2\lambda r^{a+1}}{\beta^2(a+1)} \right) F \left(1, \frac{a+1}{2b} \frac{a+1}{2b} + 1; -\frac{\alpha^2 r^{2b}}{\beta^2} \right),$$

$$Y(r) = \left( \frac{2H r}{\beta^2} \right) F \left(1, \frac{1}{2b} \frac{1}{2b} + 1; -\frac{\alpha^2 r^{2b}}{\beta^2} \right),$$

where $F(a, b; c; z)$ is the hypergeometric function. Some limiting cases of Eqs. (27)-(29) are shown in the following.

(a) The case of $H = Y(r) = 0$ was previously studied in Ref. [44].

(b) For $\alpha = 0$ and $\beta \neq 0$, we get

$$p(r) \propto \exp \left[ -\left( \frac{2\lambda}{\beta^2(a+1)} \right) r^{a+1} + \left( \frac{2H}{\beta^2} \right) r \right], \quad \text{for } a + 1 \neq 0 \tag{30}$$

$$p(r) \propto r^{-2\lambda/\beta^2} \exp \left( \frac{2H r}{\beta^2} \right), \quad \text{for } a + 1 = 0 \tag{31}$$

(c) For $\beta = 0$ and $\alpha \neq 0$, we get

$$p(r) \propto r^{-b} \exp \left[ -\left( \frac{2\lambda}{\alpha^2(a-2b+1)} \right) r^{a-2b+1} - \left( \frac{2H}{\alpha^2(2b-1)} \right) r^{-2b+1} \right],$$

for $a - 2b + 1 \neq 0, 2b - 1 \neq 0 \tag{32}$

$$p(r) \propto r^{-(2\lambda/\alpha^2 + b)} \exp \left[ -\left( \frac{2H}{\alpha^2(2b-1)} \right) r^{-2b+1} \right], \quad \text{for } a - 2b + 1 = 0 \tag{33}$$

$$p(r) \propto r^{(2H/\alpha^2 - 1/2)} \exp \left[ -\left( \frac{2\lambda}{\alpha^2 a} \right) r^a \right], \quad \text{for } 2b - 1 = 0 \ (b = 1/2) \tag{34}$$

$$p(r) \propto r^{-[2(\lambda - H)/\alpha^2 + 1/2]}, \quad \text{for } a - 2b + 1 = 0, 2b - 1 = 0 \ (a = 0, b = 1/2) \tag{35}$$

(d) In the case of $a = 1$ and $b = 1/2$, we get

$$p(r) \propto \left( r + \frac{\beta^2}{\alpha^2} \right) \left( \frac{2\lambda}{\alpha^2} \right) \exp \left[ -\left( \frac{2\lambda}{\alpha^2} \right) r \right], \tag{36}$$
which reduces, in the limit of \( \alpha = 0 \), to
\[
p(r) \propto \exp \left[ -\left( \frac{\lambda}{\alpha^2} \right) \left( r - \frac{H}{\lambda} \right)^2 \right], \quad \text{for } \alpha = 0
\] (37)

**Case III** \( F(x) = -\lambda \ln x \) and \( G(x) = x^{1/2} \) \((x > 0)\)

We get
\[
p(r) \propto r^{-(1/2)} \exp \left[ -\left( \frac{\lambda}{\alpha^2} \right) \left( \ln r - \frac{H}{\lambda} \right)^2 \right], \quad \text{for } \beta = 0
\] (38)

Figure 3(a) shows distributions \( p(r) \) for various \( \alpha \) with fixed values of \( I = 0.1, b = 1.0, \alpha = 1.0 \) and \( \beta = 0.0 \) (multiplicative noise only). With decreasing \( \alpha \), a peak of \( p(r) \) at \( r \sim 0.1 \) becomes sharper. Figure 4(a) shows distributions \( p(r) \) for various \( b \) with fixed values of \( I = 0.1, a = 1.0, \alpha = 1.0 \) and \( \beta = 0.0 \) (multiplicative only). We note that a change in the \( b \) value yields considerable changes in shapes of \( p(r) \). Figures 3(b) and 4(b) will be discussed shortly.

### 2.2.2 Distribution of \( T \)

When the temporal ISI \( T \) is simply defined by \( T = 1/r \), its distribution \( \pi(T) \) is given by
\[
\pi(T) = p \left( \frac{1}{T} \right) \frac{1}{T^2}.
\] (39)

For \( F(x) = -\lambda x \), \( G(x) = x \) and \( \beta = 0 \), Eq. (26) or (33) yields
\[
\pi(T) \propto T^{(2\lambda/\alpha^2 - 1)} \exp \left[ -\left( \frac{2H}{\alpha^2} \right) T \right],
\] (40)

which expresses the gamma distribution [see Eq. (7)] [42, 49]. For \( F(x) = -\lambda x^2 \), \( G(x) = x \) and \( \beta = 0 \), Eq. (32) yields
\[
\pi(T) \propto T^{-1} \exp \left[ -\left( \frac{2H}{\alpha^2} \right) T - \left( \frac{2\lambda}{\alpha^2} \right) \frac{1}{T} \right],
\] (41)

which is similar to the inverse Gaussian distribution [see Eq. (8)] [50]. For \( F(x) = -\ln x \), \( G(x) = x^{1/2} \) and \( \beta = 0 \), Eq. (38) leads to
\[
\pi(T) \propto T^{-3/2} \exp \left[ -\left( \frac{2\lambda}{\alpha^2} \right) \left( \ln T + \frac{H}{\lambda} \right)^2 \right],
\] (42)

which is similar to the log-normal distribution [see Eq. (9)] [51].

Figures 3(b) and 4(b) show distributions of \( T, \pi(T) \), which are obtained from \( p(r) \) shown in Figs. 3(a) and 4(a), respectively, by a change of variable [Eq. (39)]. Figure 3(b) shows that with increasing \( \alpha \), the peak of \( \pi(T) \) becomes sharper and moves left. We note in Fig. 4(b) that the form of \( \pi(T) \) significantly varied by changing \( b \) in \( G(x) = x^b \).

### 2.2.3 Distribution of \( R \)

When we consider global variables \( R(t) \) defined by
\[
R(t) = \frac{1}{N} \sum_i r_i(t),
\] (43)
the distribution $P(R, t)$ for $R$ is given by

$$P(R, t) = \int \cdots \int \Pi_i \, dr_i \, p(\{r_i\}, t) \, \delta \left( R - \frac{1}{N} \sum_j r_j \right). \quad (44)$$

Analytic expressions of $P(R)$ are obtainable only for limited cases.

(a) For $\beta \neq 0$ and $\alpha = 0$, $P(R)$ is given by

$$P(R) \propto \exp \left[ - \left( \frac{\lambda N}{\beta^2} \right) \left( R - \frac{H}{\lambda} \right)^2 \right], \quad (45)$$

where $H = H(I)$.

(b) For $H = 0$, we get

$$P(R) = \frac{1}{2\pi} \int_{-\infty}^{\infty} dk \, e^{ikR} \, \Phi(k), \quad (46)$$

with

$$\Phi(k) = \left[ \phi \left( \frac{k}{N} \right) \right]^N, \quad (47)$$

where $\phi(k)$ is the characteristic function for $p(r)$ given by

$$\phi(k) = \int_{-\infty}^{\infty} e^{-ikx} \, p(x) \, dx, \quad (48)$$

$$= 2^{1-\nu} \left( \frac{\lambda'}{k} \right)^\nu K_\nu(\lambda' \, | \, k \, |), \quad (49)$$

with

$$\nu = \frac{\lambda}{\alpha^2}, \quad (50)$$

$$\lambda' = \frac{\beta}{\alpha}, \quad (51)$$

$K_\nu(x)$ expressing the modified Bessel function.

Some numerical examples of $P(R)$ are plotted in Figs. 5, 6 and 7. Figures 5(a) and 5(b) show $P(R)$ for $\alpha = 0.0$ and $\alpha = 0.5$, respectively, when $N$ is changed. For $\alpha = 0.0$, $P(R)$ is the Gaussian whose width is narrowed by a factor of $1/\sqrt{N}$ with increasing $N$. In contrast, $P(R)$ for $\alpha = 0.5$ is the non-Gaussian, whose shape seems to approach the Gaussian as increasing $N$. These are consistent with the central-limit theorem.

Effects of an external input $I$ on $p(r)$ and $P(R)$ are examined in Figs. 6(a) and 6(b). Figure 6(a) shows that in the case of $\alpha = 0.0$ (additive noise only), $p(r)$ and $P(R)$ are simply shifted by a change in $I$. This is not the case for $\alpha \neq 0.0$, for which $p(r)$ and $P(R)$ are shifted and widen with increasing $I$, as shown in Fig. 6(b).

Figures 7(a) and 7(b) show effects of the coupling $w$ on $p(r)$ and $P(R)$. For $\alpha = 0.0$, $p(r)$ and $P(R)$ are little changed with increasing $w$. On the contrary, for $\alpha = 0.5$, an introduction of the coupling significantly modifies $p(r)$ and $P(R)$ as shown in Fig. 7(b).
2.3 Dynamical property

2.3.1 AMM

Next we will discuss the dynamical property of the rate model by using the AMM. Moments of local variables are defined by

$$\langle r_k^i \rangle = \int \Pi_i \, dr_i \, p(\{r_i\}, t) \, r_k^i. \quad (k = 1, 2, \ldots) \quad (52)$$

Equations of motions of means, variances and covariances of local variables \((r_i)\) are given by \[46\]

$$\frac{d(r_i)}{dt} = \langle F(r_i) \rangle + \langle H(u_i) \rangle + \phi \frac{\alpha^2}{2} \langle G'(r_i)G(r_i) \rangle, \quad (53)$$

$$\frac{d\langle r_i \, r_j \rangle}{dt} = \langle r_i \, F(r_j) \rangle + \langle r_j \, F(r_i) \rangle + \langle r_i \, H(u_j) \rangle + \langle r_j \, H(u_i) \rangle$$

$$+ \phi \frac{\alpha^2}{2} \langle r_i G'(r_j)G(r_j) \rangle + \frac{\phi \alpha^2}{2} \langle r_j G'(r_i)G(r_i) \rangle$$

$$+ [\alpha^2 \langle G(r_i)^2 \rangle + \beta^2] \delta_{ij}. \quad (54)$$

Equations of motions of the mean, variance and covariance of global variables \((R)\) are obtainable by using Eqs. (43), (53) and (54):

$$\frac{d\langle R \rangle}{dt} = \frac{1}{N} \sum_i \frac{d(r_i)}{dt}, \quad (55)$$

$$\frac{d\langle R^2 \rangle}{dt} = \frac{1}{N^2} \sum_i \sum_j \frac{d\langle r_i \, r_j \rangle}{dt}. \quad (56)$$

In the AMM \[56\], we define \(\mu, \gamma\) and \(\rho\) given by

$$\mu = \langle R \rangle = \frac{1}{N} \sum_i \langle r_i \rangle, \quad (57)$$

$$\gamma = \frac{1}{N} \sum_i \langle (r_i - \mu)^2 \rangle, \quad (58)$$

$$\rho = \langle (R - \mu)^2 \rangle, \quad (59)$$

where \(\mu\) expresses the mean, \(\gamma\) the averaged fluctuations in local variables \((r_i)\) and \(\rho\) fluctuations in global variable \((R)\). Expanding \(r_i\) in Eqs. (53)-(56) around the average value of \(\mu\) as

$$r_i = \mu + \delta r_i,$$

and retaining up to the order of \(< \delta r_i \delta r_j >\), we get equations of motions for \(\mu, \gamma\) and \(\rho\) given by

$$\frac{d\mu}{dt} = f_0 + f_2 \gamma + h_0 + \left( \phi \frac{\alpha^2}{2} \right) \left[ g_0 g_1 + 3(g_1 g_2 + g_0 g_3) \gamma \right], \quad (61)$$

$$\frac{d\gamma}{dt} = 2 f_1 \gamma + 2 h_1 N \left( \frac{wN}{Z} \right) \left( \rho - \frac{\gamma}{N} \right)$$

$$+ (\phi + 1)(g_1^2 + 2g_0 g_2) \alpha^2 \gamma + \alpha^2 g_0^2 + \beta^2, \quad (62)$$

$$\frac{d\rho}{dt} = 2 f_1 \rho + 2 h_1 \omega \rho + (\phi + 1)(g_1^2 + 2g_0 g_2) \alpha^2 \rho + \frac{1}{N} (\alpha^2 g_0^2 + \beta^2), \quad (63)$$
where

\[
\begin{align*}
 f_\ell & = \frac{1}{\ell!} \frac{\partial^\ell F(\mu)}{\partial x^\ell}, \quad (64) \\
 g_\ell & = \frac{1}{\ell!} \frac{\partial^\ell G(\mu)}{\partial x^\ell}, \quad (65) \\
 h_\ell & = \frac{1}{\ell!} \frac{\partial^\ell H(u)}{\partial u^\ell}, \quad (66) \\
 u & = w\mu + I. \quad (67)
\end{align*}
\]

Original \( N \)-dimensional stochastic equations given by Eqs. (10), (11) and (15) are transformed to the three-dimensional deterministic equations given by Eqs. (61)-(63).

Before discussing the dynamical property, we study the stationary property of Eqs. (61)-(63). In order to make numerical calculations, we have adopted

\[
\begin{align*}
 F(x) & = -\lambda x, \quad (68) \\
 G(x) & = x, \quad (69)
\end{align*}
\]

where \( \lambda \) stands for the relaxation ratio. Equations (61)-(63) are expressed in the Stratonovich representation by

\[
\begin{align*}
 \frac{d\mu}{dt} & = -\lambda \mu + h_0 + \frac{\alpha^2 \mu}{2}, \quad (70) \\
 \frac{d\gamma}{dt} & = -2\lambda \gamma + 2h_1 wN Z \left( \rho - \frac{\gamma}{N} \right) + 2\alpha^2 \gamma + \alpha^2 \mu^2 + \beta^2, \quad (71) \\
 \frac{d\rho}{dt} & = -2\lambda \rho + 2h_1 w\rho + 2\alpha^2 \rho + \frac{\alpha^2 \mu^2}{N} + \frac{\beta^2}{N}. \quad (72)
\end{align*}
\]

where \( h_0 = u/\sqrt{u^2 + 1}, \ h_1 = 1/(u^2 + 1)^{3/2} \) and \( h_2 = -(3u/2)/(u^2 + 1)^{5/2} \). The stability of the stationary solution given by Eqs. (70)-(72) may examined by calculating eigenvalues of their Jacobian matrix, although actual calculations are tedious.

Figure 8 shows the \( N \) dependences of \( \gamma \) and \( \rho \) in the stationary state for four sets of parameters: \((\alpha, \beta, w) = (0.0, 0.1, 0.0) \) (solid curves), \((0.5, 0.1, 0.0) \) (dashed curves), \((0.0, 0.1, 0.5) \) (chain curves) and \((0.5, 0.1, 0.5) \) (double-chain curves), with \( \beta = 0.1, \ \lambda = 1.0 \) and \( I = 0.1 \). We note that for all the cases, \( \rho \) is proportional to \( N^{-1} \), which is easily realized in Eq. (72). In contrast, \( \gamma \) shows a weak \( N \) dependence for a small \( N \) (< 10).

### 2.3.2 Response to pulse inputs

We have studied the dynamical property of the rate model, by applying a pulse input given by

\[
I(t) = A \Theta(t - t_1)\Theta(t_2 - t) + I^{(b)}, \quad (73)
\]

with \( A = 0.5, \ t_1 = 40, \ t_2 = 50 \) and \( I^{(b)} = 0.1 \) expressing the background input, where \( \Theta(x) \) denotes the Heaviside function: \( \Theta(x) = 1 \) for \( x \geq 0 \) and 0 otherwise.

Figures 9(a), 9(b) and 9(c) show the time dependence of \( \mu, \ \gamma \) and \( \rho \) when the input pulse \( I(t) \) given by Eq. (73) is applied: solid and dashed curves show the results of AMM and DS averaged over 1000 trials, respectively, with \( \alpha = 0.5, \ \beta = 1.0, \ N = 10 \) and \( w = 0.5 \).
Figures 9(b) and 9(c) show that an applied input pulse induces changes in $\gamma$ and $\rho$. This may be understood from $2a^2$ terms in Eqs. (71) and (72). The results of AMM shown by solid curves in Figs. 9(a)-(c) are in good agreement with DS results shown by dashed curves. Figure 9(d) will be discussed in the followings.

It is possible to discuss the synchrony in a neuronal cluster with the use of $\gamma$ and $\rho$ defined by Eqs. (58) and (59) \[56\]. In order to quantitatively discuss the synchronization, we first consider the quantity given by

$$P(t) = \frac{1}{N^2} \sum_{ij} < [r_i(t) - r_j(t)]^2 >= 2[\gamma(t) - \rho(t)].$$

(74)

When all neurons are in the completely synchronous state, we get $r_i(t) = R(t)$ for all $i$, and then $P(t) = 0$ in Eq. (74). On the contrary, we get $P(t) = 2(1 - 1/N)\gamma \equiv P_0(t)$ in the asynchronous state where $\rho = \gamma/N \[56\]$. We may define the synchronization ratio given by

$$S(t) = 1 - \frac{P(t)}{P_0(t)} = \left(\frac{N\rho(t)/\gamma(t) - 1}{N - 1}\right),$$

(75)

which is 0 and 1 for completely asynchronous ($P = P_0$) and synchronous states ($P = 0$), respectively. Figure 9(d) shows the synchronization ratio $S(t)$ for $\gamma(t)$ and $\rho(t)$ plotted in Figs. 9(b) and 9(c), respectively, with $\alpha = 0.5$, $\beta = 1.0$, $N = 10$ and $w = 0.5$. The synchronization at $t < 40$ and $t > 60$ is 0.15, but it is decreased to 0.03 at $40 < t < 50$ by an applied pulse. This is because $\gamma$ is more increased than $\rho$ by an applied pulse. The synchronization ratio is vanishes for $w = 0$, and it is increased with increasing the coupling strength \[56\].

Next we show some results when indices $a$ and $b$ in $F(x) = -\lambda x^a$ and $G(x) = x^b$ are changed. Figure 10(a) shows the time dependence of $\mu$ for $(a, b) = (1, 1)$ (solid curve) and $(a, b) = (2, 1)$ (dashed curve) with $\alpha = 0.0$, $\beta = 0.1$, $N = 10$ and $w = 0.0$. The saturated magnitude of $\mu$ for $\alpha = 0.5$ is larger than that for $\alpha = 0.0$. Solid and dashed curves in Fig. 10(b) show $\mu$ for $(a, b) = (1, 1)$ and $(1,0.5)$, respectively, with $\alpha = 0.5$, $\beta = 0.001$, $N = 10$ and $w = 0.0$. Both results show similar responses to an applied pulse although $\mu$ for a background input of $I^{(b)} = 0.1$ for $(a, b) = (1,0.5)$ is a little larger than that for $(a, b) = (1,1)$.

### 2.3.3 Response to sinusoidal inputs

We have applied also a sinusoidal input given by

$$I(t) = A \left[1 - \cos \left(\frac{2\pi t}{T_p}\right)\right] + I^{(b)},$$

(76)

with $A = 0.5$, $I^{(b)} = 0.1$, and $T_p = 10$ and 20. Time dependences of $\mu$ for $T_p = 20$ and $T_p = 10$ are plotted in Figs. 11(a) and 11(b), respectively, with $\alpha = 0.5$, $\beta = 1.0$, $w = 0.0$ and $N = 10$, solid and dashed curves denoting $\mu$ and $I$, respectively. The delay time of $\mu$ against an input $I(t)$ is about $\tau_d \sim 1.0$ independent of $T_p$. The magnitude of $\mu$ for $T_p = 10$ is smaller than that for $T_p = 20$.


3 Multiple neuron clusters

3.1 AMM

We have assumed a neuronal ensemble consisting of \(M\) clusters, whose \(m\)th cluster includes \(N_m\) neurons. The dynamics of firing rate \(r_{mi} (\geq 0)\) of a neuron \(i\) in the cluster \(m\) is assumed to be described by the Langevin model given by

\[
\frac{dr_{mi}}{dt} = F(r_{mi}) + H(u_{mi}) + \alpha_mG(r_{mi})\eta_{mi}(t) + \beta_m\xi_{mi}(t), \quad (m = 1 - M, \; i = 1 - N_m)
\]

with

\[
u_{mi}(t) = \left(\frac{w_{mm}}{Z_m}\right) \sum_{k(\neq i)} r_{mk}(t) + \sum_{n(\neq m)} \sum_{\ell} \left(\frac{w_{mn}}{(M - 1)N_n}\right) r_{\ell n}(t) + I_m(t), \quad (78)
\]

where \(F(x)\) and \(G(x)\) are arbitrary functions of \(x\): \(H(x)\) is given by Eq. (15); \(Z_m (= N_m - 1)\) denotes the coordination number: \(I_m(t)\) expresses an external input to the cluster \(m\): \(\alpha_m\) and \(\beta_m\) are the strengths of additive and multiplicative noises, respectively, in the cluster \(m\) given by \(\eta_{mi}(t)\) and \(\xi_{mi}(t)\) expressing zero-mean Gaussian white noises with correlations given by

\[
< \eta_{ni}(t) \eta_{mj}(t') > = \delta_{nm}\delta_{ij}\delta(t - t'), \quad (79)
\]

\[
< \xi_{ni}(t) \xi_{mj}(t') > = \delta_{nm}\delta_{ij}\delta(t - t'), \quad (80)
\]

\[
< \eta_{ni}(t) \xi_{mj}(t') > = 0. \quad (81)
\]

In the AMM [56], we define means, variances and covariances, \(\mu_m, \gamma_m\) and \(\rho_{mn}\), given by

\[
\mu_m = \langle R_m \rangle = \frac{1}{N_m} \sum_i \langle r_{mi} \rangle, \quad (82)
\]

\[
\gamma_m = \frac{1}{N_m} \sum_i \langle (r_{mi} - \mu_m)^2 \rangle, \quad (83)
\]

\[
\rho_{mn} = \langle (R_m - \mu_m)(R_n - \mu_n) \rangle, \quad (84)
\]

where the global variable \(R_m\) is defined by

\[
R_m(t) = \frac{1}{N_m} \sum_i r_{mi}(t). \quad (85)
\]

Details of deriving equations of motions for \(\mu_m, \gamma_m\) and \(\rho_{mn}\) are given in the Appendix [Eqs. (A10)-(A12)].

3.2 Stationary property

Now we consider an E-I ensemble \((M = 2)\) consisting of excitatory (E) and inhibitory (I) neuron clusters, for which we get equations of motions for \(\mu_m, \gamma_m\) and \(\rho_{mn}\) from Eqs.
(A10)-(A16):

\[
\frac{d\mu_E}{dt} = f_{E,0} + f_{E,2}\gamma_E + h_{E,0} \\
+ \left(\frac{\phi}{2}\frac{\alpha_E^2}{2}\right)[g_{E,0}g_{E,1} + 3(g_{E,1}g_{E,2} + g_{E,0}g_{E,3})\gamma_E], 
\]

\[
\frac{d\mu_I}{dt} = f_{I,0} + f_{I,2}\gamma_I + h_{I,0} \\
+ \left(\frac{\phi}{2}\frac{\alpha_I^2}{2}\right)[g_{I,0}g_{I,1} + 3(g_{I,1}g_{I,2} + g_{I,0}g_{I,3})\gamma_I],
\]

\[
\frac{d\gamma_E}{dt} = 2f_{E,1}\gamma_E + 2h_{E,1}\left[\left(\frac{w_{EE}N_E}{Z_E}\right)\left(\rho_{EE} - \frac{\gamma_E}{N_E}\right) - w_{EI}\rho_{EI}\right] \\
+ (\phi + 1)(g_{E,1} + 2g_{E,0}g_{E,2})\alpha_E^2\gamma_E + \alpha_E\gamma_{E,0} + \beta_E^2,
\]

\[
\frac{d\gamma_I}{dt} = 2f_{I,1}\gamma_I + 2h_{I,1}\left[\left(-\frac{w_{II}N_I}{Z_I}\right)\left(\rho_{II} - \frac{\gamma_I}{N_I}\right) + w_{IE}\rho_{EI}\right] \\
+ (\phi + 1)(g_{I,1} + 2g_{I,0}g_{I,2})\alpha_I^2\gamma_I + \alpha_I\gamma_{I,0} + \beta_I^2,
\]

\[
\frac{d\rho_{EE}}{dt} = 2f_{E,1}\rho_{EE} + 2h_{E,1}(w_{EE}\rho_{EE} - w_{EI}\rho_{EI}) \\
+ (\phi + 1)(g_{E,1} + 2g_{E,0}g_{E,2})\alpha_E^2\rho_{EE} + \frac{(\alpha_E^2g_{E,0}^2 + \beta_E^2)}{N_E},
\]

\[
\frac{d\rho_{II}}{dt} = 2f_{I,1}\rho_{II} + 2h_{I,1}(-w_{II}\rho_{II} + w_{IE}\rho_{EI}) \\
+ (\phi + 1)(g_{I,1} + 2g_{I,0}g_{I,2})\alpha_I^2\rho_{II} + \frac{(\alpha_I^2g_{I,0}^2 + \beta_I^2)}{N_I},
\]

\[
\frac{d\rho_{EI}}{dt} = (f_{E,1} + f_{I,1})\rho_{EI} \\
+ h_{E,1}(w_{EE}\rho_{EI} - w_{EI}\rho_{II}) + h_{I,1}(-w_{II}\rho_{EI} + w_{IE}\rho_{EE}) \\
+ \frac{(\phi + 1)}{2}[(g_{E,1} + 2g_{E,0}g_{E,2})\alpha_E^2 + (g_{I,1} + 2g_{I,0}g_{I,2})\alpha_I^2]\rho_{EI}.
\]

Here we set \(-w_{II} \leq 0\) and \(-w_{EI} \leq 0\) after convention. Equations (86)-(92) correspond to a generalized Wilson-Cowan (WC) model, because they reduce to WC model if we adopt \(F(x) = -\lambda\) and \(G(x) = x\) (see below), neglecting all fluctuations of \(\gamma\) and \(\rho_{\eta\eta'}\) (\(\eta, \eta' = E, I\)).

It is difficult to obtain the stability condition for the stationary solution of Eqs. (86)-(92) because they are seven-dimensional nonlinear equations. We find that equations of motions of \(\mu_E\) and \(\mu_I\) are decoupled from the rest of variables in the cases of \(G(x) = x\) and \(G(x) = x^{1/2}\) with \(F(x) = -\lambda x\), for which \(f_{\eta,2} = 0\) and \((g_{\eta,1}g_{\eta,2} + g_{\eta,0}g_{\eta,3}) = 0\) (\(\eta = E, I\)) in Eqs. (86) and (87). We will the discuss the stationary solutions for these two cases in the followings.

(A) \(F(x) = -\lambda x\) and \(G(x) = x\)

Equations of motions for \(\mu_E\) and \(\mu_I\) become

\[
\frac{d\mu_E}{dt} = -\left(\lambda_E - \frac{\alpha_E^2}{2}\right)\mu_E + H(w_{EE}\mu_E - w_{EI}\mu_I + I_E),
\]

\[
\frac{d\mu_I}{dt} = -\left(\lambda_I - \frac{\alpha_I^2}{2}\right)\mu_I + H(w_{IE}\mu_E - w_{II}\mu_I + I_I).
\]
The stationary solution is given by

\[ 0 = f_1(\mu_E, \mu_I) = -\left(\lambda_E - \frac{\alpha_E^2}{2}\right) \mu_E + H(w_{EE}\mu_E - w_{EI}\mu_I + I_E), \tag{95} \]

\[ 0 = f_2(\mu_E, \mu_I) = -\left(\lambda_I - \frac{\alpha_I^2}{2}\right) \mu_I + H(w_{IE}\mu_E - w_{II}\mu_I + I_I). \tag{96} \]

The stability condition for stationary solutions is given by

\[ T = -\lambda_E - \lambda_I - \frac{\alpha_E^2}{2} - \frac{\alpha_I^2}{2} - w_{EE}h_{E,1} - w_{II}h_{II,1} < 0, \tag{97} \]

\[ D = \left(\lambda_E - \frac{\alpha_E^2}{2} - w_{EE}h_{E,1}\right)\left(\lambda_I - \frac{\alpha_I^2}{2} - w_{II}h_{II,1}\right) + w_{EI}w_{IE}h_{E,1}h_{E,1,1} > 0, \tag{98} \]

where \( T \) and \( D \) denote the trace and determinant, respectively, of Jacobian matrix of Eqs. (93) and (94).

By solving Eqs. (93) and (94), we get stationary solutions of \( \mu_E \) and \( \mu_I \). Figures 12(a) and 12(b) show \( \mu_E \) and \( \mu_I \), respectively, as a function of \( w_{EE} \) for various \( \alpha \) (\( \equiv \alpha_E = \alpha_I \)) with \( \lambda_E = \lambda_I = 1.0 \), \( w_{EI} = w_{IE} = w_{II} = 1 \), \( I_E = I_I = 0 \) and \( N_E = N_I = 10 \). In the case of \( \alpha = 0 \), \( \mu_E \) and \( \mu_I \) are zero for \( w_{EE} \leq w_c \) but become finite for \( w_{EE} > w_c \) where \( w_c \) (\( = 1.5 \)) denotes the critical couplings for the ordered state. With increasing \( \alpha \), the critical value of \( w_c \) is decreased and magnitudes of \( \mu_E \) and \( \mu_I \) in the ordered state are increased. This shows that multiplicative noise works to create the ordered state [39].

(B) \( F(x) = -\lambda x \) and \( G(x) = x^{1/2} \)

Equations of motions for \( \mu_E \) and \( \mu_I \) become

\[ \frac{d\mu_E}{dt} = -\lambda_E\mu_E + \frac{\alpha_E^2}{4} + H(w_{EE}\mu_E - w_{EI}\mu_I + I_E), \tag{99} \]

\[ \frac{d\mu_I}{dt} = -\lambda_I\mu_I + \frac{\alpha_I^2}{4} + H(w_{IE}\mu_E - w_{II}\mu_I + I_I). \tag{100} \]

The stationary solution is given by

\[ 0 = f_1(\mu_E, \mu_I) = -\lambda_E\mu_E + \frac{\alpha_E^2}{4} + H(w_{EE}\mu_E - w_{EI}\mu_I + I_E), \tag{101} \]

\[ 0 = f_2(\mu_E, \mu_I) = -\lambda_I\mu_I + \frac{\alpha_I^2}{4} + H(w_{IE}\mu_E - w_{II}\mu_I + I_I). \tag{102} \]

The stability condition for stationary solution is given by

\[ T = -\lambda_E - \lambda_I - w_{EE}h_{E,1} - w_{II}h_{II,1} < 0, \tag{103} \]

\[ D = (\lambda_E - w_{EE}h_{E,1})(\lambda_I - w_{II}h_{II,1}) + w_{EI}w_{IE}h_{E,1}h_{E,1,1} > 0, \tag{104} \]

where \( T \) and \( D \) express the trace and determinant, respectively, of Jacobian matrix of Eqs. (99) and (100).

Figure 13(a) and 13(b) show the \( w_{EE} \) dependences of \( \mu_E \) and \( \mu_I \), respectively, for various \( \alpha \) (\( \equiv \alpha_E = \alpha_I \)) with \( \lambda_E = \lambda_I = 1.0 \), \( w_{EI} = w_{IE} = w_{II} = 1.0 \) and \( N_E = N_I = 10 \). Equations (99) and (100) show that multiplicative noise play a role of inputs, yielding finite \( \mu_E \) and
get

µ₁ even for no external inputs (I₄ = I₃ = 0). With increasing α, magnitudes of µₑ and µ₁ are increased and the critical value of wₑ for the ordered state is decreased. It is interesting to note that the behavior of µₑ and µ₁ at wₑEE ~ wₑ is gradually changed with increasing α.

3.3 Dynamical property

We have studied the dynamical property of the rate model, by applying pulse inputs given by

\[ Iₜ(η) = Aᵦ(η) \Theta(t - t₁) \Theta(t₂ - t) + Iₜ⁽ᵇ⁾, \quad (η = E, I) \]  (105)

with Aₑ = 0.5, Aᵦ = 0.3, Iₑ⁽ᵇ⁾ = 0.1, Iᵦ⁽ᵇ⁾ = 0.05, t₁ = 40 and t₂ = 50. The time courses of µₑ, γᵦ and ρₑᵦ (η, η' = E, I) are plotted in Figs. 14(a)-14(c), respectively, where solid, chain and dashed curves show the results of AMM and dotted curves those of DS averaged over 1000 trials for αₑ = αᵦ = 0.5, βₑ = βᵦ = 0.1, and wₑEE = wₑᵦ = wᵦₑ = wᵦᵦ = 1.0. The results of AMM are in good agreement with DS results.

Responses of µₑ and µᵦ for various sets of couplings are plotted in Figs. 15(a)-15(f): w₁001 in Fig. 15(b), for example, means that (wₑEE, wₑᵦ, wᵦₑ, wᵦᵦ) = (1,0,0,1). Figure 15(a) shows the result of no couplings (wₑEE = wₑᵦ = wᵦₑ = wᵦᵦ = 0). When intracluster couplings of wₑᵦ = 1.0 and wᵦᵦ = 1.0 are introduced, µᵦ in the inhibitory cluster is much suppressed, while the excitatory cluster is in the ordered state with µₑ = 0.73 for no input pulses, as shown in Fig. 15(b). Figure 15(c) shows that when only the intercluster coupling of wᵦᵦ is introduced, the magnitude of µₑ is decreased compared to that in Fig. 15(a). In contrast, Fig. 15(d) shows that an addition of only wᵦₑ enhances magnitude of µᵦ compared to that in Fig. 15(a). We note in Fig. 15(e) that when both intercluster couplings of wᵦᵦ and wᵦₑ are included, magnitude of µₑ is considerably reduced while that of µᵦ is slightly increased. When all couplings are added, magnitudes of both µₑ and µᵦ are increased compared to those for no couplings shown in Fig. 15(a). Figure 15(a)-15(f) clearly shows that responses of µₑ and µᵦ to inputs significantly depend on the couplings.

Figure 16(a) and 16(b) show the synchronization ratios of Sₑ and Sᵦ, respectively, defined by [see Eq. (75)]

\[ Sₜ(η) = \left( \frac{Nₜ \rhoₜ(η) / \gammaₜ(η) - 1}{Nₜ - 1} \right), \quad (η = E, I) \]  (106)

for various sets of couplings when inputs given by Eq. (105) are applied (Aₑ = 0.5, Aᵦ = 0.3, Iₑ⁽ᵇ⁾ = 0.1, Iᵦ⁽ᵇ⁾ = 0.05, αₑ = αᵦ = 0.5, βₑ = βᵦ = 0.1, and Nₑ = Nᵦ = 10). First we discuss the synchronization ratio at the period of t < 40 and t > 60 where the pulse input is not relevant. With no intra- and inter-cluster couplings (wₑEE = wₑᵦ = wᵦₑ = wᵦᵦ = 0), we get Sₑ = Sᵦ = 0. When only the intra-cluster couplings of wₑEE = 1 and wᵦᵦ = 1 are introduced, we get Sₑ = 0.15 and Sᵦ = -0.67, as shown by dashed curve in Fig. 16(b). When inter-cluster coupling of wᵦᵦ = 1 is included, the synchronization in the excitatory cluster is decreased to Sₑ = 0.08 (dotted curves in Fig. 16(a). In contrast, when inter-cluster
of $w_{IE} = 1$ is introduced, the synchrony in the inhibitory cluster is increased to $S_1 = 0.06$, as shown by dotted curve in Fig. 16(b). When inter-cluster couplings of $w_{EI} = w_{IE} = 1$ are included, the synchronization ratios almost vanish (chain curves). Solid curves show that when both intra- and inter-cluster couplings are included, we get $S_E = 0.24$ and $S_I = 0.04$. It is noted that the responses of the synchronizations to a pulse applied at $40 \leq t < 50$ are rather complicated. When an input pulse is applied at $t = 40$, the synchronization ratios are generally decreased while $S_E$ with $w0110$ increased: $S_E$ with $w0100$ is once decreased and then increased. When an applied pulse disappears at $t = 50$, the synchronization are increased in the refractory period though the synchronization ratios for $w0100$ and $w0110$ are decreased.

Figures 17(a)-17(e) show responses of an E-I ensemble with $N_E = N_I = 10$ when the input pulse shown in 17(a) is applied only to the excitatory cluster. Responses of the local rate of $r_\eta$ of single neurons in the excitatory ($\eta = E$) and inhibitory clusters ($\eta = I$) are shown by solid and dashed curves, respectively, in Fig. 17(b). Local rates in Fig. 17(b) which are obtained by DS with a single trial, have much irregularity induced by additive and multiplicative noises with $\alpha_E = \alpha_I = 0.1$ and $\beta_E = \beta_I = 0.1$. Figure 17(c) shows the population-averaged rates of $R_\eta(t)$ obtained by DS with a single trial. The irregularity shown in Fig. 17(c) is reduced compared to that of $r_\eta(t)$ in Fig. 17(b), which demonstrates the advantage of the population code. When DS is repeated and the global variable is averaged over 100 trials, we get the result of $R_\eta(t)$ whose irregularity is much reduced by the average over trials, as shown in Fig. 17(d). The AMM results of $\mu_\eta(t)$ shown in Fig. 17(e) are in good agreement with those shown in Fig. 17(d).

4 Discussion and conclusion

We may calculate the stationary distributions in the E-I ensemble. Figures 18(a)-18(c) show global distributions of $P_E(R)$ and $P_I(R)$ which are averaged within the excitatory and inhibitory clusters, respectively. We have studied how distributions are varied when couplings are changed: $w0110$ in Fig. 18(b), for example, means $(w_{EE}, w_{EI}, w_{IE}, w_{II}) = (0.1, 1, 0)$. Figure 18(a) shows the results without couplings, for which distributions of $P_E(R)$ and $P_I(R)$ have peaks at $R \sim 0.1$ and 0.05, respectively, because of applied background inputs ($I_E^{(b)} = 0.1$ and $I_I^{(b)} = 0.05$). When intercluster couplings of $w_{EI} = 1.0$ and $w_{IE} = 1.0$ are introduced, the peak of $P_E(R)$ locates at $R \sim 0.02$, while that of $P_I(R)$ is at $R \sim 0.08$: their relative positions are interchanged compared to the case of no couplings shown in Fig. 18(a). When all couplings with $w_{EE} = w_{EI} = w_{IE} = w_{II} = 1.0$ are included, we get the distributions shown in Fig. 18(c), where both $P_E(R)$ and $P_I(R)$ have wider distributions than those with no couplings shown in Fig. 18(a). Our calculations show that the distributions are much influenced by the magnitudes of couplings.

We have proposed the rate model given by Eqs. (10) and (11), in which the relaxation process is given by a single $F(x)$. Instead, when the relaxation process consists of two terms:

$$ F(x) \rightarrow c_1 F_1(x) + c_2 F_2(x), \quad (107) $$
with \( c_1 + c_2 = 1 \), the distribution becomes

\[
p(r) = [p_1(r)]^{c_1} [p_2(r)]^{c_2},
\]

(108)

where \( p_k(r) \) \((k = 1, 2)\) denotes the distribution only with \( F(x) = F_1(x) \) or \( F(x) = F_1(x) \).

In contrast, when multiplicative noises arise from two independent origins:

\[
\alpha x\eta(t) \rightarrow c_1\alpha_1 x\eta_1(t) + c_2\alpha_2 x\eta_2(t),
\]

(109)

the distribution for \( \beta = H = 0 \) becomes

\[
p(r) \propto r^{-\left[2\lambda/(c_1\alpha_1^2 + c_2\alpha_2^2) + 1\right]}.
\]

(110)

Similarly, when additive noises arise from two independent origins:

\[
\beta\xi(t) \rightarrow c_1\beta_1 \xi_1(t) + c_2\beta_2 \xi_2(t),
\]

(111)

the distribution for \( \alpha = H = 0 \) becomes

\[
p(r) \propto e^{-\lambda/(c_1\alpha_1^2 + c_2\alpha_2^2)}.
\]

(112)

Equations (108), (110) and (112) are quite different from the form given by

\[
p(r) = c_1p_1(r) + c_2p_2(r),
\]

(113)

which has been conventionally adopted for a fitting of theoretical distributions to that obtained by experiments.

It is an interesting subject to decode the stimulus from the observed spiking rate of neurons. In BMI, stimulus \( \hat{y}(t) \) is decoded from observed rate signals \( \hat{r}(t-u) \) with the use of Eq. (4). In the AMM, the relation between the input \( I(t) \) and the averaged rate of \( R(t) \), \( \mu(t) \), given by Eq. (70) yields that \( I(t) \) is expressed in terms of \( \mu(t) \) and \( d\mu(t)/dt \) as

\[
I(t) = \frac{[d\mu/dt + (\lambda - \alpha^2/2)\mu(t)]}{\sqrt{1 - [d\mu/dt + (\lambda - \alpha^2/2)\mu(t)]^2}} - w\mu(t),
\]

(114)

\[
\sim \frac{d\mu}{dt} + \left(\lambda - \frac{\alpha^2}{2} - w\right)\mu(t), \quad \text{for small } \mu(t)
\]

(115)

The \( d\mu/dt \) term plays an important role in decoding dynamics of \( \mu(t) \). In an approach using the Bayesian statistics [70], the conditional probability of an input \( I \) for a given rate \( R \), \( P(I \mid R) \), is expressed by

\[
P(I \mid R) \propto P(R \mid I) P(I),
\]

(116)

where \( P(R \mid I) \) is the conditional probability of \( R \) for a given \( I \) and \( P(I) \) the likelihood of \( I \). An estimation of the value of \( I \) which yields the maximum of \( P(I \mid R) \), is known as the maximum a posteriori (MAP) estimate. Since \( P(R \mid I) \) is obtainable with the use of our rate model, as shown in Figs. 6(a) and 6(b), we may estimate \( P(I \mid R) \) by Eq. (116) if \( P(I) \) is provided. We note that \( I(t) \) given by Eq. (114) corresponds to the center of gravity
of $P(I \mid R)$, which is expected to be nearly the same as the maximum value obtained by MAP estimate. More sophisticate Bayesian approach using the recursive method has been proposed \cite{70}, although it is not unclear whether such Bayesian networks may be implemented by real neurons.

The structures of neuronal networks have been discussed based on the theory on complex networks \cite{71,72}. The neural network of nematode worm $C.~elegans$ is reported to be small-world network. It has been recently observed by the functional magnetic resonance imaging (fMRI) that the functional connectivity in human brain has the behavior of the scale-free \cite{73} or small-world network \cite{74,75}. Most of theoretical studies have assumed the local or all-to-all coupling in neuron networks, as we have made in our study. In real neural networks, however, the couplings are neither local nor global. A new approach extending the AMM has been proposed to take into account the couplings from local to global and/or from regular to random couplings \cite{60}. It has been shown that the synchronization in the small-world networks is worse than that in the regular networks due to the randomness introduced in the small-world networks.

In recent years, it becomes increasingly popular to study the distributed information processing by using cultured neuronal networks which are cultivated in an artificial way \cite{76}. It is possible that every cell in the cultured network may be observed, monitored, stimulated and manipulated with high temporal and spatial resolutions. The observed ISI distributions of the cultured networks with 50-10$^6$ neurons are reported to obey the scale-free distribution \cite{77}. Although our AMM study in Sec. 3 has been made for an E-I ($M = 2$) cluster, it would be interesting to investigate the dynamics of larger ensembles modeling complex networks and cultured networks, which is left for our future study.

To summarize, we have discussed the stationary and dynamical properties of the generalized rate model by using the FPE and AMM. The proposed rate model is a phenomenological one and has no biological basis. Nevertheless, the generalized rate model is expected to be useful in discussing various properties of neuronal ensembles. Indeed, the proposed rate model has an interesting property, yielding various types of stationary non-Gaussian distributions such as gamma, inverse-Gaussian and log-normal distributions, which have been experimentally observed \cite{47,51}. The stationary distribution and dynamical responses of neuronal clusters have been shown to considerably depend on the model parameters such as strengths of noises and couplings. A disadvantage of our AMM is that its applicability is limited to weak-noise cases. On the contrary, an advantage of the AMM is that we can easily discuss dynamical property of an $N$-unit neuronal cluster. In DS and FPE, we have to solve the $N$-dimensional stochastic Langevin equations and the $(N + 1)$-dimensional partial differential equations, respectively, which are more laborious than the three-dimensional ordinary differential equations in the AMM. We hope that the proposed rate model in the AMM is adopted for a wide class of study on neuronal ensembles.
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APPENDIX

A AMM for multiple clusters

We will present a detail of an application of the AMM to the rate model describing multiple clusters given by Eqs. (77) and (78). The Fokker-Planck equation for the distribution of $p\{r_{mi}\}, t\}$ is given by

$$\frac{\partial}{\partial t} p\{r_{mi}\}, t\} = -\sum_{mk} \frac{\partial}{\partial r_{mk}} \left\{ \left[ F(r_{mk}) + \frac{\phi \alpha^2_m}{2} G'(r_{mk}) G(r_{mk}) + H(u_{mk}) \right] p\{r_{mi}\}, t\} \right\} + \frac{1}{2} \sum_{mk} \frac{\partial^2}{\partial r_{mk}^2} \left\{ \left[ \alpha^2_m G(r_{mk})^2 + \beta^2_m \right] p\{r_{mi}\}, t\} \right\},$$

(A1)

where $G'(x) = dG(x)/dx$, and $\phi = 1$ and $0$ in the Stratonovich and Ito representations, respectively.

When we consider global variables of the cluster $m$ given by

$$R_m(t) = \frac{1}{N_m} \sum_i r_{mi}(t),$$

(A2)

the distribution $P(R_m, t)$ for $R_m$ is given by

$$P(R_m, t) = \int \cdots \int \Pi_i dr_{mi} p\{r_{mi}\}, t\} \delta\left( R_m - \frac{1}{N_m} \sum_j r_{mj}\right).$$

(A3)

Variances and covariances of local variables are defined by

$$\langle r_{mi} r_{nj}' \rangle = \int \Pi_i dr_{mi} p\{r_{mi}\}, t\} r_{mi} r_{nj}' \delta_{ij'} \delta_{mn}.$$  

(k, $k' = 1, 2, ..$)  

(A4)

Equations of motions of means, variances and covariances of local variables ($r_{mi}$) are given by

$$\frac{d\langle r_{mi}\rangle}{dt} = \langle F(r_{mi}) \rangle + \langle H(u_{mi}) \rangle + \frac{\phi \alpha^2_m}{2} (G'(r_{mi}) G(r_{mi})),$$

(A5)

$$\frac{d\langle r_{mi} r_{nj}\rangle}{dt} = \langle r_{mi} F(r_{nj}) \rangle + \langle r_{nj} F(r_{mi}) \rangle + \langle r_{mi} H(u_{mi}) \rangle + \langle r_{nj} H(u_{nj}) \rangle + \frac{\phi \alpha^2_m}{2} (r_{mi} G'(r_{nj}) G(r_{nj})) + \frac{\phi \alpha^2_m}{2} (r_{nj} G'(r_{mi}) G(r_{mi})) + \left[ \alpha^2_m (G(r_{mi})^2 + \beta_m^2) \delta_{ij} \delta_{mn} \right].$$

(A6)

Equations of motions of the mean, variance and covariance of global variables ($R_m$) are obtainable by using Eqs. (A3), (A5) and (A6):

$$\frac{d\langle R_m\rangle}{dt} = \frac{1}{N_m} \sum_i \frac{d\langle r_{mi}\rangle}{dt},$$

(A7)
\[ \frac{d\langle R_m R_n \rangle}{dt} = \frac{1}{N_m N_n} \sum_i \sum_j \frac{d\langle r_{mi} r_{nj} \rangle}{dt}. \quad (A8) \]

Variances and covariances, \( \mu_m, \gamma_m \) and \( \rho_{mn} \) are given by Eqs. (82)-(84). Expanding \( r_{mi} \) in Eqs. (A5)-(A8) around the average value of \( \mu_m \) as

\[ r_{mi} = \mu_m + \delta r_{mi}, \quad (A9) \]

and retaining up to the order of \( < \delta r_{mi} \delta r_{mj} > \), we get equations of motions for \( \mu_m, \gamma_m \) and \( \rho_{mn} \) given by

\[
\frac{d\mu_m}{dt} = f_{m,0} + f_{m,2} \gamma_m + h_{m,0} + \left( \frac{\phi \alpha_m^2}{2} \right) [g_{m,0} g_{m,1} + 3(g_{m,1} g_{m,2} + g_{m,0} g_{m,3}) \gamma_m], \quad (A10)
\]

\[
\frac{d\gamma_m}{dt} = 2f_{m,1} \gamma_m + 2h_{m,1} \left[ \left( \frac{w_{mm} N_m}{Z_m} \right) \left( \rho_{mm} - \frac{\gamma_m}{N_m} \right) + \left( \frac{1}{M - 1} \right) \sum_{n(\neq m)} w_{mn} \rho_{mn} \right] + (\phi + 1) (g_{m,1}^2 + 2g_{m,0} g_{m,2}) \alpha_m^2 \gamma_m + \alpha_m^2 g_{m,0}^2 + \beta_m^2, \quad (A11)
\]

\[
\frac{d\rho_{mn}}{dt} = (f_{m,1} + f_{n,1}) \rho_{mn} + h_{m,1} \left[ w_{mm} \rho_{mn} + \left( \frac{1}{M - 1} \right) \sum_{n'(\neq m)} w_{mn'} \rho_{nn'} \right] + h_{n,1} \left[ w_{nn} \rho_{mn} + \left( \frac{1}{M - 1} \right) \sum_{n'(\neq n)} w_{n'n} \rho_{mn'} \right] + \frac{\phi + 1}{2} \left[ (g_{m,1}^2 + 2g_{m,0} g_{m,2}) \alpha_m^2 + (g_{n,1}^2 + 2g_{n,0} g_{n,2}) \alpha_n^2 \right] \rho_{mn} + \delta_{mn} \left( \frac{\alpha_m^2 g_{m,0}^2 + \beta_m^2}{N_m} \right), \quad (A12)
\]

where

\[
\begin{align*}
  f_{m,\ell} &= \frac{1}{\ell!} \frac{\partial^\ell F(\mu_m)}{\partial x^\ell}, \\
  g_{m,\ell} &= \frac{1}{\ell!} \frac{\partial^\ell G(\mu_m)}{\partial x^\ell}, \\
  h_{m,\ell} &= \frac{1}{\ell!} \frac{\partial^\ell H(u_m)}{\partial u^\ell}, \\
  u_m &= w_{mm} \mu_m + \left( \frac{1}{M - 1} \right) \sum_{n(\neq m)} w_{mn} \mu_n + I_m.
\end{align*}
\]

For a two-cluster \( (M = 2) \) ensemble consisting of excitatory and inhibitory clusters, equations of motions given by Eqs. (A10)-(A12) reduce to Eqs. (86)-(92).
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Figure 1: Response of a 10-unit FN neuron cluster subjected to additive and multiplicative noises: (a) input signal $I(t)$, (b) a local membrane potential $[v(t)]$ and (c) a global membrane potential $[V(t) = (1/N) \sum v_i(t)]$ obtained by direct simulation (DS) with a single trial: (d) a global membrane potential $[V(t)]$ calculated by DS with 100 trials: (e) the result of the AMM $[\mu(t)]$.

Figure 2: (a) Distributions $p(r)$ of the (local) firing rate $r$ for various $\alpha$ with $\lambda = 1.0$, $\beta = 0.1$, $I = 0.1$ and $w = 0.0$, (b) $p(r)$ for various $\beta$ with $\lambda = 1.0$, $\alpha = 1.0$, $I = 0.1$ and $w = 0.0$, and (c) $p(r)$ for various $I$ with $\lambda = 1.0$, $\alpha = 0.5$, $\beta = 0.1$ and $w = 0.0$.

Figure 3: (a) Distributions $p(r)$ of the (local) firing rate $r$ and (b) $\pi(T)$ of the ISI $T$ for $a = 0.8$ (chain curves), $a = 1.0$ (solid curves), $a = 1.5$ (dotted curves) and $a = 2.0$ (dashed curves) with $b = 1.0$, $\lambda = 1.0$, $\alpha = 1.0$, $\beta = 0.0$ and $I = 0.1$.

Figure 4: (a) Distributions $p(r)$ of the (local) firing rate $r$ and (b) $\pi(T)$ of the ISI $T$ for $b = 0.5$ (dashed curves), $b = 1.0$ (solid curves), $b = 1.5$ (dotted curves) and $b = 2.0$ (chain curves) with $a = 1.0$, $\lambda = 1.0$, $\alpha = 1.0$, $\beta = 0.0$ and $I = 0.1$: results for $b = 1.5$ and $b = 2$ should be multiplied by factors of 2 and 5, respectively.

Figure 5: Distributions $P(R)$ of the (global) firing rate $R$ for (a) $\alpha = 0.0$ and (b) $\alpha = 0.5$, with $N = 1, 10$ and 100: $\lambda = 1.0$, $\beta = 0.1$, $w = 0.0$ and $I = 0.1$.

Figure 6: Distributions $p(r)$ (dashed curves) and $P(R)$ (solid curves) for (a) $\alpha = 0.0$ and (b) $\alpha = 0.5$ with $I = 0.1$ and $I = 0.2$: $N = 10$, $\lambda = 1.0$, $\beta = 0.1$ and $w = 0.0$.

Figure 7: Distributions $p(r)$ (dashed curves) and $P(R)$ (solid curves) for (a) $\alpha = 0.0$ and (b) $\alpha = 0.5$ with $w = 0.0$ and $w = 0.5$: $N = 10$, $\lambda = 1.0$, $\beta = 0.1$ and $I = 0.1$.

Figure 8: The $N$ dependence of $\gamma$ and $\rho$ in the stationary states for four sets of parameters: $(\alpha, \beta, w) = (0.0, 0.1, 0.0)$ (solid curves), $(0.5, 0.1, 0.0)$ (dashed curves), $(0.0, 0.1, 0.5)$ (chain curves) and $(0.5, 0.1, 0.5)$ (double-chain curves): $\lambda = 1.0$, $N = 10$ and $I = 0.1$.

Figure 9: Time courses of (a) $\mu(t)$, (b) $\gamma(t)$, (c) $\rho(t)$ and (d) $S(t)$ for a pulse input $I(t)$ given by Eq. (73) with $\lambda = 1.0$, $\alpha = 0.5$, $\beta = 0.1$, $N = 10$ and $w = 0.5$, solid and chain curves denoting results of AMM and dashed curves expressing those of DS result with 1000 trials.

Figure 10: (a) Response of $\mu(t)$ to input pulse $I(t)$ given by Eq. (73) for $(a, b) = (1, 1)$ (solid curve) and $(a, b) = (2, 1)$ (dashed curve) with $\alpha = 0.0$, $\beta = 0.1$, $N = 10$ and $I = 1.0$.

(b) Response of $\mu(t)$ to input pulse $I(t)$ for $(a, b) = (1, 1)$ (solid curve) and $(a, b) = (1, 0.5)$ (dashed curve) with $\alpha = 0.5$, $\beta = 0.001$, $N = 10$, $\lambda = 1.0$ and $w = 0.0$.

Figure 11: Response of $\mu(t)$ (solid curves) to sinusoidal input $I(t)$ (dashed curves) given by Eq. (73) for (a) $T_p = 20$ and (b) $T_p = 10$ with $A = 0.5$, $\lambda = 1.0$, $\alpha = 0.5$, $\beta = 0.1$, $w = 0$ and $N = 10$ ($a = 1$ and $b = 1$).

Figure 12: Stationary values of (a) $\mu_E$ and (b) $\mu_I$ in an E-I ensemble as a function of $w_{EE}$ for various values of $\alpha$ ($= \alpha_E = \alpha_I$) for the case of $G(x) = x$ with $\lambda_E = \lambda_I = 1.0$, $w_{EI} = w_{IE} = w_{II} = 1.0$ and $I_E = I_I = 0$ and $N_E = N_I = 10$. 
Figure 13: Stationary values of (a) $\mu_E$ and (b) $\mu_I$ in an E-I ensemble as a function of $w_{EE}$ for various values of $\alpha$ ($= \alpha_E = \alpha_I$) for the case of $G(x) = x^{1/2}$ with $\lambda_E = \lambda_I = 1.0$, $w_{EI} = w_{IE} = w_{II} = 1.0$ and $I_E = I_I = 0$ and $N_E = N_I = 10$.

Figure 14: Time courses of (a) $\mu_E$ and $\mu_I$, (b) $\gamma_E$ and $\gamma_I$, and (c) $\rho_{EE}$, $\rho_{II}$ and $\rho_{EI}$, for pulse inputs given by Eq. (105) with $\alpha_E = \alpha_I (= \alpha) = 0.5$, $\beta_E = \beta_I (= \beta) = 0.1$, $N_E = N_I = 10$ and $w_{EE} = w_{EI} = w_{IE} = w_{II} = 1.0$: solid, dashed and chain curves denote the results of AMM and dotted curves express those of DS with 1000 trials.

Figure 15: Responses of $\mu_E$ (solid curves) and $\mu_I$ (dashed curves) of an E-I ensemble to pulse inputs given by Eq. (105); (a) $(w_{EE}, w_{EI}, w_{IE}, w_{II}) = (0, 0, 0, 0)$, (b) $(1.0, 0.1)$, (c) $(0.1, 0.0)$, (d) $(0.0, 1.0)$, (e) $(0.1, 1.0)$ and (f) $(1.1, 1.1)$: $w_{1001}$, for example, expresses the case of (b): $\alpha_E = \alpha_I = 0.5$, $\beta_E = \beta_I = 0.1$, $A_E = 0.5$, $A_I = 0.3$, $I_E^{(b)} = 0.1$, $I_I^{(b)} = 0.05$ and $N_E = N_I = 10$.

Figure 16: Synchronization ratios of (a) $S_E$ and (b) $S_I$ of an E-I ensemble to pulse inputs given by Eq. (105) with $A_E = 0.5$, $A_I = 0.3$, $I_E^{(b)} = 0.1$, $I_I^{(b)} = 0.05$, $\alpha_E = \alpha_I = 0.5$, $\beta_E = \beta_I = 0.1$, and $N_E = N_I = 10$: $w_{1001}$, for example, denotes $(w_{EE}, w_{EI}, w_{IE}, w_{II}) = (1.0, 0.1)$.

Figure 17: Responses of an E-I ensemble; (a) input signal $I_E(t)$, (b) local rates $r_\eta(t)$ and (c) global rate $R_\eta(t)$ ($\eta = E$ and $I$) obtained by direct simulation (DS) with a single trial: (d) global rates $R_\eta(t)$ calculated by DS with 100 trials: (e) the result of the AMM $\mu_\eta(t)$: $\alpha_E = \alpha_I = 0.5$, $\beta_E = \beta_I = 0.1$, $w_{EE} = w_{EI} = w_{IE} = w_{II} = 1.0$, $A_E = 0.5$, $A_I = 0.0$, $I_E^{(b)} = 0.1$, $I_I^{(b)} = 0.05$ and $N_E = N_I = 10$. Solid and dashed curves in (b)-(e) denote the results for excitatory (E) and inhibitory (I) clusters, respectively.

Figure 18: Stationary global distributions in E $[P_E(R)]$ and I clusters $[P_I(R)]$ for (a) $(w_{EE}, w_{EI}, w_{IE}, w_{II}) = (0.0, 0.0, 0)$, (b) $(0.1, 1.0)$ and (c) $(1.1, 1.1)$ with $I_E^{(b)} = 0.1$, $I_I^{(b)} = 0.05$, $\alpha_E = \alpha_I (= \alpha) = 0.5$, $\beta_E = \beta_I (= \beta) = 0.1$ and $N_E = N_I = 10$, solid and dashed curves denoting $P_E(R)$ and $P_I(R)$, respectively.
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