Population rate codes carried by mean, fluctuation and synchrony of neuronal firings

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A population of firing neurons is expected to carry information not only by the mean firing rate but also by fluctuation and synchrony among neurons. In order to examine this possibility, we have studied responses of neuronal ensembles to three kinds of inputs: mean-, fluctuation- and synchrony-driven inputs. The generalized rate-code model including additive and multiplicative noise [H. Hasegawa, Phys. Rev. E 75 (2007) 051904] has been studied by direct simulations (DSs) and the augmented moment method (AMM) in which equations of motion for mean firing rate, fluctuation and synchrony are derived. Results calculated by the AMM are in good agreement with those by DSs. The independent component analysis (ICA) of our results has shown that mean firing rate, fluctuation (or variability) and synchrony may carry independent information in the population rate-code model. The input–output relation of mean firing rates is shown to have higher sensitivity for larger multiplicative noise, as recently observed in prefrontal cortex. A comparison is made between results obtained by the integrate-and-fire (IF) model and our rate-code model.

1. Introduction

One of the most important and difficult problems in neuroscience is to understand how neurons communicate in a brain. There has been a long-standing controversy between the temporal- and rate-code hypotheses in which information is assumed to be encoded in firing timings and rates, respectively [1–3]. A recent success in brain-machine interface (BMI) [4, 5], however, suggests that the population rate code is employed in sensory and motor neurons, though it is still controversial which of rate, temporal or other codes is adopted in higher-level cortical neurons.

In recent years, much attention has been paid to a study on the effects of mean firing rate, fluctuation and synchrony (or spatial correlation) of input signals (for a review on rate and synchrony, see Ref. [6]). The precise role of synchrony in information transmission and the relationship among the firing rate, fluctuation and synchrony are not clear at the moment [6–12]. The firing rate and synchrony are reported to be simultaneously modulated by different signals. For example, in motor tasks of monkeys, firing rate and synchrony are considered to encode behavioral events and cognitive events, respectively [7]. During visual tasks, rate and synchrony are suggested to encode task-related signals and expectation, respectively [8]. A change in synchrony may amplify behaviorally relevant signals in V4 of monkeys [9]. An increase in synchrony of input signals is expected to yield an increase in output firing rate. The synchrony of neurons in the extrastriate visual cortex is, however, reported to be modulated by selective attention even when there is only a small change in firing rate [12]. Rate-independent modulations in synchrony are linked to expectation, attention and rivalry [6]. Fluctuations of input signals have been reported to modify the f–I relation between an applied dc current I and autonomous firing frequency f although its sensitivity to input fluctuation seems to depend on a kind of neurons [13–15]. The f–I curve of prefrontal cortex

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The gain function for the population code hypothesis. The AMM has been nicely applied to various subjects of neuronal ensembles and complex networks. The AMM has the same purpose to effectively study the properties of neuronal ensembles as approaches based on the population-code hypothesis. The AMM has been nicely applied to various subjects of neuronal ensembles and complex networks.

We have assumed in I that input signals are the same for all neurons in the ensemble. In the present study, input signals are allowed to fluctuate and to be spatially correlated. We will derive equations of motion for mean, fluctuation and synchrony of firing rates with the use of the AMM, in order to investigate the response to mean-, fluctuation- and synchrony-driven inputs. This study clarifies, to some extent, their respective roles in information transmission.

The paper is organized as follows. In Section 2, we discuss an application of the AMM to the generalized rate model, studying the input–output relations of mean fluctuation and synchrony. In Section 3, stationary and dynamical properties are discussed with numerical model calculations. By using the independent component analysis (ICA) [47], we investigate a separation of signals when two or three kinds of inputs are simultaneously applied. Discussions are presented in Section 4, where the results obtained by spiking IF model are compared with those by our rate-code model. The final Section 5 is devoted to the conclusion.

2. Formulation

2.1. Adopted model

For a study of the properties of a neuron ensemble containing finite $N$ neurons, we have adopted the generalized rate-code model [34,45] in which a neuron is regarded as a transducer from input to output signals, both of which are expressed in terms of firing rates. The dynamics of the firing rate $r_i(t) (\geq 0)$ of a neuron $i (i = 1$ to $N)$ is given by

$$\frac{dr_i}{dt} = F(r_i) + H(u_i) + G(r_i)\eta_i(t) + \xi_i(t),$$

with

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

$$H(u) = \frac{u}{\sqrt{u^2 + 1}} \Theta(u).$$

Here $F(r)$ and $G(r)$ are arbitrary functions of $r$, $Z (= N - 1)$ denotes the coordination number, $I_i(t)$ an input signal from external sources, $w$ the coupling strength, and $\Theta(u)$ the Heaviside function: $\Theta(u) = 1$ for $u > 0$ and $\Theta(u) = 0$ otherwise. Additive and multiplicative noises are included by $\xi_i(t)$ and $\eta_i(t)$, respectively, expressing zero-mean Gaussian white noise with correlations given by

$$\langle \eta_i(t)\eta_i(t') \rangle = \alpha^2 [\delta_{ij} + c_i (1 - \delta_{ij})] \delta(t - t'),$$

$$\langle \xi_i(t)\xi_i(t') \rangle = \beta^2 [\delta_{ij} + c_0 (1 - \delta_{ij})] \delta(t - t'),$$

$$\langle \eta_i(t)\xi_i(t') \rangle = 0,$$

where the bracket $\langle \cdot \rangle$ denotes the average over the distribution of $p(\{r_i\}, t)$ [Eq. (A.1)], $\alpha$ ($\beta$) stands for the magnitudes of multiplicative (additive) noise, and $c_i$ ($c_0$) expresses the degree of the spatial correlation in multiplicative (additive) noise. The gain function $H(u)$ in Eq. (3) expresses the response of a rate output ($r$) to a rate input ($u$). It has been shown that, when spike inputs with mean firing rate $r_i$ are applied to a Hodgkin-Huxley neuron, mean firing rate $r_o$ of output signals is $r_o \simeq r_i$ for $r_i \simeq 60$ [Hz], above which $r_o$ shows the saturation behavior [48,49]. The nonlinear, saturating behavior in $H(u)$ arises

(PFC) retains the increased sensitivity to input fluctuations at large $I$, while that of somatosensory cortex (SSC) is insensitive to input fluctuation though its linearity is increased at small $I$ [15].

This kind of problems discussed above has been extensively studied by using spiking neuron models such as the Hodgkin-Huxley model [16] and integrate-and-fire (IF) model with diffusion and mean-field approximations [17–33]. The purpose of the present paper is to examine the same problem by using the rate-code model, which is an alternative theoretical model to the spiking model. In a previous paper [34] (referred to as I hereafter), we proposed the generalized rate-code model for coupled neuron ensembles with finite populations, which are subjected to additive and multiplicative noises. It seems natural to include multiplicative noise besides additive noise in our rate-code model because the noise intensity is expected to generally depend on the state of neurons. Actually effects of multiplicative noise in the spiking neuron model are extensively examined by using conductance-based inputs which yield multiplicative noise [35–37]. Our calculation in I has shown that the introduced multiplicative noise leads to the non-Gaussian stationary distribution of firing rate, yielding interspike-interval (ISI) distributions such as the gamma, inverse-Gaussian and log-normal distributions, which have been experimentally observed. We discussed in I the dynamical properties of neuron population, by using the augmented moment method (AMM) which was developed for a study of stochastic systems with finite populations [38]. In the AMM, we pay attention to global properties of neuronal ensembles, taking account of mean and fluctuations of local and global variables.

The AMM has the same purpose to effectively study the properties of neuronal ensembles as approaches based on the population-code hypothesis [39–43]. The AMM has been nicely applied to various subjects of neuronal ensembles and complex networks [46].
from the fact that a neuron cannot fire with the rate of \( r > 1/\tau_r (= r_{\text{max}}) \) where \( \tau_r \) denotes the refractory period. The function \( H(u) \) has the rectifying property because the firing rate is positive, which is expressed by the Heaviside function in Eq. (3). Although our results to be present in the following are valid for any choice of \( H(x) \), we have adopted, in this study, a simple analytic expression given by Eq. (3), where the rate is normalized by \( r_{\text{max}} \).

With the use of the diffusion-type approximation, a spatially correlated input signal \( I_i(t) \) in Eq. (2) is assumed to be given by

\[
I_i(t) = \mu_i(t) + \delta I_i(t),
\]

with

\[
\langle \delta I_i(t) \rangle = 0,
\]

\[
\langle \delta I_i(t) \delta I_j(t') \rangle = \gamma(t) [\delta_{ij} + (1 - \delta_{ij}) S_{ij} \delta(t - t')],
\]

where variance \( \gamma_i \) and covariance \( S_{ij} \) are given by

\[
\gamma_i = \frac{1}{N} \sum_i \langle \delta I_i(t)^2 \rangle,
\]

\[
S_{ij} = \frac{1}{NZ} \sum_i \sum_{j \neq i} \langle \delta I_i(t) \delta I_j(t) \rangle,
\]

\( S_i(t) \) expressing the degree of the spatial correlation. We will discuss responses of the neuronal ensemble described by Eqs. (1)–(3) to the spatially correlated input given by Eqs. (7)–(9) with given \( \mu_i \), \( \gamma_i \) and \( S_{ij} \), by using both direct simulations (DSs) and the AMM [34,38].

2.2. Augmented moment method

In the AMM [38], we define the three quantities of \( \mu \), \( \gamma \) and \( \rho \) given by

\[
\mu(t) = \langle R(t) \rangle = \frac{1}{N} \sum_i \langle r_i(t) \rangle,
\]

\[
\gamma(t) = \frac{1}{N} \sum_i \{ \langle r_i(t) - \mu(t) \rangle^2 \},
\]

\[
\rho(t) = \frac{1}{N^2} \sum_i \sum_j \{ \langle r_i(t) - \mu(t) \rangle \langle r_j(t) - \mu(t) \rangle \},
\]

where \( R = (1/N) \sum r_i \), \( \mu(t) \) expresses the mean, and \( \gamma(t) \) and \( \rho(t) \) denote the averaged, auto and mutual correlations, respectively, of firing rates. By using the Fokker–Planck equation (FPE), we obtain equations of motion for \( \langle r_i \rangle \) and \( \langle r_i r_j \rangle \) (for details see Appendix A). Expanding \( r_i \) in Eqs. (A.2) and (A.3) around the average value of \( \mu \) as

\[
r_i(t) = \mu(t) + \delta r_i(t),
\]

and retaining up to the order of \( \langle \delta r_i \delta r_j \rangle \), we obtain equations of motion for \( \mu \), \( \gamma \) and \( \rho \). AMM equations in the Stratonovich representation are given by (the argument \( t \) being suppressed)

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

\[
\frac{d\gamma}{dt} = 2f_1 \gamma + \frac{2h_1 w}{Z} (N \rho - \gamma) + 2(g_1^2 + 2g_0 g_2) \alpha^2 \gamma + \gamma + \alpha^2 g_0^2 + \beta^2,
\]

\[
\frac{d\rho}{dt} = 2f_1 \rho + 2h_1 w \rho + 2(g_1^2 + 2g_0 g_2) \alpha^2 \rho + \frac{1}{N} (\gamma + \alpha^2 g_0^2 + \beta^2) + \frac{Z}{N} (\gamma S_i + c_1 \alpha^2 g_0^2 + c_0 \beta^2),
\]

where \( f_i = (1/\ell^2)(\partial^i F(\mu)/\partial \mu^i) \), \( g_i = (1/\ell^2)(\partial^i G(\mu)/\partial \mu^i) \), \( h_i = (1/\ell^2)(\partial^i H(u)/\partial u^i) \) and \( u = w \mu + \mu_1 \). Original \( N \)-dimensional stochastic DESs given by Eqs. (1)–(3) are transformed to the three-dimensional deterministic DESs given by Eqs. (16)–(18). For \( \gamma = S_i = c_0 = c_1 = 0 \), equations of motion given by Eqs. (16)–(18) reduce to those obtained in our previous study [34]. From \( \mu \), \( \gamma \) and \( \rho \) obtained by Eqs. (16)–(18), we may calculate important quantities of synchrony and variability. Then, they may be expressed in physically more transparent forms, as will be discussed in the following [Eqs. (23)–(25)].
2.3. Rate synchronization and variability

2.3.1. Synchronization ratio

The synchronization is conventionally discussed for firing timings (temporal synchronization) or phase (phase synchronization). We discuss, in this paper, the synchronization for firing rate (rate synchronization). In order to quantitatively discuss the synchronization, we first consider the quantity \( P(t) \) given by

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

(19)

When all neurons are firing with the same rate (the completely synchronous state), we obtain \( r_i(t) = R(t) \) for all \( i \), and then \( P(t) = 0 \) in Eq. (19). On the contrary, we obtain \( P(t) = 2(1 - 1/N)\gamma(t) \equiv P_0(t) \) in the asynchronous state where \( \rho = \gamma/N \) [34,38]. We may define the normalized ratio for the synchrony of firing rates given by [38]

\[
S(t) \equiv 1 - \frac{P(t)}{P_0(t)} = \left( \frac{N\rho(t)/\gamma(t) - 1}{N - 1} \right).
\]

(20)

\( S(t) \) is 0 and 1 for completely asynchronous \((P = P_0)\) and synchronous states \((P = 0)\), respectively.

2.3.2. Variability

The variability in the ISI is usually defined by by \( C_V^I = \sqrt{\gamma^I/\mu^I} \) where \( \mu^I \) and \( \gamma^I \) stand for mean and variance of ISI, respectively. We here define the rate variability given by

\[
C_V(t) = \frac{\sqrt{\langle (\delta r_I)^2 \rangle}}{\mu(t)} = \frac{\sqrt{\gamma(t)}}{\mu(t)}.
\]

(21)

Similarly, the variability in input rate signals is given by

\[
C_V(t) = \frac{\sqrt{\langle (\delta I_I)^2 \rangle}}{\mu_I(t)} = \frac{\sqrt{\gamma_I(t)}}{\mu_I(t)}.
\]

(22)

We may show that if the temporal firing rate is given by \( r_i(t) = 1/T_i(t) \), we obtain \( C_V(t) \simeq C_V^I(t) \), where \( T_i(t) \) denotes the ISI of firing times in a neuron \( i \).

2.4. AMM equations for \( \mu, \gamma \) and \( S \)

It is noted that the variability and synchrony are related to the second-order statistics of local \((\gamma)\) and global fluctuations \( (\rho) \), respectively, of firing rates. Employing the relations given by Eq. (20), we may transform equations of motion for \( \mu, \gamma \) and \( \rho \) given by Eqs. (16)–(18) to those for \( \mu, \gamma \) and \( S \) given by

\[
\frac{d\mu}{dt} = f_0 + h_0 + f_2\gamma + \left( \frac{\alpha^2}{2} \right) [g_0g_1 + 3(g_1g_2 + g_0g_1)\gamma].
\]

(23)

\[
\frac{d\gamma}{dt} = 2f_1\gamma + 2h_1\gamma S + 2(g_1^2 + 2g_0g_2)\alpha^2\gamma + \gamma_1 + \alpha^2g_0^2 + \beta^2,
\]

(24)

\[
\frac{dS}{dt} = -\frac{1}{\gamma} (\gamma_1 + \alpha^2g_0^2 + \beta^2)S + \left( \frac{1}{\gamma} \right) (\gamma S_1 + c_1\alpha^2g_0^2 + c_0\beta^2) + \left( \frac{2h_1w}{Z} \right) (1 + ZS)(1 - S).
\]

(25)

Eqs. (23)–(25) express a response of \((\mu, \gamma, S)\) to a given input of \((\mu_I, \gamma_I, S_I)\). Input signals in which information is encoded in \( \mu_I, \gamma_I \) and \( S_I \) are hereafter referred to as mean-driven, fluctuation-driven and synchrony-driven inputs, respectively. Eqs. (23)–(25) show that \( \gamma_1 \) plays the same role as independent noise while \( \gamma S_1 \) as correlated noise.

When we adopt \( F(r) \) and \( G(r) \) given by

\[
F(r) = -\lambda r^a, \quad G(r) = r^b, \quad (a, b \geq 0)
\]

(26)

(27)

Eqs. (23)–(25) become

\[
\frac{d\mu}{dt} = -\lambda \mu^a + h_0 - \left( \frac{\lambda}{2} \right) [\alpha (a - 1)\mu^{a-2}\gamma + \left( \frac{\alpha^2}{2} \right) [b\mu^{2b-1} + b(b - 1)(2b - 1)\mu^{2b-3}\gamma]],
\]

(28)

\[
\frac{d\gamma}{dt} = -2\lambda a\mu^{a-1}\gamma + 2h_1\gamma S + 2b(2b - 1)\alpha^2\mu^{2b-2}\gamma + \gamma_1 + \alpha^2\mu^{2b} + \beta^2,
\]

(29)

\[
\frac{dS}{dt} = -\frac{1}{\gamma} (\gamma_1 + \alpha^2\mu^{2b} + \beta^2)S + \left( \frac{1}{\gamma} \right) (\gamma S_1 + c_1\alpha^2\mu^{2b} + c_0\beta^2) + \left( \frac{2h_1w}{Z} \right) (1 + ZS)(1 - S),
\]

(30)
where \( \lambda \) expresses the relaxation rate. We note that for (i) \( a = 0 \) or 1 and (ii) \( b = 0, 1/2 \) or 1, a motion of \( \mu \) is decoupled from the rest of variables because the \( a(a-1) \) and \( b(b-1)(2b-1) \) in the third and fourth terms of Eq. (28) vanish. Eq. (30) shows that a motion of \( S \) is ostensibly independent of the index \( a \) of \( F(r) \) although it depends on \( a \) through \( \gamma \).

### 3. Model calculations

#### 3.1. Stationary properties

In order to get an insight to the present method, we will show some model calculations. When we consider a special case of \( a = b = 1.0 \) in Eqs. (26) and (27),

\[
F(r) = -\lambda r, \\
G(r) = r.
\]

Eqs. (28)–(30) are expressed by

\[
\begin{align*}
\frac{d\mu}{dt} &= -\lambda \mu + h_0 + \frac{\alpha^2 \mu}{2}, \\
\frac{d\gamma}{dt} &= -2\lambda \gamma + 2h_1 w \gamma S + 2\alpha^2 \gamma + \gamma_1 + \alpha^2 \mu^2 + \beta^2, \\
\frac{dS}{dt} &= -\frac{S}{\gamma} \left[ (\gamma_1 + \alpha^2 \mu^2 + \beta^2) + \frac{1}{\gamma} (\gamma_1 S_1 + c_1 \alpha^2 \mu^2 + c_0 \beta^2) + \left( \frac{2h_1 w}{Z} \right) (1 + ZS) (1 - S). \right]
\end{align*}
\]

The stationary solution of Eqs. (33)–(35) is given by

\[
\begin{align*}
\mu &= \frac{h_0}{(\lambda - \alpha^2/2)}, \\
\gamma &= \frac{(\gamma_1 + \alpha^2 \mu^2 + \beta^2)}{2(\lambda - \alpha^2 - h_1 w S)}, \\
S &= \frac{Z(\lambda - \alpha^2)(\gamma_1 S_1 + c_1 \alpha^2 \mu^2 + c_0 \beta^2) + h_1 w(\gamma_1 + \alpha^2 \mu^2 + \beta^2)}{(\gamma_1 + \alpha^2 \mu^2 + \beta^2)(Z(\lambda - \alpha^2) - h_1 w(Z - 1)] + h_1 w \gamma S_1}, \\
&= \frac{(\gamma_1 S_1 + c_1 \alpha^2 \mu^2 + c_0 \beta^2)}{(\gamma_1 + \alpha^2 \mu^2 + \beta^2)}, \quad \text{for } w = 0 \\
&= \frac{h_1 w}{[Z(\lambda - \alpha^2) - h_1 w(Z - 1)]}, \quad \text{for } c_0 = c_1 = S_1 = 0.
\end{align*}
\]

We note in Eq. (36) that \( \mu \) is increased as \( \mu_1 \) is increased with an enhancement factor of \( 1/(\lambda - \alpha^2/2) \), but \( \mu \) is independent of \( \gamma_1 \) and \( S_1 \). Local fluctuation \( \gamma \) is increased with increasing input fluctuation \( (\gamma_1) \) and/or noise \( (\alpha, \beta) \) as Eq. (37) shows. Eq. (38) shows that \( S \) is increased with increasing \( S_1, c_0, c_1 \) and/or \( w \), as expected.

The stability condition around the stationary state may be examined from eigenvalues of the Jacobian matrix of Eqs. (33)–(35), which are given by (for details, see Appendix B)

\[
\begin{align*}
\lambda_1 &= -\lambda + \frac{\alpha^2}{2} + h_1 w, \\
\lambda_2 &= -2\lambda + 2\alpha^2 - \frac{2h_1 w}{Z}, \\
\lambda_3 &= -2\lambda + 2\alpha^2 + 2h_1 w.
\end{align*}
\]

The first eigenvalue of \( \lambda_1 \) arises from an equation of motion for \( \mu \), which is decoupled from the rest of variables. The stability condition for \( \mu \) is given by

\[
h_1 w < (\lambda - \alpha^2/2).
\]

In contrast, the stability condition for \( \gamma \) and \( \rho \) is given by

\[
-Z(\lambda - \alpha^2) < h_1 w < (\lambda - \alpha^2).
\]

Then for \( \lambda - \alpha^2 < h_1 w < \lambda - \alpha^2/2 \), \( \gamma \) and \( \rho \) are unstable but \( \mu \) remains stable.

The parameters in our model are \( \alpha, \beta, w \) and \( N \): we hereafter set \( \lambda = 1.0 \) and \( c_1 = c_0 = 0.0 \) to reduce the number of model parameters. Input signals are characterized by \( \mu_1, \gamma_1 \) and \( S_1 \). We will present some numerical calculations for mean-, fluctuation- and synchrony-driven inputs which are calculated with the use of Eqs. (36)–(38) for \( \alpha = 0.0, \beta = 0.1 \) and \( N = 100 \).
3.1.1. Mean-driven inputs

Fig. 1 shows the $\mu_I$ dependence of $\mu$ and $S$ for $w = 0.0$ (dashed curves) and $w = 0.5$ (solid curves) with $\gamma_I = 0.2$ and $S_I = 0.1$ ($\lambda = 1.0, \alpha = 0.0, \beta = 0.1$, and $N = 100$), the chain curve expressing $\mu = \mu_I$.

3.1.2. Fluctuation-driven inputs

Fig. 2 shows $C_V$ and $S$ against $C_{VI}$ ($= \sqrt[4]{\gamma_I}/\mu_I$) for $w = 0.0$ (dashed curves) and $w = 0.5$ (solid curves) with $\mu_I = 0.2$ and $S_I = 0.2$ ($\lambda = 1.0, \alpha = 0.0, \beta = 0.1$, and $N = 100$), the chain curve expressing $C_V = C_{VI}$.

3.1.3. Synchrony-driven inputs

Fig. 3 shows the $S_I$ dependence of $\mu$ and $S$ for $w = 0.0$ (dashed curves) and $w = 0.5$ (solid curves) with $\mu_I = 0.2$ and $\gamma_I = 0.2$. For $w = 0.0$, an increase in $C_{VI}$ yields an increase in $C_V$ and $S$, while $\mu$ is independent of $C_{VI}$ as Eqs. (36)–(38) show. The chain curve shows $C_V = C_{VI}$: the region where $C_V < C_{VI}$ is realized for $C_{VI} > 0.51$ for $w = 0.0$ and $C_{VI} > 0.22$ for $w = 0.5$.

It is necessary to point out that the $\mu_I$ dependence of $\mu$ is modified by multiplicative noise ($\alpha$). An example of the $\mu_I$ dependence of $\mu$ is plotted in Fig. 4 for various $\alpha$. With increasing $\alpha$, $\mu$ shows a steeper increase for larger $\alpha$ because of the $(\lambda - \alpha^2/2)$ factor in Eq. (36). This reminds us the recent experiment of prefrontal cortex (PFC) showing that the $f-I$ curve
Fig. 3. (Color online) Stationary values of $\mu$ and $S$ as a function of $S_I$ for $w = 0.0$ (dashed curves) and $w = 0.5$ (solid curves) with $\mu_I = 0.2$ and $\gamma_I = 0.2$ ($\lambda = 1.0, \alpha = 0.1, \beta = 0.0$, and $N = 100$), the chain curve expressing $S = S_I$.

Fig. 4. $\mu$ as a function of $\mu_I$ for various $\alpha$ values with $\lambda = 1.0$ and $w = 0.0$.

has the increased sensitivity at large $l$ with increasing input fluctuation [15]. This is interpreted as due to a shorten, effective refractory period by fluctuation in the calculation using the IF model [15].

The dependence of $S$ on $S_I$ is plotted in Fig. 5 for various values of $N$ ($\alpha = 0.5, \beta = 0.2, w = 0.5$). It is shown that the synchrony $S$ is more increased in smaller system. The result for $N = 100$ is nearly the same as that for $N = \infty$.

3.2. Dynamical properties

In order to study the dynamical properties of the neuronal ensemble given by Eqs. (1)–(3), we have performed DSs by using the Heun method [50,51] with a time step of 0.0001: DS results are averages of 100 trials. AMM calculations have been performed for Eqs. (33)–(35) by using the fourth-order Runge–Kutta method with a time step of 0.01. We consider, as a typical example, an ensemble with $\lambda = 1.0, \alpha = 0.1, \beta = 0.1, w = 0.5$ and $N = 100$. If we adopt a larger $N$ in our model calculations, fluctuations in DS results are decreased and we may obtain smoother results, although it needs much computational time. Among $\mu$, $\gamma$ and $S$, the strongest $N$ dependence is realized in $S$ [Eqs. (36)–(38)]. Fig. 5 shows that the synchrony $S$ almost saturates at $N > 100$ where it has little $N$ dependence. This is a reason why we have adopted $N = 100$ for our model calculations. Calculated responses to mean-, fluctuation- and synchrony-driven pulse inputs are shown in Figs. 6–8, respectively, where solid and dashed curves show results of the AMM and DS, respectively.

3.2.1. Mean-driven inputs

First we apply a mean-driven pulse input given by

$$\mu_I(t) = A \Theta(t - 40) \Theta(60 - t) + A_0, \quad (46)$$
Fig. 5. $S$ as a function of $S_I$ for various $N$ with $\mu_I = 0.1, \gamma_I = 0.0, \lambda = 1.0, \alpha = 0.5, \beta = 0.2$ and $w = 0.5$.

Fig. 6. (Color online) Time courses of (a) $\mu(t)$, (b) $\gamma(t)$, (c) $S(t)$ and (d) $C_V(t)$ for mean-driven pulse input $\mu_I(t)$ given by Eq. (46) ($A = 0.4, A_b = 0.1$) with $\gamma_I(t) = 0.1$ and $S_I(t) = 0.1$, calculated by the AMM (solid curves) and DS (dashed curves): chain curves in (a), (b) and (c) express inputs of $\mu_I(t)$, $\gamma_I(t)$ and $S_I(t)$, respectively ($\lambda = 1.0, \alpha = 0.1, \beta = 0.1, w = 0.5$ and $N = 100$).

with $A = 0.4, A_b = 0.1, \gamma_I(t) = 0.1$ and $S_I(t) = 0.1$. Responses of $\mu(t)$, $\gamma(t)$, $S(t)$ and $C_V(t)$ calculated by the AMM (solid curves) and DS (dashed curves) are shown in Fig. 6(a), (b), (c) and (d), respectively: input signals of $\mu_I(t)$, $\gamma_I(t)$ and $S_I(t)$ are plotted by chain curves in (a), (b) and (c), respectively. An increase in an applied mean-driven input at $40 \leq t < 60$ induces an increase in $\mu(t)$ and decreases in $\gamma(t)$ and $S(t)$ which arise from the $h_1$ term in Eq. (35). By an applied pulse input, $C_V(t)$ is decreased because of the increased $\mu$. The results of the AMM are in fairly good agreement with those of DS.
Fig. 7. (Color online) Time courses of (a) $\mu(t)$, (b) $\gamma(t)$, (c) $S(t)$ and (d) $C_V(t)$ for fluctuation-driven pulse input $\gamma_I(t)$ given by Eq. (47) ($B = 0.2, B_b = 0.05$) with $\mu_I(t) = 0.1$ and $S_I(t) = 0.1$. Calculated by the AMM (solid curves) and DS (dashed curves): chain curves in (a), (b) and (c) express inputs of $\mu_I(t)$, $\gamma_I(t)$ and $S_I(t)$, respectively ($\lambda = 1.0, \alpha = 0.1, \beta = 0.1, w = 0.5$ and $N = 100$).

3.2.2. Fluctuation-driven inputs

Next we apply a fluctuation-driven input given by

$$\gamma_I(t) = B\Theta(t - 40)\Theta(60 - t) + B_b,$$

with $B = 0.2, B_b = 0.05, \mu_I(t) = 0.1$ and $S_I(t) = 0.1$. Fig. 7(a)–(d) show calculated responses of $\mu(t)$, $\gamma(t)$, $S(t)$ and $C_V(t)$. When the magnitude of $\gamma_I(t)$ is increased at $40 \leq t < 60$, $\gamma(t)$ and $C_V(t)$ are much increased, while there is no changes in $\mu(t)$. $S(t)$ is modified only at $t \sim 40$ and $t \sim 60$, where the input pulse is on and off.

3.2.3. Synchrony-driven inputs

We apply a synchrony-driven input given by

$$S_I(t) = C\Theta(t - 40)\Theta(60 - t) + C_b,$$

with $C = 0.4, C_b = 0.1, \mu_I(t) = 0.1$ and $\gamma_I(t) = 0.1$, whose results are plotted in Fig. 8(a)–(d). An increase in synchrony-driven input at $40 \leq t < 60$ induces increases in $S(t)$, $\gamma(t)$ and $C_V(t)$, but no changes in $\mu(t)$. This is because $\mu(t)$ is decoupled from the rest of variables in Eqs. (33)–(35) for the case of $F(r) = -\lambda r$ and $G(r) = r$.

3.3. Independent component analysis

It is interesting to estimate multivariate input signals from multiple output signals. Such a procedure has been provided in various methods such as Bayesian estimation and ICA [47]. Here we consider ICA, which was originally developed for a linear mixing system, and then it has been extended to linear and nonlinear dynamical systems. ICA has revealed many interesting applications in various fields such as biological signals and image processing. A vector $x$ of output signals is a real function $F$ of a vector $s$ of input sources:

$$x = \hat F(s).$$

The dimension of $s$ is assumed to be the same or smaller than that of $x$. If components of $s$ are statistically independent and if only one of the source signals is allowed to have a Gaussian distribution, ICA may extract a vector $y$ with a function $\hat G$ given
Fig. 8. (Color online) Time courses of (a) $\mu(t)$, (b) $\gamma(t)$, (c) $S(t)$ and (d) $C_V(t)$ for synchrony-driven pulse input $S_I(t)$ given by Eq. (48) ($C = 0.4, C_b = 0.1$) with $\mu_I(t) = 0.1$ and $\gamma_I(t) = 0.1$ calculated by the AMM (solid curves) and DS (dashed curves); chain curves in (a), (b) and (c) express inputs of $\mu_I(t)$, $\gamma_I(t)$ and $S_I(t)$, respectively ($\lambda = 1.0, \alpha = 0.1, \beta = 0.1, w = 0.5$ and $N = 100$).

by

$$y = \hat{G}(x),$$

from which we may estimate the original source as $s \simeq y$ [47].

### 3.3.1 Coexistence of $\mu_I$ and $S_I$

We will discuss the case when mean- and synchrony-driven inputs are simultaneously applied to the neuronal model. We consider the mean-driven sinusoidal input and synchrony-driven sawtooth input, given by

$$\mu_I(t) = 0.1[1 - \cos(2\pi t/20)] + 0.1,$$

$$S_I(t) = 0.01 \text{mod} (t, 50),$$

with $\gamma_I(t) = 0.1$ where $\text{mod}(a, b)$ denotes the mod function expressing the residue of $a$ divided by $b$. Two panels in Fig. 9(a) show input signals of $\mu_I(t)$ and $S_I(t)$, and two panels in Fig. 9(b) show output signals of $\mu(t)$ and $S(t)$ calculated by the AMM. We note a little distortion in $S(t)$ due to crosstalk from $\mu(t)$. Assuming $s = (\mu_I, S_I)^\top$ and $x = (\mu, S)^\top$, we have made an analysis of our result by using ICA. Two panels in Fig. 9(c) show two components of $y$ extracted from output signals of $x = (\mu, S)^\top$ shown in Fig. 9(b) with the use of the fast ICA program [52]. Although the program is designed for linear, mixing signals, we have employed it for our qualitative discussion. We note that results in Fig. 9(c) fairly well reproduce the original, sinusoidal and sawtooth signals shown in Fig. 9(a).

### 3.3.2 Coexistence of $\mu_I$, $\gamma_I$ and $S_I$

Next we consider the case where three kinds of inputs are simultaneously applied. They are mean-driven sinusoidal signal, fluctuation-driven sawtooth signal and synchrony-driven square pulse signal, given by

$$\mu_I(t) = 0.1[1 - \cos(2\pi t/20)] + 0.1,$$

$$\gamma_I(t) = 0.002 \text{mod} (t, 50),$$

$$S_I(t) = 0.5\Theta[-\cos(2\pi t/120)].$$

Three panels in Fig. 10(a) show the input signals of $\mu_I(t)$, $\gamma_I(t)$ and $S_I(t)$. Output signals of $\mu(t)$, $\gamma(t)$ and $S(t)$ calculated in the AMM are shown in three panels of Fig. 10(b), where $\gamma(t)$ and $S(t)$ are a little distorted by crosstalk. We have made an
ICA analysis of our result, assuming $s = (\mu_I, \gamma_I, S_I)^\top$ and $x = (\mu, \gamma, S)^\top$. Three panels of Fig. 10(c) show signals extracted by ICA. Extracted sinusoidal and square signals in Fig. 10(c) are similar to those of input signals shown in Fig. 10(a), though the fidelity of a sawtooth signal is not satisfactory. This is partly due to the fact that the fast ICA program adopted in our analysis is developed for linear mixing models, but not for dynamical nonlinear models [52].

These ICA analyses show that the mean, fluctuation and synchrony may independently carry information in our population rate-code model.

4. Discussion

4.1. A comparison with previous studies

Various attempts have been proposed to obtain the firing-rate model, starting from spiking neuron models [53–57]. It is difficult to analytically calculate the firing rate based on the firing model, except for the IF-type model [19–33]. Calculations with the use of the IF model have shown the followings:

1. increased input firing rate decreases output variability [32].
2. increased input firing rate decreases synchrony [20,22].
3. increased input fluctuation raises firing rate [15,26].
4. increased input synchrony increases firing rates [6,12,18,22,24], and
5. increased input synchrony increases variability [21].

The items (1), (2) and (5) are consistent with our result shown in Figs. 6 and 7. In contrast, items (3) and (4) seem to inconsistent with our result showing that $\mu(t)$ is independent of $\gamma_I(t)$ and $S_I(t)$, as given by Eq. (33). It is noted, however,
that the model calculation given in the preceding section has been made for the case of $F(r) = -\lambda r$ and $G(r) = r$, in which a motion of $\mu(t)$ is decoupled from those of $\gamma(t)$ and $S(t)$. This is not the case in general. We note in Eq. (28) that $\mu(t)$ is not decoupled from $\gamma(t)$ and $S(t)$ except for the case in which $(a = 0 \text{ or } 1)$ and $(b = 0, 1/2 \text{ or } 1)$. For example, in the case of $F(r) = -\lambda r$ and $G(r) = r^2$, equations of motion given by Eqs. (28)–(30) become

\[
\frac{d\mu}{dt} = -\lambda \mu + h_0 + \alpha^2 (\mu^3 + 3\mu \gamma),
\]

\[
\frac{d\gamma}{dt} = -2\lambda \gamma + 2h_1 \gamma S + 12\alpha^2 \mu^2 \gamma + \gamma_1 + \alpha^2 \mu^4 + \beta^2,
\]

\[
\frac{dS}{dt} = -\frac{1}{\gamma}(\gamma_1 + \alpha^2 \mu^4 + \beta^2)S + \frac{1}{\gamma}(\gamma_0 S + s_1 \alpha^2 \mu^4 + c_0 \beta^2) + \left(\frac{2h_1 w}{Z}\right)(1 + ZS)(1 - S),
\]

Eqs. (56)–(58) clearly show that $\mu(t)$ is coupled with $\gamma(t)$ and $S(t)$.

Fig. 11 shows time courses of $\mu(t)$, $\gamma(t)$ and $S(t)$ calculated with the use of Eqs. (56)–(58) when a mean-driven input $\mu_0(t)$ given by Eq. (46) with $A = 0.4, A_0 = 0.1, \gamma_0(t) = 0.2$ and $S_0(t) = 0.2$ is applied to a neuron ensemble with $\alpha = 0.35$, $\beta = 0.1, w = 0.5, c_0 = 0.0$ and $N = 100$. We note that $\gamma(t)$ is modified by an applied $\mu_0(t)$ at $40 \leq t < 60$, showing the coupling between $\mu(t)$ and $\gamma(t)$ in the case of $F(r) = -\lambda r$ and $G(r) = r^2$, while there are no couplings between them in the case of $F(r) = -\lambda r$ and $G(r) = r$ as shown in Fig. 6.

A number of neuronal experiments have not reported a systematic change in firing rates while the synchronization within an area is modulated [6]. In particular, the synchrony is modified without a change in firing rate in some experiments [7, 9, 11]. It has been pointed out that such phenomenon may be accounted for by a mechanism of a rapid activation of a few
Fig. 11. (Color online) Time courses of (a) $\mu(t)$, (b) $\gamma(t)$, (c) $S(t)$ and (d) $C(t)$ for mean-driven input $\mu(t)$ given by Eq. (46) ($A = 0.4, A_b = 0.1$) with $\gamma_I(t) = 0.2$ and $S_I(t) = 0.2$ calculated by the AMM (solid curves) for $F(r) = -\lambda r$ and $G(r) = r^2$ with Eqs. (56)–(58); chain curves in (a), (b) and (c) express inputs of $\mu_I(t)$, $\gamma_I(t)$ and $S_I(t)$, respectively ($\lambda = 1.0, \alpha = 0.4, \beta = 0.1, w = 0.5$ and $N = 100$).

selected interneurons [12]. Recently the absence of a change in firing rate is shown to be explained if the ratio of excitatory to inhibitory synaptic weights of long-range couplings is kept constant in neuron ensembles described by the IF model [33].

5. Conclusion

We have discussed the rate code of firings neuron population, studying the responses of the generalized rate-code model [34,45] to three kinds of inputs: mean-, fluctuation- and synchrony-driven inputs. The ICA analyses of our results have suggested that mean rate, fluctuation (or variability) and synchrony may carry independent information. It would be interesting to examine this possibility by neuronal experiments using in vivo or in vitro neuron ensembles.

One of advantages of our rate-code model given by Eqs. (1)–(3) is that we can easily discuss various properties of neuronal ensembles, by changing $F(r)$, $G(r)$, $H(u)$ and model parameters. It is possible to theoretically examine various cases of $F(r)$ and $G(r)$ in a systematic way. We hope that our rate-code model shares advantages with phenomenological neuronal models such as the Hopfield [58] and Wilson–Cowan models [59].

The Tsallis and Fisher information entropies are very important quantities expressing information measures in nonextensive systems [60]. It is challenging to calculate information entropies in neuronal ensembles with spatially correlated variability [61]. The plasticity of synapses (depression and facilitation) is known to play important roles in the activity of neurons. Indeed, memory in the brain is accounted for by the plasticity of synapses in the Hopfield model [58]. A variety of activity in prefrontal cortex in response to sensory stimuli is expected to be explained by dynamic synapses. It is promising to take into account dynamic synapses in our approach, which is left as our future study.

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Appendix A. Derivation of AMM equations given by Eqs. (16)–(18)

The Fokker–Planck equation (FPE) for the Langevin equation given by Eq. (1) in the Stratonovich representation is given by [62,63]
\[
\frac{\partial}{\partial t} p(\{r_k\}, t) = \sum_i \frac{\partial}{\partial r_i} \{F(\{r_i\}) + H(\{u_i\})\} p(\{r_k\}, t) + \frac{\beta^2}{2} \sum_i \sum_j \frac{\partial^2}{\partial r_i \partial r_j} \{\delta_{ij} + c_0 (1 - \delta_{ij})\} p(\{r_k\}, t),
\]
\[+ \frac{\alpha^2}{2} \sum_i \sum_j \{\delta_{ij} + c_1 (1 - \delta_{ij})\} \frac{\partial}{\partial r_i} \{G(\{r_i\}) \frac{\partial}{\partial r_j} [G(\{r_i\}) p(\{r_k\}, t)]\}. \quad (A.1)
\]
Equations of motion for moments, \( \langle r_i \rangle \) and \( \langle r_i r_j \rangle \), are derived with the use of FPE \[34]:
\[
\frac{d\langle r_i \rangle}{dt} = \langle F(\{r_i\}) + H(\{u_i\}) \rangle + \frac{\alpha^2}{2} \langle G(\{r_i\}) G(\{r_i\}) \rangle, \quad (A.2)
\]
\[
\frac{d\langle r_i r_j \rangle}{dt} = \{\langle r_i [F(\{r_j\}) + H(\{u_i\})] \rangle + \langle r_j [F(\{r_i\}) + H(\{u_i\})] \rangle \} + \frac{\alpha^2}{2} \{\langle r_i G(\{r_j\}) G(\{r_j\}) \rangle + \langle r_j G(\{r_i\}) G(\{r_i\}) \rangle \}
\]
\[+ \delta_{ij} [\gamma_1 + \alpha^2 \langle G(\{r_i\})^2 \rangle + \beta^2] + (1 - \delta_{ij}) [\gamma_2 s_i + c_1 \alpha^2 \langle G(\{r_i\}) G(\{r_j\}) \rangle + c_0 \beta^2]. \quad (A.3)
\]
We may obtain Eqs. (16)-(18), by using the expansion given by
\[r_i = \mu + \delta r_i, \quad (A.4)\]
and the relations given by
\[
\frac{d\mu}{dt} = \frac{1}{N} \sum_i \frac{d\langle r_i \rangle}{dt}, \quad (A.5)
\]
\[
\frac{dy}{dt} = \frac{1}{N} \sum_i \frac{d\langle (\delta r_i)^2 \rangle}{dt}, \quad (A.6)
\]
\[
\frac{d\rho}{dt} = \frac{1}{N^2} \sum_i \sum_j \frac{d(\delta r_i \delta r_j)}{dt}. \quad (A.7)
\]
For example, Eq. (16) for \( d\mu/dt \) is obtained as follows.
\[
\frac{1}{N} \sum_i \langle F(\{r_i\}) \rangle = f_0 + f_2 \gamma, \quad (A.8)
\]
\[
\frac{1}{N} \sum_i \langle H(\{u_i\}) \rangle = h_0, \quad (A.9)
\]
\[
\frac{1}{N} \sum_i \langle G(\{r_i\}) G(\{r_i\}) \rangle = g_0 g_1 + 3 (g_0 g_3 + g_1 g_2) \gamma. \quad (A.10)
\]
Eqs. (17) and (18) are obtainable in a similar way. By using Eq. (20), we obtain equations of motion for \( \mu(t), \gamma(t) \) and \( S(t) \) given by Eqs. (23)-(25).

**Appendix B. Jacobian matrix of Eqs. (33)-(35)**

In making a linear stability analysis, it is better to adopt the basis of \( (\mu, \gamma, \rho) \) than that of \( (\mu, \gamma, S) \). In the former basis, equations of motion for \( F(r) = -\lambda r \) and \( G(r) = r \) given by Eqs. (16)-(18) become
\[
\frac{d\mu}{dt} = -\lambda \mu + h_0 + \frac{\alpha^2 \mu}{2}, \quad (B.1)
\]
\[
\frac{dy}{dt} = -2\lambda \gamma + \frac{2h_1 w N}{Z} \left( \rho - \frac{\gamma}{N} \right) + 2\alpha^2 \gamma + \gamma_1 + \alpha^2 \mu^2 + \beta^2, \quad (B.2)
\]
\[
\frac{d\rho}{dt} = -2\lambda \rho + 2h_1 w \rho + 2\alpha^2 \rho + \frac{1}{N} (\gamma_1 + \alpha^2 \mu^2 + \beta^2) + \frac{Z}{N} (\gamma_2 s_i + c_1 \alpha^2 \mu^2 + c_0 \beta^2). \quad (B.3)
\]
The stability of the stationary state may be examined by the Jacobian matrix of Eqs. (B.1)-(B.3). With the use of \( c_{12} = c_{13} = c_{32} = 0 \) in the matrix, we obtain its eigenvalues given by
\[
\lambda_1 = c_{11} = -\lambda + \frac{\alpha^2}{2} + h_1 w, \quad (B.4)
\]
\[
\lambda_2 = c_{22} = -2\lambda + 2\alpha^2 - \frac{2h_1 w}{Z}, \quad (B.5)
\]
\[
\lambda_3 = c_{33} = -2\lambda + 2\alpha^2 + 2h_1 w, \quad (B.6)
\]
from which the stability condition given by Eqs. (44) and (45) is obtained.
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