Dynamics of the Langevin model subjected to colored noise: Functional-integral method

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Abstract

We have discussed the dynamics of Langevin model subjected to colored noise, by using the functional-integral method (FIM) combined with equations of motion for mean and variance of the state variable. Two sets of colored noise have been investigated: (a) one additive and one multiplicative colored noise, and (b) one additive and two multiplicative colored noise. The case (b) is examined with relevance to a recent controversy on the stationary subthreshold voltage distribution of an integrate-and-fire model including stochastic excitatory and inhibitory synapses and a noisy input. We have studied the stationary probability distribution and dynamical responses to time-dependent (pulse and sinusoidal) inputs of the linear Langevin model. Model calculations have shown that results of the FIM are in good agreement with those of direct simulations (DSs). A comparison is made among various approximate analytic solutions such as the universal colored noise approximation (UCNA). It has been pointed out that dynamical responses to pulse and sinusoidal inputs calculated by the UCNA are rather different from those of DS and the FIM, although they yield the same stationary distribution.

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1. Introduction

Nonlinear stochastic dynamics of physical, chemical, biological and economical systems has been extensively studied (for a recent review, see Ref. [1]). In most theoretical studies, Gaussian white noise is employed as random driving force because of its mathematical simplicity. The white-noise approximation is appropriate to systems in which the time scale characterizing the relaxation of the noise is much shorter than the characteristic time scale of the system. There has been a growing interest in the theoretical study of nonlinear dynamical systems subjected to colored noise with the finite correlation time (for a review on colored noise, see Ref. [2] and the related references therein). It has been realized that colored noise gives rise to new intriguing effects such as the reentrant phenomenon in a noise-induced transition [3] and a resonant activation in bistable systems [4].
The original model for a system driven by colored noise is expressed by non-Markovian stochastic differential equation. This problem may be transformed to a Markovian one, by extending the number of relevant variables and including an additional differential equation describing the Orstein–Uhlenbeck (OU) process. It is difficult to analytically solve the Langevin model subjected to colored noise. For its analytical study, two approaches have been adopted: (1) to construct the multi-dimensional Fokker–Planck equation (FPE) for the multivariate probability distribution, and (2) to derive the effective one-dimensional FPE equation. The presence of multi-variables in the approach (1) makes a calculation of even the stationary distribution much difficult. In a recent study on the Langevin model subjected to additive (non-Gaussian) colored noise [5], we employed approach (1), analyzing the multivariate FPE with the use of the second-order moment method. A typical example of approach (2) is the universal colored noise approximation (UCNA) [6], which interpolates between the limits of zero and infinite relaxation times, and which has been widely adopted for a study of colored noise [2]. Another example of the approach (2) is the path-integral and functional-integral methods [7–12] obtaining the effective FPE, with which stationary properties such as the non-Gaussian stationary distribution have been studied [2].

Theoretical study on the Langevin model driven by colored noise has been mostly made for its stationary properties such as the stationary probability distribution and the phase diagram of noise-induced transition [2]. As far as we are aware of, little theoretical study has been reported on dynamical properties such as the response to time-dependent inputs. Refs. [13,14] have discussed the filtering effect, in which the high-frequency response of the system is shown to be improved by colored noise. The purpose of the present paper is to extend the functional-integral method (FIM) such that we may discuss the dynamical properties of the Langevin model subjected to colored noise. We consider, in this paper, two sets of colored noise: (a) one additive and one multiplicative colored noise, and (b) one additive and two multiplicative colored noise. The case (b) is included to clarify, to some extent, a recent controversy on the subthreshold voltage distribution of a leaky integrate-and-fire model including conductance-based stochastic excitatory and inhibitory synapses as well as noisy inputs [15–18].

The paper is organized as follows. The FIM is applied to the above-mentioned cases (a) and (b) in Sections 2 and 3, respectively, where the stationary distribution and the response to time-dependent inputs are studied. In Section 4, we will discuss the recent controversy on the subthreshold voltage distribution of a leaky integrate-and-fire model [15–18]. A comparison is made among the results of some approximate analytical theories such as the UCNA [2,6]. The final Section 5 is devoted to conclusion.

2. Langevin model subjected to one additive and one multiplicative colored noise

2.1. Effective Langevin equation

We have considered the Langevin model subjected to additive and multiplicative colored noise given by

$$\frac{dx}{dt} = F(x) + \eta_0(t) + G(x)\eta_1(t),$$

(1)

with

$$\frac{d\eta_m(t)}{dt} = -\frac{\eta_m}{\tau_m} + \frac{\sqrt{2D_m}}{\tau_m} \xi_m(t), \quad (m = 0 \text{ and } 1)$$

(2)

where $F(x)$ and $G(x)$ denote arbitrary functions of $x$: $\eta_0(t)$ and $\eta_1(t)$ stand for additive and multiplicative noise, respectively: $\tau_m$ and $D_m$ express the relaxation times and the strengths of colored noise for additive ($m = 0$) and multiplicative noise ($m = 1$): $\eta_m(t)$ express independent zero-mean Gaussian white noise with correlations given by

$$\langle \xi_m(t)\xi_n(t') \rangle = \delta_{mn}\delta(t - t').$$

(3)

The distribution and correlation of $\eta_m$ are given by

$$p(\eta_m) \propto \exp\left(-\frac{\tau_m}{2D_m}\eta_m^2\right),$$

(4)

$$c_{mn}(t, t') = \langle \eta_m(t)\eta_n(t') \rangle = \delta_{mn}\frac{D_m}{\tau_m}\exp\left(-\frac{|t - t'|}{\tau_m}\right).$$

(5)
By applying the FIM to the Langevin model given by Eqs. (1) and (2), we obtain the effective FPE given by (details being given in the Appendix)

\[ \frac{\partial}{\partial t} p(x, t) = -\frac{\partial}{\partial x} \tilde{F}(x) p(x, t) + \tilde{D}_0 \frac{\partial^2}{\partial x^2} p(x, t) + \tilde{D}_1 \frac{\partial}{\partial x} G(x) \frac{\partial}{\partial x} G(x) p(x, t), \]

from which the effective Langevin model is derived as

\[ \frac{dx}{dt} = \tilde{F}(x) + \sqrt{2\tilde{D}_0} \xi_0(t) + \sqrt{2\tilde{D}_1} G(x) \xi_1(t), \]

with

\[ \tilde{F} = F, \]
\[ \tilde{D}_0 = \frac{D_0}{(1 - \tau_0(F'))}, \]
\[ \tilde{D}_1 = \frac{D_1}{[1 - \tau_1((F') - (FG'/G))]} . \]

Here \( F' = dF/dx \) and \( G' = dG/dx \), and the bracket \( \langle \cdot \rangle \) expresses the average over \( p(x, t) \) to be discussed shortly [Eq. (11)]. It is noted that we will temporally evaluate \( \langle F' \rangle \) etc. in order to discuss the dynamics of the system, while they are conventionally evaluated for the stationary value as \( F'(x_s) \) etc. with \( x_s = \langle x(t = \infty) \rangle \) [7,11].

### 2.2. Equations of motion for mean and variance

With the use of the effective FPE given by Eq. (7), an equation of motion for the average of \( Q(x) \):

\[ \langle Q \rangle = \int Q(x) p(x, t) dx, \]

is given by [19]

\[ \frac{d\langle Q \rangle}{dt} = \langle Q' \tilde{F} \rangle + \tilde{D}_0 \langle Q'' \rangle + \tilde{D}_1 \langle (Q'G)'G \rangle, \]

which yields (for \( Q = x, x^2 \))

\[ \frac{d\langle x \rangle}{dt} = \langle \tilde{F} \rangle + \tilde{D}_1 \langle G'G \rangle, \]
\[ \frac{d\langle x^2 \rangle}{dt} = 2\langle \tilde{F} \rangle + 2\tilde{D}_0 + 2\tilde{D}_1 \langle G^2 + xG'G \rangle. \]

Mean (\( \mu \)) and variance (\( \gamma \)) are defined by

\[ \mu = \langle x \rangle, \]
\[ \gamma = \langle x^2 \rangle - \langle x \rangle^2. \]

Expanding Eqs. (13) and (14) around the mean value of \( \mu \), and retaining up to the second order of \( \langle (\Delta x_i)^2 \rangle \), we get equations of motion for \( \mu \) and \( \gamma \) expressed by [19]

\[ \frac{d\mu}{dt} = \tilde{f}_0 + \tilde{f}_2 \gamma + \tilde{D}_1 [2g_0 g_1 + 3(g_1g_2 + g_0g_3)] \gamma, \]
\[ \frac{d\gamma}{dt} = 2\tilde{f}_1 \gamma + 4\tilde{D}_1 \gamma (g_1^2 + 2g_0g_2) + 2\tilde{D}_1 g_0^2 + 2\tilde{D}_0, \]

where \( \tilde{f}_0 = (1/\ell!) \tilde{F}(\mu)/\partial x^\ell \) and \( g_\ell = (1/\ell!) \tilde{G}(\mu)/\partial x^\ell \). It is noted that \( \tilde{D}_0 \) and \( \tilde{D}_1 \) in Eqs. (17) and (18) are given by Eqs. (9) and (10), respectively.
In the case of $F(x) = -\lambda x + I$ and $G(x) = x$ where $\lambda$ and $I$ denote the relaxation rate and an external input, respectively, the FIM yields equations of motion for $\mu$ and $\gamma$ given by

\[
\frac{d\mu}{dt} = -\lambda \mu + \tilde{D}_1 \mu + I, \quad (19)
\]
\[
\frac{d\gamma}{dt} = -2\lambda \gamma + 4\tilde{D}_1 \gamma + 2\tilde{D}_1 \mu^2 + 2\tilde{D}_0, \quad (20)
\]
with

\[
\tilde{D}_0 = \frac{D_0}{(1 + \lambda \tau_0)}, \quad (21)
\]
\[
\tilde{D}_1 = \frac{D_1}{[1 + (\tau_1 I/\mu)]}. \quad (22)
\]

We have to solve Eqs. (19)--(22) for $\mu$, $\gamma$, $\tilde{D}_0$ and $\tilde{D}_1$ in a self-consistent way.

Stationary values of $\mu$ and $\gamma$ are implicitly given by

\[
\mu_s = \frac{I}{(\lambda - \tilde{D}_1)}, \quad (23)
\]
\[
\gamma_s = \frac{(\tilde{D}_0 + \tilde{D}_1 \mu_s^2)}{(\lambda - 2\tilde{D}_1)}. \quad (24)
\]

with $\tilde{D}_0$ and $\tilde{D}_1$ given by Eqs. (21) and (22), respectively, with $\mu = \mu_s$. Eqs. (23) and (24) show that $\mu_s$ and $\gamma_s$ diverge for $\tilde{D}_1 > \lambda$ and $\tilde{D}_1 > \lambda/2$, respectively. The divergence of moments is common in systems subjected to multiplicative noise, because its stationary distribution has a long-tail power-law structure [19–21]. From Eqs. (22) and (23), we get

\[
\tilde{D}_1 = \left(\frac{D_1}{1 + \lambda \tau_1}\right) \left[1 + \frac{\tau_1 D_1}{(1 + \lambda \tau_1)^2} + 2 \frac{\tau_1^2 D_1^2}{(1 + \lambda \tau_1)^4} + \cdots\right], \quad (25)
\]
\[
\simeq \frac{D_1}{1 + \lambda \tau_1} \equiv \tilde{D}_1^{\text{APP}}. \quad \text{for } \tau_1 D_1/(1 + \lambda \tau_1)^2 \ll 1. \quad (26)
\]

Eq. (27) implies that the approximation of $\tilde{D}_1^{\text{APP}}$ is valid both for (i) $\tau_1 \ll (1/\lambda, 1/D_1)$ and (ii) $\tau_1 \gg (1/\lambda, D_1/\lambda^2)$.

2.3. Stationary distribution

From the effective FPE given by Eq. (7), we get the stationary distribution $p(x)$ given by

\[
\ln p(x) = -\left(\frac{1}{2}\right) \ln[\tilde{D}_0 + \tilde{D}_1 G(x)^2] + Z(x), \quad (28)
\]
with

\[
Z(x) = \int \frac{F(x)}{[\tilde{D}_0 + \tilde{D}_1 G(x)^2]} \, dx. \quad (29)
\]

Because of the presence of multiplicative noise, the stationary distribution generally has non-Gaussian power-law structure [19–21].
Fig. 1. The ratio of $\tilde{D}_1/D_1$ vs. $\tau_1$ calculated by the FIM (solid curve), the approximation (APP) given by Eq. (27) (dashed curve) and the difference of (FIM–APP) x 10 (chain curve) with $I = 0.5, \lambda = 1.0, D_0 = 0.01, D_1 = 0.2$ and $\tau_0 = 0.01$.

In the white-noise limit ($\tau_m = 0$), the stationary distribution for the Langevin equation given by Eq. (1) with $\eta_m = \sqrt{2D_m}$ is expressed by Eqs. (28) and (29) with $\tilde{D}_m = D_m$ in the Stratonovich representation. Then the stationary distribution for colored noise is expressed by

$$p(x; D_0, D_1, \tau_0, \tau_1) = p(x; \tilde{D}_0, \tilde{D}_1, 0, 0) \equiv p_{wn}(x; \tilde{D}_0, \tilde{D}_1),$$  \hspace{1cm} (30)

where $p_{wn}(x; \tilde{D}_0, \tilde{D}_1)$ expresses the stationary distribution for white noise.

In the case of $F(x) = -\lambda x + I$ and $G(x) = x$, we get

$$p(x) \propto (\tilde{D}_0 + \tilde{D}_1 x^2)^{-1/2} \exp[Y(x)],$$  \hspace{1cm} (31)

with

$$Y(x) = \frac{I}{\sqrt{\tilde{D}_0 \tilde{D}_1}} \tan^{-1}\left(\sqrt{\frac{\tilde{D}_1}{\tilde{D}_0}} x\right),$$  \hspace{1cm} (32)

$$\tilde{D}_0 = \frac{D_0}{(1 + \lambda \tau_0)},$$  \hspace{1cm} (33)

$$\tilde{D}_1 = \frac{D_1}{[1 + (\tau_1 I/\mu_s)]},$$  \hspace{1cm} (34)

where $\mu_s$ expresses the stationary value of $\mu$ [Eq. (23)].

2.4. Model calculations

2.4.1. Stationary properties

In order to demonstrate the feasibility of our analytical theory, we have performed model calculations. Direct simulations (DSs) for Eqs. (1) and (2) have been performed by using the fourth-order Runge–Kutta method for a period of 1000 with a time mesh of 0.01. Results of DSs are the average over hundred thousands trials otherwise noticed. All quantities are dimensionless.

The $\tau_1$ dependence of the ratio of $\tilde{D}_1/D_1$ is depicted in Fig. 1, where results calculated by the FIM and the approximation (APP) given by Eq. (27) are shown by solid and dashed curves, respectively, for $\lambda = 1.0, D_0 = 0.01, D_1 = 0.2$ and $\tau_0 = 0.01$. $\tilde{D}_1$ calculated by the APP is in good agreement with that by the FIM, and the effective noise strength is decreased with increasing $\tau_1$. The difference between $\tilde{D}_1/D_1$ of the FIM and APP, plotted by the chain curve, is zero at $\tau_1 = 0$ with a maximum at $\tau_1 \sim 0.5$, and decreased at larger $\tau_1 (>1)$. The APP is fairly good for small $\tau_1$ and large $\tau_1$, as discussed after Eq. (27).
Fig. 2. (Color online) The stationary distributions $p(x)$ for $\tau_1 = 0.1$ [(a), (b)], $\tau_1 = 1.0$ [(c), (d)] and $\tau_1 = 5.0$ [(e), (f)] calculated by the FIM (solid curves), DS (dashed curves), the approximation given by Eq. (27) (APP; chain curves) and in the white-noise limit (WN; double chain curves) with $I = 0.5$, $\lambda = 1.0$, $D_0 = 0.01$, $D_1 = 0.2$ and $\tau_0 = 0.01$: (a), (c) and (e) are in normal scale, and (b), (d) and (f) are in log scale.

Fig. 2(a)–(f) show the stationary distribution $p(x)$ calculated by the FIM (solid curves), DS (dashed curves), with the APP (chain curves) and in the white-noise limit (WN: double chain curves) when $\tau_1$ is changed for fixed values of $\lambda = 1.0$, $D_0 = 0.01$, $D_1 = 0.2$ and $\tau_0 = 0.01$: (a), (c) and (e) in normal scale, and (b), (d) and (f) in log scale. Calculations show that with increasing $\tau_1$, $p(x)$ becomes narrower, deviating from the results of WN. Results of the FIM and APP are in fairly good agreement with those of DS: results of the APP is indistinguishable from those of the FIM.

Fig. 2(b), (d) and (f) plotting $p(x)$ in log scale show that results of the FIM and APP are in fairly good agreement with that of DS up to the order of $10^{-2}$ for $\tau_1 = 1.0$ and of $10^{-4}$ for $\tau_1 = 5.0$.

2.4.2. Dynamical properties

We have investigated the response to an applied pulse input given by

$$
I(t) = A \Theta(t - t_b) \Theta(t_e - t) + B,
$$

where $A = 0.5$, $B = 0.1$, $t_b = 100$ and $t_e = 200$, and $\Theta(t)$ is the Heaviside function. Time courses of $\mu(t)$ and $\gamma(t)$ are shown in Fig. 3(a)–(f), where $\tau_1$ is changed for fixed values of $\lambda = 1.0$, $D_0 = 0.01$, $D_1 = 0.2$ and $\tau_0 = 0.01$. 
With increasing $\tau_1$, $\mu(t)$ and $\gamma(t)$ induced by an applied pulse at $t_b < t < t_e$ are decreased. This is because they are given by

$$\mu(t) = \frac{(A + B)}{\lambda - \tilde{D}_1}, \quad \gamma(t) = \frac{\tilde{D}_0}{\lambda - 2\tilde{D}_1} + \frac{(A + B)^2 \tilde{D}_1}{(\lambda - 2\tilde{D}_1)(\lambda - \tilde{D}_1)^2}, \text{ for } t_b < t < t_e$$

where $\tilde{D}_1$ is decreased with increasing $\tau_1$ as Fig. 1 shows. The results of the FIM and APP are again in good agreement with that of the DS: the FIM yields slightly better results than the APP as shown in Fig. 3(b) and (f).

Next we study the response to a sinusoidal input given by

$$I(t) = C \sin \omega t,$$
where $C = 0.5$, $\omega = 2\pi / T_p$, and $T_p = 100$. Fig. 4(a), (c) and (f) show time courses of $\mu(t)$, and Fig. 4(b), (d) and (f) those of $\gamma(t)$ when $\tau_1$ is changed for fixed values of $\lambda = 1.0$, $D_0 = 0.01$, $D_1 = 0.2$ and $\tau_0 = 0.01$. With increasing $\tau_1$, the magnitude of $\mu(t)$ is decreased. This is understood from an analysis with the use of Eq. (19), which yields

$$
\mu(t) = \frac{C}{\sqrt{(\lambda - \bar{D}_1)^2 + \omega^2}} \sin(\omega t - \phi),
$$

(39)

with

$$
\phi = \tan^{-1}\left(\frac{\omega}{\lambda - \bar{D}_1}\right).
$$

(40)

Eq. (39) shows that with increasing $\omega$ (i.e. decreasing $T_p$), the magnitude of $\mu(t)$ is decreased, representing a character of the low-pass filter.
3. Langevin model subjected to one additive and two multiplicative colored noise

3.1. Effective Langevin equation

We have assumed the Langevin model subjected to one additive ($\eta_0$) and two multiplicative colored noise ($\eta_1$, $\eta_2$), as given by

$$\frac{dx}{dt} = F(x) + \eta_0(t) + G_1(x)\eta_1(t) + G_2(x)\eta_2(t),$$

with

$$\frac{d\eta_m(t)}{dt} = -\frac{1}{\tau_m}\eta_m + \frac{\sqrt{2D_m}}{\tau_m}\xi_m(t), \quad (m = 0, 1, 2)$$

where $F(x)$, $G_1(x)$ and $G_2(x)$ express arbitrary functions of $x$, and $\xi_m$ are independent zero-mean white noise with correlation:

$$\langle \xi_m(t)\xi_n(t') \rangle = \delta_{mn}\delta(t - t').$$

Applying the FIM to the model under consideration, we get the effective FPE given by (details being given in the Appendix):

$$\frac{\partial}{\partial t} p(x, t) = -\frac{\partial}{\partial x} \tilde{F}(x) p(x, t) + \tilde{D}_0 \frac{\partial^2}{\partial x^2} p(x, t) + \tilde{D}_1 \frac{\partial}{\partial x} G_1(x) \frac{\partial}{\partial x} G_1(x) p(x, t) + \tilde{D}_2 \frac{\partial}{\partial x} G_2(x) \frac{\partial}{\partial x} G_2(x) p(x, t),$$

from which we get the effective Langevin equation:

$$\frac{dx}{dt} = F(x) + \sqrt{2\tilde{D}_0\tilde{\xi}_0(t)} + \sqrt{2\tilde{D}_1 G_1(x)\tilde{\xi}_1(t)} + \sqrt{2\tilde{D}_2 G_2(x)\tilde{\xi}_2(t)},$$

with

$$\tilde{D}_0 = \frac{D_0}{(1 - \tau_0(F'))},$$

$$\tilde{D}_m = \frac{D_m}{[1 - \tau_m((F') - (FG'_m/G_m))]}, \quad (m = 1, 2)$$

where $F' = dF/dx$ and $G'_m = dG_m/dx$, and the bracket $\langle \cdot \rangle$ stands for the average over $p(x, t)$:

$$\langle Q(x) \rangle = \int Q(x) p(x, t) dx.$$  

3.2. Equations of motion for mean and variance

By using the effective FPE given by Eq. (45), we can obtain the equations of motion for mean ($\mu$) and variance ($\gamma$) defined by

$$\mu = \langle x \rangle,$$

$$\gamma = \langle x^2 \rangle - \langle x \rangle^2.$$  

When $F(x)$ and $G_m(x)$ are given by

$$F(x) = -\lambda x + I,$$

$$G_m = a_m(x - e_m), \quad (m = 1, 2)$$

the equations of motion for mean and variance become

$$\frac{d\mu}{dt} = -\lambda \mu + I,$$

$$\frac{d\gamma}{dt} = -2\lambda \gamma + 2\lambda^2 \mu - \lambda^2 I.$$
where $\lambda$ is the relaxation rate, $I$ an external input, and $a_m$ and $e_m$ constants, we get the equations of motion for $\mu$ and $\gamma$ given by [19]

$$\frac{d\mu}{dt} = -\lambda \mu + I + \tilde{D}_1(\mu - e_1) + \tilde{D}_2(\mu - e_2),$$

$$\frac{d\gamma}{dt} = -2\lambda \gamma + 4(\tilde{D}_1 + \tilde{D}_2)\gamma + 2\tilde{D}_2(\mu - e_1)^2 + 2\tilde{D}_2(\mu - e_2)^2 + 2\tilde{D}_0,$$

with

$$\tilde{D}_0 = \frac{D_0}{(1 + \lambda \tau_0)},$$

$$\tilde{D}_m = \frac{D_m}{[1 + \tau_m(-\lambda e_m + I)/(\mu - e_m)]}.$$  \hspace{1cm} \text{(for $m = 1, 2$)}

It is necessary to self-consistently solve Eqs. (53)–(56) for $\mu$, $\gamma$, $\tilde{D}_0$, $\tilde{D}_1$ and $\tilde{D}_2$.

Stationary values of $\mu$ and $\gamma$ are implicitly given by

$$\mu_s = \frac{(I - \tilde{D}_1 e_1 - \tilde{D}_2 e_2)}{(\lambda - \tilde{D}_1 - \tilde{D}_2)},$$

$$\gamma_s = \frac{[\tilde{D}_0 + \tilde{D}_1(\mu_s - e_1)^2 + \tilde{D}_2(\mu_s - e_2)^2]}{[\lambda - 2(\tilde{D}_1 + \tilde{D}_2)].}$$

with $\tilde{D}_m (m = 0, 1, 2)$ given by Eqs. (55) and (56) with $\mu = \mu_s$. Eqs. (57) and (58) show that $\mu_s$ and $\gamma_s$ diverge for $(\tilde{D}_1 + \tilde{D}_2) > \lambda$ and $(\tilde{D}_1 + \tilde{D}_2) > \lambda/2$, respectively. Eqs. (56) and (57) suggest that the approximation given by

$$\tilde{D}_m \simeq \frac{D_m}{(1 + \lambda \tau_m)} \equiv \tilde{D}_m^{\text{APP}}, \quad \text{for} \quad \tau_m D_m/(1 + \lambda \tau_m)^2 \ll 1 (m = 1, 2)$$

may be valid both for small $\tau_m$ and large $\tau_m$, as will be numerically shown in Figure 5 [22].

3.3. Stationary distribution

From the effective FPE of Eq. (45), we get the stationary distribution $p(x)$ given by [19]

$$\ln p(x) = -\left(\frac{1}{2}\right) \ln[D_0 + \tilde{D}_1 G^2_1(x) + \tilde{D}_2 G^2_2(x)] + Z(x),$$

with

$$Z(x) = \int \frac{F(x)}{[D_0 + \tilde{D}_1 G^2_1(x) + \tilde{D}_2 G^2_2(x)]} \, dx.$$  \hspace{1cm} \text{(61)}

In the white-noise limit ($\tau_m = 0$), the stationary distribution of the Langevin model given by Eq. (41) with $\eta_m = \sqrt{\Sigma D_m}$ ($m = 0, 1, 2$), is expressed by [19–21]

$$\ln p(x) = Z(x) - \left(\frac{1}{2}\right) \ln[D_0 + D_1 G^2_1(x) + D_2 G^2_2(x)],$$

with

$$Z(x) = \int \frac{F(x)}{[D_0 + D_1 G^2_1(x) + D_2 G^2_2(x)]} \, dx,$$  \hspace{1cm} \text{(63)}

in the Stratonovich representation. It agrees with the distribution given by Eqs. (60) and (61) with $\tilde{D}_m = D_m$.

When $F(x)$ and $G_m(x)$ are given by Eqs. (51) and (52), we get

$$p(v) \propto (d_2 v^2 + d_1 v + d_0)^{-(\lambda/2d_2)^{1/2}} \exp[Y(v)],$$

where

$$Y(v) = \int \frac{F(x)}{[D_0 + D_1 G^2_1(x) + D_2 G^2_2(x)]} \, dx.$$  \hspace{1cm} \text{(64)}
with

\[ Y(v) = \left( \frac{2d_2 + \lambda d_1}{d_2\sqrt{4d_0d_2 - d_1^2}} \right) \tan^{-1}\left( \frac{2d_2v + d_1}{\sqrt{4d_0d_2 - d_1^2}} \right), \]  

(65)

where

\[ \tilde{D}_0 = \frac{D_0}{1 + \lambda \tau_0}, \]  

(66)

\[ \tilde{D}_m = \frac{D_m}{\left\{ 1 + \tau_m(-\lambda e_m + I)/(\mu - e_m) \right\}}, \quad (\text{for } m = 1, 2) \]  

(67)

\[ d_0 = \tilde{D}_0 + \tilde{D}_1a_1^2e_1^2 + \tilde{D}_2a_2^2e_2^2, \]  

(68)

\[ d_1 = -2(\tilde{D}_1a_1^2e_1 + \tilde{D}_2a_2^2e_2), \]  

(69)

\[ d_2 = \tilde{D}_1a_1^2 + \tilde{D}_1a_2^2, \]  

(70)

\( \mu \), denoting the stationary value [Eqs. (57) and (58)].

It is easy to see that for additive noise only \((D_1 = D_2 = 0)\), the distribution becomes the Gaussian given by

\[ p(x) \propto \exp \left[ -\frac{\lambda}{2d_0} \left( x - \frac{I}{\lambda} \right)^2 \right]. \]  

(71)

When multiplicative noise is included, \( p(x) \) becomes the non-Gaussian distribution with power-law tails.

3.4. Model calculations

3.4.1. Stationary properties

Fig. 5 shows \( \tilde{D}_m / D_m \) \((m = 1, 2)\) as a function of \( \tau_1 \) calculated by the FIM for \( m = 1 \) (solid curve) and \( m = 2 \) (dashed curve) with fixed values of \( \tau_2/\tau_1 = 10, \lambda = 1.0, D_0 = 0.01, D_1 = 0.1, D_2 = 0.2 \) and \( \tau_0 = 0.01 \). With increasing \( \tau_1 \) \((= \tau_2/10)\), \( \tilde{D}_1 / D_1 \) and \( \tilde{D}_2 / D_2 \) are gradually decreased. In order to examine the validity of the approximation (APP) given by \( \tilde{D}_m^{\text{APP}} \) in Eq. (59), we show the differences between \( \tilde{D}_m / D_m \) of the FIM and APP for \( m = 1 \) (chain curve) and \( m = 2 \) (double-chain curve). Both the differences start from zero at \( \tau_1 = 0 \), have maxima at \( \tau_1 \sim 0.5 \), and are decreased at larger \( \tau_1 \). This shows that the APP is valid both for small \( \tau_1 \) and large \( \tau_1 \), whose behavior is similar to that shown in Fig. 1.
Fig. 6. (Color online) The stationary distributions $p(x)$ for $\tau_1 = 0.05$, $\tau_2 = 0.5$ [(a), (b)], $\tau_1 = 0.5$, $\tau_2 = 5.0$ [(c), (d)] and $\tau_1 = 5.0$, $\tau_2 = 50.0$ [(e), (f)] calculated by the FIM (solid curves), DS (dashed curves), the approximation given by Eq. (59) (chain curves) and in the white-noise limit (double-chain curves) with $I = 0.5$, $\lambda = 1.0$, $D_0 = 0.01$, $D_1 = 0.1$, $D_2 = 0.2$ and $\tau_0 = 0.01$: (a), (c) and (e) are in normal scale, and (b), (d) and (f) are in log scale.

Fig. 6(a)–(f) show the stationary distribution $p(x)$ calculated by the FIM (solid curves), DS (dashed curves), the APP (chain curves) and in the white-noise limit (double-chain curves), when $\tau_1$ and $\tau_2$ are changed with a fixed ratio of $\tau_2/\tau_1 = 10$, and $\tau_0 = 0.01$, $I = 0.5$, $\lambda = 1.0$, $D_0 = 0.01$, $D_1 = 0.1$ and $D_2 = 0.2$: Fig. 6(a), (c) and (e) are plotted in normal scale while Fig. 6(b), (d) and (f) are plotted in log scale. With increasing the relaxation time for multiplicative colored noise, the width of $p(x)$ is decreased and its profile approaches the Gaussian.

3.4.2. Dynamical properties

Responses of $\mu(t)$ to a pulse input given by Eq. (35) are shown in Fig. 7(a), (c) and (e) by changing the relaxation time with a fixed value of $\tau_2/\tau_1 = 10$. They are calculated by the FIM (solid curves), DS (dashed curves), the APP (chain curves) and in the white-noise limit (WN: double-chain curves). Similarly the response of $\gamma(t)$ are plotted in Fig. 7(b), (d) and (f). With increasing the relaxation time of colored noise, the effective noise strength is decreased, and then the values of $\mu(t)$ and $\gamma(t)$ at $100 < t < 200$ is decreased, as shown by Eqs. (39) and (40). Fig. 7(d) and (f)
show that the FIM yield slightly better results than the APP. The general trend of the effect of the relaxation time on $p(x)$, $\mu(t)$ and $\gamma(t)$ shown in Figs. 6 and 7 is the same as that shown in Figs. 2 and 3.

4. Discussion

4.1. A controversy on the subthreshold voltage distribution

In recent years, a controversy has been made on the subthreshold voltage distribution of a leaky integrate-and-fire model [15–18]. The adopted model includes conductance-based stochastic excitatory and inhibitory synapses as well as noisy inputs, as given by [15–18]

$$ C \frac{dv}{dt} = -g_L(v - E_L) - \frac{1}{a} I_{syn}(t), $$ (72)
with
\[ I_{\text{syn}}(t) = g_e(v - E_e) + g_i(v - E_i) - I_I(t). \] (73)

Here \( C \) denotes the membrane capacitance, \( a \) the membrane area, \( g_L \) and \( E_L \) the leak conductance and reversal potential, and \( g_{e,i} \) and \( E_{e,i} \) are the noisy conductances and reversal potentials of excitatory \((e)\) and inhibitory \(i\) synapses, respectively. Stochastic \( g_{e,i} \) and noisy additional input \( I_I(t) \) are assumed to be described by the OU process given by
\[
\frac{dg_e}{dt} = -\frac{1}{\tau_e}(g_e - g_{e0}) + \sqrt{\frac{2\sigma_e^2}{\tau_e}}\xi_e(t),
\]
(74)
\[
\frac{dg_i}{dt} = -\frac{1}{\tau_i}(g_i - g_{i0}) + \sqrt{\frac{2\sigma_i^2}{\tau_i}}\xi_i(t),
\]
(75)
\[
\frac{dI_I}{dt} = -\frac{1}{\tau_I}(I_I - I_0) + \sqrt{\frac{2\sigma_I^2}{\tau_I}}\xi_I(t),
\]
(76)
where \( \xi_\kappa \) are independent zero-mean white noise with correlation:
\[ \langle \xi_\kappa(t)\xi_\kappa(t') \rangle = \delta_{\kappa}\delta(t-t'). \] \((\kappa = I, e, i)\)
(77)

In the first paper of Rudolph and Destexhe \((RD1)\) [15], they derived an expression for the stationary distribution function of the system described by Eqs. \((72)-(76)\). In their second paper \((RD2)\) [16], they modified their expression to cover a larger parameter regime. Lindner and Longtin [17] criticized that the result of \(RD1\) does not reconcile the result of white-noise limit and that the extended expression of \(RD2\) does not solve the colored-noise problem though it is much better than that of \(RD1\). In the third paper of Rudolph and Destexhe \((RD3)\) [18], they claimed that the result of \(RD2\) is the best from a comparison among various approximate analytic expressions for the stationary distribution. It has been controversy which of approximate analytic expressions having been proposed so far may best explain the result of DSs.

It is worthwhile to apply our method mentioned in Section 3 to the system given by Eqs. \((72)-(76)\), which are rewritten as
\[
\frac{dv}{dt} = F(v) + G_I\eta_I(t) + G_e(v)\eta_e(t) + G_i(v)\eta_i(t),
\]
(78)
with
\[ \frac{\partial \eta_\kappa(t)}{\partial t} = -\frac{1}{\tau_\kappa}\eta_\kappa + \frac{\sqrt{2D_\kappa}}{\tau_\kappa}\xi_\kappa(t), \quad (\kappa = e, i, I) \]
(79)
where
\[ F(v) = -\frac{1}{C}g_L(v - E_m) - \frac{1}{Ca}[g_{e0}(v - E_e) + g_{i0}(v - E_i) - I_0], \]
(80)
\[ G_I = \frac{1}{Ca}, \]
(81)
\[ G_{e,i}(v) = -\frac{1}{Ca}(v - E_{e,i}), \]
(82)
\[ D_{I,e,i} = \tau_{I,e,i}\sigma_{I,e,i}^2. \]
(83)

By using Eqs. \((64)-(70)\), we get the stationary distribution \(p(v)\) given by
\[ p(v) \propto (d_2v^2 + d_1v + d_0)^{-\lambda/2d_2+1/2} \exp[Y(v)], \]
(84)
with

\[ Y(v) = \left( \frac{2c_0d_2 + \lambda d_1}{d_2 \sqrt{4d_0d_2 - d_1^2}} \right) \tan^{-1} \left( \frac{2d_2v + d_1}{\sqrt{4d_0d_2 - d_1^2}} \right), \]  

(85)

where

\[ \lambda = \frac{1}{C} g_L + \frac{1}{C_a} (g_{e0} + g_{i0}), \]  

(86)

\[ c_0 = \frac{1}{C} g_L E_m + \frac{1}{C_a} (g_{e0}E_e + g_{i0}E_i + I_{I0}), \]  

(87)

\[ d_0 = \frac{1}{C^2a^2} (\tilde{D}_I + \tilde{D}_e E_e^2 + \tilde{D}_i E_i^2), \]  

(88)

\[ d_1 = -\frac{2}{C^2a^2} (\tilde{D}_e E_e + \tilde{D}_i E_i), \]  

(89)

\[ d_2 = \frac{1}{C^2a^2} (\tilde{D}_e + \tilde{D}_i). \]  

(90)

With the use of Eqs. (57) and (58), \( \tilde{D}_e \) in Eqs. (88)–(90) are expressed by

\[ \tilde{D}_I = \frac{D_I}{(1 + \lambda \tau_I)}, \]  

(91)

\[ \tilde{D}_e = \frac{D_e}{[1 + \tau_e (\lambda E_e + c_0)/(\mu_s - E_e)]}, \]  

(92)

\[ \tilde{D}_i = \frac{D_i}{[1 + \tau_i (\lambda E_i + c_0)/(\mu_s - E_i)]}. \]  

(93)

Here \( \mu_s \) denotes the stationary value of \( v \) which is determined by the self-consistent equations for \( \mu_s, \gamma_s, \tilde{D}_e \) and \( \tilde{D}_i \) [as Eqs. (57) and (58)], though their explicit expressions are not necessary for our discussion.

In the limit of small relaxation times, Eqs. (92) and (93) yield

\[ \tilde{D}_e \simeq \frac{D_e}{(1 + \lambda \tau_e)}, \text{ (for } \tau_e D_e \ll 1) \]  

(94)

\[ \tilde{D}_I \simeq \frac{D_I}{(1 + \lambda \tau_I)}, \text{ (for } \tau_I D_I \ll 1) \]  

(95)

This is nothing but the approximation introduced in RD2 [16].

In the white-noise limit (\( \tau_{I,e,i} = 0 \)), the stationary distribution of the model given by Eq. (78) with \( \eta_\kappa = \sqrt{2D_\kappa} \) (\( \kappa = I, e, i \)) is given by [19–21]

\[ \ln p_{wa}(v; D_I, D_e, D_I) = Z(v) - \left( \frac{1}{2} \right) \ln\left[D_I G_I^2 + D_e G_e^2(v) + D_i G_i^2(v)\right], \]  

(96)

with

\[ Z(v) = \int \frac{F(v)}{[D_I G_I^2 + D_e G_e^2(v) + D_i G_i^2(v)]} dv, \]  

(97)

in the Stratonovich representation. We note that our stationary distribution given by Eqs. (84)–(90) is consistent in the white-noise limit, and that the distribution for colored noise, is expressed by

\[ p(v; D_I, D_e, D_i, \tau_I, \tau_e, \tau_i) = p_{wa}(v; \tilde{D}_I, \tilde{D}_e, \tilde{D}_i), \]  

(98)
where $\tilde{D}_I$, $\tilde{D}_e$ and $\tilde{D}_i$ given by Eqs. (91)–(93) take account of effects of relaxation times. If we adopt approximate expressions for $D_e$ and $D_i$ given by Eqs. (94) and (95), we get

$$p(v; D_I, D_e, D_i, \tau_I, \tau_e, \tau_i) = p_{wn} \left( v; \frac{D_I}{1 + \lambda \tau_I}, \frac{D_e}{1 + \lambda \tau_e}, \frac{D_i}{1 + \lambda \tau_i} \right).$$

(for $\tau_e D_e \ll 1$ and $\tau_i D_i \ll 1$) \hspace{1cm} (99)

Lindner and Longtin have pointed out that the first solution of $RD1$ is given by [17]

$$p_{RD1}(v; D_I, D_e, D_i, \tau_I, \tau_e, \tau_i) = p_{wn} \left( v; \frac{D_I}{2}, \frac{D_e}{2}, \frac{D_i}{2} \right).$$

(100)

With the use of the Fourier transform of stochastic equations, Rudolph and Destexhe have obtained in $RD2$ [16], the stationary distribution with $D_I = 0$ given by

$$p_{RD2}(v; D_I = 0, D_e, D_i, \tau_I, \tau_e, \tau_i) = p_{wn} \left( v; D_I = 0, \frac{D_e}{1 + \lambda \tau_e}, \frac{D_i}{1 + \lambda \tau_i} \right).$$

(101)

It is noted that Eq. (101) coincides with Eq. (99) for $D_I = 0$. Model calculations in Section 3.4 have shown that the approximation given by Eq. (59) yields a good result. This is true also for the approximation given by Eqs. (94) and (95). This explains to some extent the reason why the approximation adopted in $RD2$ provides us with good results, as claimed in $RD3$ [18].

### 4.2. A comparison with previous approximations

We have discussed, in Section 2, the dynamics of the Langevin model subjected to colored noise, by using the FIM. It is interesting to make a comparison among several approximate, analytical methods having been proposed so far for the Langevin model subjected to colored noise:

$$\frac{dx}{dt} = F(x) + G(x) \eta_1(t),$$

(102)

where $\eta_1(t)$ is described by the OU process of Eq. (2).

First we apply the UCNA to Eq. (102) [2,6]. Taking the derivative of Eq. (102) with respect to $t$, eliminating the variable $\eta_1$ with the use of Eq. (2), and neglecting the $\ddot{x}$ term after the UCNA, we get the effective Langevin equation given by

$$\frac{dx}{dt} = \tilde{F}(x) + \tilde{D}_I G(x) \xi_1(t),$$

(103)

with

$$\tilde{F}_U = \frac{F(x)}{[1 - \tau_t (F' - FG' / G)]},$$

(104)

$$\tilde{D}_I^U = \frac{D_I}{[1 - \tau_t (F' - FG' / G)]^2}.$$

(105)

The stationary distribution is given by

$$p(x) \propto \exp[- \ln G(x) + Y(x)],$$

(106)

with

$$Y(x) = \left( \frac{1}{D_I} \right) \int \frac{\tilde{F}(x)}{G(x)^2} \, dx.$$

(107)

In the case of $F(x) = -\lambda x$ and $G(x) = x$, we get

$$p(x) \propto x^{-[\lambda(1 + \lambda \tau_I) / D_I + 1]},$$

(108)

which agrees with Eqs. (31) and (32) with $I = Y = 0$. 

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*Note: The content continues with more equations and discussions regarding the stationary distribution and the comparison with previous approximations.*

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Similarly, when the system is subjected to additive colored noise only
\[ \frac{dx}{dt} = F(x) + \eta_0(t), \] (109)
the UCNA yields the effective Langevin equation given by
\[ \frac{dx}{dt} = \tilde{F}(x) + \tilde{D}_0 \xi(t), \] (110)
with
\[ \tilde{F}^U = \frac{F(x)}{(1 - \tau_0 F')}, \] (111)
\[ \tilde{D}^U_0 = \frac{D_0}{(1 - \tau_0 F')^2}. \] (112)
The stationary distribution is given by
\[ p(x) \propto \exp[Z(x)], \] (113)
with
\[ Z(x) = \left(1 - \frac{\tau_0 F'}{D_0}\right) \int F(x) \, dx. \] (114)

When a system is subjected to multiplicative colored noise only, as given by Eq. (102), we may employ the method of a change of variable, with which it is transformed to that subjected to additive noise [23]:
\[ \frac{dy}{dt} = \tilde{F}(y) + \eta_1(t), \] (115)
where
\[ y = \int \frac{dx}{G(x)} \equiv K(x), \] (116)
\[ \tilde{F}(y) = \frac{F(K^{-1}(y))}{G(K^{-1}(y))}. \] (117)
We get the effective Langevin equation given by Eq. (103) with
\[ \tilde{F}^C = F(x), \] (118)
\[ \tilde{D}^C_1 = \frac{D_1}{1 - \tau_1 (F' - FG' / G)}. \] (119)
In the case of \( F(x) = -\lambda x \) and \( G_1(x) = x \), we get the distribution of \( p(x) \) given by
\[ p(x) \propto x^{-[\lambda(1+\lambda\tau_1)/D_1+1]}, \] (120)
which agrees with Eq. (108).

Table 1 summarizes a comparison among various approximate methods. It is noted that although the effective Langevin equation is rather different depending on the methods, the stationary distribution given by Eq. (108) or (120) agrees with each other in the linear Langevin model for which the ratio of \( \tilde{F}(x) / \tilde{D}_1(x) \) is the same [Eq. (107)]. Difference among the methods may be, however, realized in dynamical properties. Fig. 8(a) and (b) show responses of \( \mu(t) \) and \( \gamma(t) \), respectively, to an applied pulse input given by Eq. (35), calculated by the FIM (solid curves), DS (dashed curves) and the UCNA (chain curves) with \( \lambda = 1.0, D_1 = 0.2 \) and \( \tau_1 = 1.0 \). We note that \( \mu(t) \) and \( \gamma(t) \) at \( 100 < t < 200 \) calculated by the FIM is in good agreement with those of DS. Those of the UCNA are, however, much larger than those of DS. This is easily understood by Eqs. (36), (37), (104) and (105), from which we get (for \( D_0 \ll D_1 \))
A comparison among various methods yielding the effective equation given by

\[ \dot{\xi} = \tilde{F}(x) + \sqrt{2D_0}\xi(t) + \sqrt{2D_1}G(x)\xi_1(t) \]

for the Langevin model: \( \dot{\xi} = \tilde{F}(x) + \eta_0(t) + G(x)\eta_1(t) \) subjected to colored noise \( \eta_0 \) with the relaxation time \( \tau_m \) (for UCNA) (122)

\[ \gamma F (t) \approx (A + B)^2 D_1/(1 + \lambda \tau_1)^2 \]

\[ \lambda \tau_1 = 2, \lambda \tau_2 = 6, \lambda \tau_3 = 10 \]

Table 1

| Method       | \( \tilde{F} \) | \( D_0 \) | \( D_1 \) | \( \dot{\xi} \) |
|--------------|----------------|-----------|-----------|----------------|
| FIM          | \( D_0/(1 - \tau_0 F') \) | \( D_1/(1 - \tau_1 (F' - FG'/G)) \) | FIM\(^a\) |
| DS          | \( D_0/(1 - \tau_0 F') \) | \( D_1/[1 - \tau_1 (F' - FG'/G)] \) | FIM\(^b\) |
| UCNA        | \( D_0/(1 - \tau_0 F') \) | \( D_1/[1 - \tau_1 (F' - FG'/G)] \) | UCNA\(^d\) |
| CV          | \( D_0/(1 - \tau_0 F') \) | \( D_1/[1 - \tau_1 (F' - FG'/G)] \) | UCNA\(^e\) |
| MM          | \( D_0/(1 - \tau_0 F') \) | \( D_1/[1 - \tau_1 (F' - FG'/G)] \) | MM\(^f\) |

\(^a\) The functional-integral method (FIM; present study).
\(^b\) FIM (Refs. [11,12]).
\(^c\) A change of variable (CV) for multiplicative colored noise only (after Ref. [23]).
\(^d\) UCNA calculation for multiplicative colored noise only (Ref. [6]).
\(^e\) UCNA calculation for additive colored noise only (Ref. [6]).
\(^f\) FIM for additive colored noise only (Ref. [10]).
\(^g\) Moment method (MM) for additive colored noise only (Ref. [5]).

\[ \mu^F (t) \approx \frac{(A + B)}{[\lambda - D_1/(1 + \lambda \tau_1)]} \], (for FIM) \hspace{1cm} (121)

\[ \mu^U (t) \approx (1 + \lambda \tau_1)\mu^F (t), \] (for UCNA) \hspace{1cm} (122)

\[ \gamma^F (t) \approx \frac{(A + B)^2 D_1/(1 + \lambda \tau_1)}{[\lambda - 2D_1/(1 + \lambda \tau_1)]^2}, \] (for FIM) \hspace{1cm} (123)
\[ y^U(t) \simeq (1 + \lambda \tau_1)^2 y^F(t). \quad \text{(for UCNA).} \] (124)

Similar results are obtained also for sinusoidal inputs: responses of \( \mu(t) \) and \( \gamma(t) \) to a sinusoidal input given by Eq. (38) are shown in Fig. 8(c) and (d), respectively. We note that their magnitudes calculated by the UCNA are again much larger than those of DS and the FIM.

It has been claimed that the UCNA is justified by the FIM [8–10]. Although the FIM starts from the formally exact expression for the probability distribution, an actual evaluation has to adopt some kinds of approximations such as \( \bar{x} = 0 \) and \( \bar{\bar{x}} = 0 \) for \( n \geq 2 \) just as in the UCNA [2,6]. The result of Refs. [8–10] obtained by the FIM is different from that of Refs. [7,11,12] derived by the alternative FIM: the final result using the FIM depends on the adopted approximations.

5. Conclusion

We have extended the FIM approach such that we may discuss the dynamics of the Langevin model subjected to additive and/or multiplicative colored noises, combined with the equations of motion for mean and variance of a state variable \( x \). The stationary probability distribution and the dynamical response to time-dependent inputs have been discussed for two cases of colored noise: (a) one additive and one multiplicative colored noise, and (b) one additive and two multiplicative colored noise. Our conclusions are summarized as follows:

(i) calculated results for the both cases (a) and (b) of the FIM are in good agreement with those of DS for not only stationary but also dynamical properties: the latter cannot be well accounted for by the existing, approximate analytical methods like the UCNA [6],

(ii) with increasing the relaxation time of colored noise, the width of the stationary distribution \( p(x) \) becomes narrower and its non-Gaussian form approaches the Gaussian because the effective noise strength of \( D_m \) becomes smaller than the original noise strength of \( D_m \), and

(iii) the approximations given by Eqs. (27) and (59) for the cases (a) and (b), respectively, derived by the FIM are valid for both small and large relaxation times, which supports the result of \( RD2 \) and \( RD3 \) [16,18].

Item (i) implies that the present FIM approach may be applicable to a wide class of realistic models for physical systems subjected to noise sources with finite correlation time. Recently we have proposed a generalized Langevin-type rate-code neuronal model including multiplicative white noise [24,25]. It would be interesting to study effects of finite correlation time of colored noise on firing rates in neuronal ensembles based on the rate-code hypothesis, which is an alternative to the temporary-code hypothesis [26,27].

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Appendix. Derivation of the effective Fokker–Planck equation

By applying the functional-integral method to the Langevin model given by

\[ \frac{dx}{dt} = F(x) + \sum_m G_m(x) \eta_m(t), \] (A.1)

with

\[ \frac{d\eta_m(t)}{dt} = - \frac{1}{\tau_m} \eta_m + \frac{\sqrt{2D_m}}{\tau_m} \xi_m(t), \] (A.2)

\[ \langle \xi_m(t) \xi_n(t') \rangle = \delta_{mn} \delta(t - t'), \] (A.3)

we may obtain the expression for the probability distribution: \( p(x, t) = \langle \delta(x(t) - x) \rangle \) given by [7,11]

\[ \frac{\partial}{\partial t} p(x, t) = - \frac{\partial}{\partial x} F(x) p(x, t) - \sum_m \frac{\partial}{\partial x} G_m(x) \langle \eta_m(t) \delta(x(t) - x) \rangle, \] (A.4)
where the bracket $\langle \cdot \rangle$ denotes the average over $p(x, t)$. Although Eq. (A.4) is a formally exact expression, it is evitable to employ some approximations to perform actual calculations. In order to evaluate the average $\langle \eta_m(t) \delta(x(t) - x) \rangle$, we use the Novikov theorem [28]:

$$\langle \eta_m(t) \Phi(q_1, q_2) \rangle = \int_0^t dt' \sum_n c_{mn}(t, t') \left( \frac{\delta \Phi(q_1, q_2)}{\delta \eta_n} \right),$$

(A.5)

where $\Phi(q_1, q_2)$ denotes a function of $q_1$ and $q_2$, and $c_{mn}$ is their correlation function given by Eq. (5). From Eqs. (5) and (A.5), we get

$$\langle \eta_m(t) \delta(x(t) - x) \rangle = -\int_0^t dt' c_{mm}(t, t') \left( \frac{\delta \delta(x(t) - x)}{\delta x} \right),$$

(A.6)

$$= -\frac{\partial}{\partial x} \int_0^t dt' c_{mm}(t, t') \left( \delta(x(t) - x) \frac{\delta x}{\delta \eta_m(t')} \right).$$

(A.7)

After integrating Eq. (1), we get

$$x(t) = x(0) + \int_0^t ds \left[ F(x(s)) + \sum_n G_m(x(s)) \eta_m(s) \right].$$

(A.8)

The functional derivative of $x(t)$ of Eq. (A.8) with respect to $\eta_m(t')$ becomes

$$\frac{\delta x(t)}{\delta \eta_m(t')} = G_m(x(t')) + \int_0^t ds \left[ F'(x(s)) + \sum_n G'_n(x(s)) \eta_m(s) \right] \frac{\delta x(s)}{\delta \eta_m(t')}.$$

(A.9)

The derivative of Eq. (A.9) with respect to $t$ is given by

$$\frac{\partial}{\partial t} \left[ \frac{\delta x(t)}{\delta \eta_m(t')} \right] = G_m(x(t)) \frac{\delta x(t)}{\delta \eta_m(t')}.$$

(A.10)

The formal solution of Eq. (A.10) with the initial condition:

$$\frac{\partial}{\partial t} \left[ \frac{\delta x(t)}{\delta \eta_m(t')} \right] = G_m(x(t)),$$

(A.11)

is given by

$$\frac{\delta x(t)}{\delta \eta_m(t')} = G_m(x(t')) \exp \left[ \int_0^t ds [F'(x(s)) + \sum_n G'_n(x(s)) \eta_n(x(s))] \right].$$

(A.12)

The derivative of $G_m(x(t))$ with respect to $t$ becomes

$$\frac{d}{dt} G_m(x(t)) = G'_m(x(t)) \frac{dx(t)}{dt},$$

(A.13)

$$= G'_m(x(t)) \left[ F(x(t)) + \sum_n G_n(x(t)) \eta_n(t) \right].$$

(A.14)

The integral of Eq. (A.14) yields

$$G_m(x(t')) = G_m(x(t)) \exp \left[ \int_0^{t'} ds \left( \frac{G'_m(x(s))}{G_m(x(s))} \right) [F(x(s)) + \sum_n G_n(x(s)) \eta_n(x(s))] \right].$$

(A.15)

Substituting Eqs. (A.12) and (A.15) to Eq. (A.9), we get

$$\frac{\delta x(t)}{\delta \eta_m(t')} \simeq G_m(x(t)) \exp \left( \int_0^{t'} ds \left[ F'(x(s)) - \frac{G'_m(x(s))}{G_m(x(s))} F(x(s)) \right] \right),$$

(A.16)
where contributions from terms including $\eta_n$ in Eqs. (A.12) and (A.15) are neglected. Combining Eq. (A.7) with Eq. (A.16), we get

$$\langle \eta_m(t) \delta(x(t) - x) \rangle = -\frac{\partial}{\partial x} G_m(x(t)) \int_0^t dt' \left[ c_m \left( \delta(x(t) - x) \exp \left( \int_{t'}^t ds' \left[ F'(x(s)) - \frac{G_m'(x(s))}{G_m(x(s))} F(x(s)) \right] \right) \right) \right].$$  \hspace{1cm} (A.17)

By using the decoupling approximation given by

$$\left\langle \delta(x(t) - x) \exp \left( \int_{t'}^t ds' \left[ F'(x(s)) - \frac{G_m'(x(s))}{G_m(x(s))} F(x(s)) \right] \right) \right\rangle \simeq \left\langle \delta(x(t) - x) \right\rangle \exp \left( \left[ F'(x(t)) - \frac{G_m'(x(t))}{G_m(x(t))} F(x(t)) \right] (t - t') \right),$$  \hspace{1cm} (A.18)

we get

$$\langle \eta_m(t) \delta(x(t) - x) \rangle \simeq \tilde{D}_m \frac{\partial}{\partial x} G_m(x) p(x, t),$$  \hspace{1cm} (A.20)

with

$$\tilde{D}_m = \frac{D_m}{[1 - \tau_m (\langle F' \rangle - \langle FG' / G \rangle)]},$$  \hspace{1cm} (A.21)

where $F' = dF/dx$ and $G_m' = dG_m/dx$, and the bracket $\langle \cdot \rangle$ expresses the average over $p(x, t)$. Substituting Eq. (A.20) to Eq. (A.4), we finally get the effective FPE given by

$$\frac{\partial}{\partial t} p(x, t) = -\frac{\partial}{\partial x} F(x) p(x, t) + \sum_m \tilde{D}_m \frac{\partial}{\partial x} G_m(x) \frac{\partial}{\partial x} G_m(x) p(x, t),$$  \hspace{1cm} (A.22)

from which we get the effective Langevin equation given by

$$\frac{dx}{dt} = F(x) + \sum_m \sqrt{2\tilde{D}_m G_m(x)} \xi_m(t),$$  \hspace{1cm} (A.23)

with

$$\langle \xi_m(t) \rangle = 0,$$  \hspace{1cm} (A.24)

$$\langle \xi_m(t) \xi_n(t') \rangle = \delta_{mn} \delta(t - t').$$  \hspace{1cm} (A.25)

References

[1] B. Lindner, J. García-Ojalvo, A. Neiman, L. Schimansky-Geier, Phys. Rep. 392 (2004) 321.
[2] P. Hänggi, P. Jung, Adv. Chem. Phys. 89 (1995) 239.
[3] S. Mangioni, R. Deza, H.S. Wio, R. Toral, Phys. Rev. Lett. 79 (1997) 2389; S.E. Mangioni, R.R. Deza, R. Toral, H.S. Wio, Phys. Rev. E 61 (2000) 223.
[4] Ch.R. Doering, J.C. Gadoua, Phys. Rev. Lett. 69 (1992) 2318.
[5] H. Hasegawa, Physica A 384 (2007) 241.
[6] P. Jung, P. Hänggi, Phys. Rev. A 35 (1987) 4464.
[7] J.M. Sancho, M. San Miguel, S.L. Katz, J.D. Gunton, Phys. Rev. 26 (1982) 1589.
[8] P. Colet, H.S. Wio, M. San Miguel, Phys. Rev. A 39 (1989) 6094.
[9] H.S. Wio, P. Colet, M. San Miguel, L. Pesquera, M.A. Rodriguez, Phys. Rev. A 40 (1989) 7312.
[10] M.A. Fuentes, R. Toral, H.S. Wio, Physica A 303 (2002) 91.
[11] G.Y. Liang, L. Cao, D.J. Wu, Physica A 335 (2004) 371.
[12] D. Wu, X. Luo, S. Zhu, Physica A 373 (2007) 203.
[13] N. Brunel, F.S. Chance, N. Fourcaud, L.F. Abbott, Phys. Rev. Lett. 86 (2001) 2186.
[14] N. Fourcaud, N. Brunel, Neural Comput. 14 (2002) 2057.
[15] M. Rudolph, A. Destexhe, Neural Comput. 15 (2003) 2577.
It would be possible to analytically show that the approximation given by Eq. (59) is valid for small and large relaxation times, though we have not succeeded in it. In a simple case of $a_1 = a_2$, $e_1 = e_2$ and $\tau_1 = \tau_2$, Eqs. (56) and (57) yield $\tilde{D} \equiv \tilde{D}_1 + \tilde{D}_2 = (D_1 + D_2)/[1 + \tau_1(\lambda - \tilde{D})]$, from which we get an approximate expression of $\tilde{D}_m \simeq D_m/[(1 + \lambda \tau_1)(m = 1, 2)$ valid for $\tau_1(D_1 + D_2)/(1 + \lambda \tau_1) \ll 1$, or alternatively valid for (i) $\tau_1 \ll (1/\lambda, 1/(D_1 + D_2))$ and (ii) $\tau_1 \gg (1/\lambda, (D_1 + D_2)/\lambda^2)$, just as Eq. (27) implies.