Growth of stochastic resonance in neuronal ensembles with the input signal intensity

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The presence of noise can improve the response of certain nonlinear systems to input signals through the effects of stochastic resonance (SR). The optimal noise intensity for SR is proportional to the signal frequency if the signal is periodic, but proportional to the signal intensity if the signal is aperiodic. Here, we demonstrate using linear response theory that the optimal noise intensity for SR is necessarily dependent on the signal intensity even if the signal is periodic. We also demonstrate that the SR curves grow according to the signal intensity from a bell-shaped curve to a plateau, resulting in the manifestation of SR without tuning. In particular, we present a theoretical analysis indicating that the SR peak shifts with the signal intensity due to the scaling of the stationary neuronal firings. The growth of SR may serve as a useful design principle for many noise-exploiting applications.

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I. INTRODUCTION

The response of a nonlinear system to input signals is improved by the presence of external noise of an optimal intensity. This noise-induced phenomenon, stochastic resonance (SR), occurs regardless of whether the input signal is periodic or aperiodic, weak (subthreshold) or strong (suprathreshold), and regardless of whether the system is in an excitable or oscillatory regime. SR from an aperiodic signal is specifically categorized as aperiodic SR (ASR) [1–4], and SR in response to suprathreshold signals is categorized as suprathreshold SR (SSR) [5–12]. Many nonlinear systems such as electronic circuits [13], neuronal systems [14,15], biological sensors [16–19] and actuators [20,21], and geometric Brownian particles [22] exhibit SR behavior. SR has also been reported in metaphysical systems such as human perception [16,23–25].

Past research has indicated that the optimal noise intensity for SR performance is determined by the signal frequency if the signal is periodic [26] or by the signal intensity if the signal is aperiodic [1]. Here, we demonstrate that the optimal noise intensity in SR is intrinsically proportional to the signal intensity even if the signal is periodic. Furthermore, we demonstrate that the SR profile grows according to the signal intensity, changing from a bell-shaped curve to a plateau, which results in the manifestation of SR without the need for tuning (SR without tuning). We also provide a theoretical framework based on linear response theory [27–30] that accounts for the SR peak growth with signal intensity.

In this article, we use FitzHugh-Nagumo (FHN) model neurons for the numerical simulations, and piecewise-linear FitzHugh-Nagumo (pFHN) model neurons for the theoretical analysis. We provide a theoretical analysis that the linear response of a neuronal ensemble involves four different response modes. We further provide experimental data implicating that the FHN model adaptively switches the linear response mode depending on the input signal frequency. We demonstrate that the increase in signal intensity modulates the SR peak locations and realizes SR without tuning, not only in the neuronal excitable and oscillatory regimes but also in the excitation-blocked regime where neuron firing is inhibited by the overwhelmingly strong excitatory input.

II. NUMERICAL SIMULATION

A. FHN neuron ensemble model

For numerical simulations of neuronal ensemble SR, it is conventional to use the FHN model neurons [1,4,26]. We consider here the neuron ensemble used in Refs. [1,4,6], wherein the neurons are driven by a common input signal and independent noise, although in this paper we deal with both periodic and aperiodic signals. Each neuron follows a common input signal $s(t)$, and an independent noise $\xi(t)$ present, the FHN model neuron is described as

$$\begin{align*}
\epsilon V_i &= V_i(1-2/3)(1-V_i) - W_i + b + s_0(t), \\
W_i &= V_i - W_i + \sqrt{2D_0}\xi_i(t),
\end{align*}$$

(1a)

(1b)

where $V(t)$ is a voltage variable, $W(t)$ is a recovery variable, $\epsilon = 0.005$, and $b$ is a constant activation signal. The Gaussian noise $\xi(t)$ has an intensity $D_0$. The FHN neuron is, approximately, in the excitable regime for $b < 0.275$, in the oscillatory regime for $0.275 \leq b \leq 0.8$, and in the excitation-blocked regime for $b > 0.8$. We consider two input signal profiles: a periodic signal $s_0(t) = g_0 \sin(\omega t)$ and an aperiodic signal $s_0(t) = g_0 \sum_j e^{-\omega(t-t_j^0)}\Theta(t-t_j)$, where $g_0$ is the uniform gain and $w_0/w_i$ is an irrational number. Note that the second signal type is aperiodic in the sense that there is no period $T$ that satisfies $s(t+T) = s(t)$ for any arbitrary $t$. For the purpose of generality, we also mention the aperiodic signal $s_0(t) = g_0 \sum_j e^{-\omega(t-t_j)}\Theta(t-t_j)$, where $\Theta(t-t_j)$ denotes the Heaviside step function.

B. Computation of correlation coefficient $C_1$

Here, we use the correlation coefficient $C_1$ to measure the effect of SR as follows:

$$C_1 = \frac{C_0}{(s_0(t)^2 - \langle s_0(t)^2 \rangle)^{1/2} (R_{\Sigma}(t)^2 - \langle R_{\Sigma}(t)^2 \rangle)^{1/2}}. \tag{2}$$
where the time average is denoted by the overline and \( C_0 \) is the cross correlation,
\[
C_0 = \langle s_0(t + \alpha) - \bar{s}_0(t) \rangle \langle R_{x}(t) - \bar{R}_{x}(t) \rangle,
\]
where \( \alpha \) is a phase shift to compute the cross correlation. The term \( R_{x}(t) \) is a measure corresponding to the cumulative mean firing rate and is constructed as
\[
R_{x}(t) = \frac{1}{N} \sum_{i=1}^{N} R_{\gamma,i}(t), \quad R_{\gamma,i}(t) = \begin{cases} 1, & V_i > 0.5, \\ 0, & V_i \leq 0.5, \end{cases}
\]
where 0.5 is a threshold for detecting spikes of a neuron.

### III. THEORETICAL ANALYSIS

#### A. Two driving modes of the pIFHN model

The original FHN model neuron does not provide a good basis for a linear response theoretical analysis due to its strong nonlinearity [31]. Based on the conventional approaches in Refs. [29,30,32], we reduce the FHN model into two coupled linear systems in the resting and firing states that jump to each other at their source and sink points to obtain

\[
\begin{align*}
\tau \dot{x}_i(t) &= -x_i(t) + \sqrt{2D_x}N_i(t), \\
\tau \dot{y}_i(t) &= -y_i(t) + \sqrt{2D_y}N_i(t),
\end{align*}
\]

where \( x \) and \( y \) denote the slow variable in the resting and firing states, respectively. We note that there are two different modes for how the signal \( s_0(t) \) drives the system, which results in different effective signal amplitudes and source and sink point locations.

In the first mode, \( s_0(t) \) is directly coupled with \( W_j \). Thus, we change the variables in Eq. (1) such that
\[
\begin{align*}
\tilde{v}_j &= \frac{1}{6} F(v_i) - \frac{v_i}{2w_i} + 2\sqrt{3}\left(b - \frac{1}{2}\right), \\
\tau \tilde{w}_j &= \frac{6}{7\gamma}v_i - \frac{1}{7w_i} + \frac{12\sqrt{3}}{\gamma} [s_0(t) - \bar{s}_0(t)] + \tilde{\xi}_i(t),
\end{align*}
\]

where \( \tilde{\xi}_i(t) = \sqrt{\frac{12\sqrt{3}}{\gamma}}\xi(t) \), \( F(v_i) = 2 - v_i, \) \( v_i \geq 1, \) \( -1 < v_i < 1, \) \( -2 - v_i, \) \( v_i \leq 1, \)

where \( \bar{s}_0(t) = 0 \) [30], and applying the following further variable changes:

\[
\begin{align*}
x(t) &= w(t) - \tilde{b}_x - \bar{s}_0(t), \\
y(t) &= w(t) - \tilde{b}_y - \bar{s}_0(t),
\end{align*}
\]

where \( \bar{s}_0(t) = g \sum_{j=1}^{N_j} [A_0^1(\tilde{\alpha}_j)e^{\tilde{\omega}_1(t-t_0)} + A_0^1(\tilde{\alpha}_j)e^{\tilde{\omega}_2(t-t_0)}] \\
+ g \sum_{m=n}^{N_n} A_0^1(\tilde{\alpha}_m)e^{\tilde{\omega}_1(t-t_n)} \Theta(t - t_n), \quad (7c)
\]

\[
A_0^1(\tilde{\alpha}) = \frac{72\sqrt{3}(1 + 7\tau \tilde{\alpha})}{7\gamma(1 + \tau \tilde{\alpha})}, \quad (7d)
\]

where \( \tilde{b}_x = \frac{12}{7\gamma}(-1 + 6\sqrt{3})(b - \frac{1}{2}), \) \( \tilde{b}_y = \frac{12}{7\gamma}(1 + 6\sqrt{3})(b - \frac{1}{2}), \) and \( g = \frac{\alpha}{\gamma N_j}. \) The source points \( X_+ \) and \( Y_+ \) and sink points \( X_- \) and \( Y_- \) are

\[
X_\pm = x_\pm + s(\tilde{t}), \quad Y_\pm = y_\pm + s(\tilde{t}), \quad (8a)
\]

\[
s(t) = g \sum_{j=1}^{N_j} [A^1(\tilde{\alpha}_j)e^{\tilde{\omega}_1(t-t_0)} + A^1(\tilde{\alpha}_j)e^{\tilde{\omega}_2(t-t_0)}] \\
+ g \sum_{m=n}^{N_n} A^1(\tilde{\alpha}_m)e^{\tilde{\omega}_1(t-t_n)} \Theta(t - t_n), \quad (8b)
\]

\[
A^1(\tilde{\alpha}) = \frac{72\sqrt{3}(1 + 7\tau \tilde{\alpha})}{7\gamma(1 + \tau \tilde{\alpha})}, \quad (8c)
\]

where \( x_\pm = \frac{12\sqrt{3} - 6\sqrt{3} + 12\sqrt{3}}{7\gamma} \) and \( y_\pm = \frac{-12\sqrt{3} - 6\sqrt{3} + 12\sqrt{3}}{7\gamma} \).

In contrast, in the second mode we change the variables in Eq. (1) such that \( V = \frac{1}{2\sqrt{3}}v + \frac{1}{2} \) and \( W = \frac{1}{2\sqrt{3}}w \) \( W \) and then have different effective signal amplitudes \( A^H_0(\tilde{\alpha}) \) and \( A^H(\tilde{\alpha}): \)

\[
A^H_0(\tilde{\alpha}) = \frac{72\sqrt{3}}{7\gamma(1 + \tau \tilde{\alpha})}, \quad A^H(\tilde{\alpha}) = \frac{12\sqrt{3}(1 + 7\tau \tilde{\alpha})}{7(1 + \tau \tilde{\alpha})}, \quad (9)
\]

(see the Appendix for a detailed derivation).

Hereafter, for the sake of brevity, we use the following notation to represent the periodic and aperiodic input components: \( s_{a_0}(t) = A^H_0(\omega_j)e^{\tilde{\omega}_j(t-t_0)} \) and \( s_{a_0}(t,t) = A^H(\omega)e^{\tilde{\omega}_j(t-t)} \) \( \Theta(t - t_j) \), respectively. Furthermore, we use \( \tau = 1 \) and \( \gamma = 1 \), as the system behavior is independent of the scaling parameters \( \tau \) and \( \gamma \).

#### B. Fokker-Planck equations and the stationary solution

The Fokker-Planck equations (FPEs) that are equivalent to Eq. (5) can be written as

\[
\partial_t \Phi_x = \partial_x(s + D \partial_x)\Phi_x + J \delta(x_+ - x), \quad (10a)
\]

\[
\partial_t \Phi_y = \partial_y(s + D \partial_y)\Phi_y + J_0 \delta(x - y_+), \quad (10b)
\]

where \( \delta \) is the Dirac delta function, \( J_0 \) is the probability flux, and the effective noise intensity \( D \) is expressed as \( D = \frac{12\sqrt{3}}{\gamma^2}D_0 \). The distribution functions of the neurons are fully specified by the FPEs, the following boundary conditions:

\[
\begin{align*}
\Phi_x(x_+ + s(t),t) = 0, \quad & \Phi_y(x_+ - s(t),t) = 0, \quad (11a) \\
\{\Phi_x(x,t)\}_{x_+ + s(t)} = 0, \quad & \{\Phi_y(y,t)\}_{y_+ - s(t)} = 0, \quad (11b) \\
\left. \frac{\partial \Phi_x(x,t)}{\partial x} \right|_{x_+ + s(t)} = -\left. \frac{\partial \Phi_y(y,t)}{\partial y} \right|_{y_+ - s(t)}, \quad (11c)
\end{align*}
\]
and the normalization condition:
\[
\int_{y^{-}(t)}^{\infty} \phi(x,t) dx + \int_{y^{-}(t)}^{-\infty} \phi(y,t) dy = 1, \tag{12}
\]
where \( f(y) = f(c+0) - f(c-0) \) \([27,30]\). In the absence of an input signal, i.e., \( s(t) = 0 \), the stationary solutions of Eqs. (10a)–(11d) can be expressed as
\[
\phi(x) = \frac{J_0}{D} e^{-x^2/(2D)} \int_{y^{-}}^{y} dz e^{z^2/(2D)} \Theta(x_+ - x), \tag{13a}
\]
and
\[
\phi(y) = \frac{J_0}{D} e^{-y^2/(2D)} \int_{y^{-}}^{y} dz e^{z^2/(2D)} \Theta(y_+ - y). \tag{13b}
\]
Here, \( J_0 \) denotes the stationary flux and is obtained by solving the normalization condition
\[
\int_{y^{-}}^{\infty} \phi(x) dx + \int_{y^{-}}^{-\infty} \phi(y) dy = 1. \tag{14}
\]

The mean value of the stationary cumulative firing rate is obtained by \( R_0 = R_0(t) = \int_{y^{-}}^{\infty} \phi(y) dy \). After some algebra, we obtain the numerically satisfactory form of \( R_0 \) as follows:
\[
\frac{R_0}{\pi D} + \frac{1}{\pi D} = \frac{\frac{\pi}{\Gamma(1/\sqrt{2})}}{\frac{1}{\pi D} + \frac{1}{\pi D} + \frac{1}{\pi D} + \frac{1}{\pi D}}. \tag{16}
\]

The time average and variance of the time series \( R_0(t) \) are identical because \( R_0(t) \) is a Poisson process. Therefore, the stationary cumulative firing rate of a neuron \( R_0(t) \) is expressed as \( R_0(t) = R_0 + \eta(t) \), where \( \langle \eta(t) \eta(t') \rangle = R_0 \).

C. Linear response of the distribution functions \( \Phi_x \) and \( \Phi_y \) to input signal

In keeping with linear response theory \([27,30]\), we assume that the solutions of the FPEs in the presence of a signal \( s(t) \) are in the form of linearly input unperturbed stationary solutions \( \phi(x) \) and \( \phi(y) \):
\[
\Phi_x(x,t) = \phi(x) + g \left( \sum_{j} \left[ s_{\omega_j}(t) p_s(\omega_j, x) + s_{\omega_j}(t) p_s(\omega_j, y) \right] \right) e^{x^2}, \tag{17a}
\]
\[
\Phi_y(y,t) = \phi(y) + g \left( \sum_{j} \left[ s_{\omega_j}(t) p_s(\omega_j, y) + s_{\omega_j}(t) p_s(\omega_j, y) \right] \right) e^{y^2}. \tag{17b}
\]

Substituting Eqs. (17a) and (17b) into Eqs. (10a) and (10b), respectively, yields the standard solutions \( \psi(\omega_j, z) = U(\omega, z) \) and \( \psi_2(\omega_j, z) = V(\omega, z) \), where \( U(\omega, z) \) and \( V(\omega, z) \) denote the Whittaker and Watson functions:
\[
U(\omega, z) = D_{-\omega} \frac{e^{-z}}{\sqrt{D}}, \tag{18a}
\]
\[
V(\omega, z) = D_{-\omega} \frac{\sin(\pi \omega) D_{-\omega} \frac{e^{-z}}{\sqrt{D}}}{\pi / \Gamma(\omega + \frac{1}{2})}. \tag{18b}
\]

Here, \( D_{-\omega}(z) \) denotes the parabolic cylinder function \([33]\). Note that it is also possible to obtain a numerically satisfactory pair of the standard solutions by combining the following four linearly independent functions: \( D_{-\omega}(z) \), \( D_{-\omega}(\xi z) \), \( D_{-\omega}(z) \), and \( D_{-\omega}(\xi z) \). In fact, the linear response functions built by \( \psi(\omega, z) = U(\omega, z) \) and \( \psi_2(\omega, z) = V(\omega, z) \), and by \( \psi(\omega, z) = D_{-\omega}(\xi z) \) and \( \psi_2(\omega, z) = D_{-\omega}(\xi z) \) (where \( \xi \) is either \(+1\) or \(-1\)), are different only in terms of the stability of the numerical evaluation in the limit \( D \to 0 \). Therefore, we use \( U(\omega, z) \) and \( V(\omega, z) \) as the pair of standard solutions unless otherwise stated.

The Wronskian of \( \psi(\omega, z) \) and \( \psi_2(\omega, z) \) is
\[
W_\xi(\omega, z) = \psi(\omega, z) \psi_2(\omega, z) - \psi(\omega, z) \psi_2(\omega, z). \tag{19}
\]

Because \( \frac{\partial}{\partial \xi} W(\omega, z) = 0 \), \( W_\xi \) is constant with respect to \( \xi \) and a function of \( \omega \) and \( D \):
\[
W_\xi(\omega, z) = W_z(\omega, 0) = k_\xi = \frac{2 \Gamma(\frac{1}{2})}{\sqrt{D \pi \Gamma(\omega + \frac{1}{2})}}, \tag{20}
\]

We further assume that \( p_s(\omega, x) \) and \( p_s(\omega, y) \) may take the following two modes \([34]\), i.e., either
\[
p_1^x = \begin{cases} c_{11}^x \psi(\omega, x) & (x_- \leq x < x_+), \\ c_{12}^x \psi(\omega, x) + c_{13}^x \psi_2(\omega, x) & (x > x_+), \end{cases} \tag{21a}
\]
\[
p_1^y = \begin{cases} c_{11}^y \psi(\omega, y) & (y_- < y \leq y_+), \\ c_{12}^y \psi(\omega, y) + c_{13}^y \psi_2(\omega, y) & (y < y_+), \end{cases} \tag{21b}
\]
or

\[ p^2_x = \begin{cases} c_1^2 \psi(\omega, x) + c_2^2 \psi_2(\omega, x), & (x_- \leq x < x_+) \smallskip \vspace{1.5ex} \\
- c_3^2 \psi(\omega, x), & (x > x_+) \end{cases} \]  \hspace{1cm} (22a)

\[ p^2_y = \begin{cases} c_1^2 \psi(\omega, y) + c_2^2 \psi_2(\omega, y), & (y_- < y \leq y_+) \smallskip \vspace{1.5ex} \\
- c_3^2 \psi(\omega, y), & (y < y_+) \end{cases} \]  \hspace{1cm} (22b)

The coefficients \( c_1^1, c_2^1, c_3^1 \) and \( c_1^2, c_2^2, c_3^2 \) can be explicitly determined by considering the boundary conditions given in Eqs. (11a)-(11d). To deal with the boundary conditions that are determined by the signal input, we consider approximations of the boundary conditions by taking the Taylor series around \( g = 0 \) to first order. The expansion is such that \( \Phi_i(x_- + s(t), t) \) in Eq. (11a) is given by

\[ \Phi_i(x_- + s(t), t) \approx \Phi_i(x_-) + s(t) \Phi_i'(x_-) \]  \hspace{1cm} (23)

The other boundary conditions take a similar form. Substituting Eqs. (21) and (22) into the approximated boundary conditions yields simultaneous equations of \( c_1 \) and \( c_2 \). By using the assignment \( W_r(\omega, z) \rightarrow k_r \) and the notation \( \psi_{zz} = \psi(\omega, z_+), \psi_{xz} = \psi(\omega, z_-), \psi_x = \partial_x \psi(\omega, z), \text{ and } \psi_x' = \partial_x \psi_x(\omega, z) \), we obtain the \( c_1^1 \) and \( c_1^2 \) as follows (the coefficients of \( p^2_y \) and \( p^2_z \) are not listed here as they are particularly long):

\[ c_{1,1}^1 = - \frac{e^{2i\pi} J_0}{D \psi_{y,1}} \]  \hspace{1cm} (24a)

\[ c_{1,2}^1 = \frac{J_0}{k_1} \left( \frac{e^{2i\pi} y_- \psi_{x,1} + e^{2i\pi} x_+ \psi_{x,1} + e^{2i\pi} \psi_{x,1}'}{2D^2} \right) \]  \hspace{1cm} (24b)

\[ c_{1,3}^1 = \frac{e^{2i\pi} J_0}{k_1} \left( \frac{\psi_{x,1}'}{D \psi_{x,-}} - \frac{y_- \psi_{x,1} + x_+ \psi_{x,1} + \psi_{x,1}'}{2D^2} \right) \]  \hspace{1cm} (24c)

\[ c_{1,1}^2 = - \frac{e^{2i\pi} J_0}{k_1} \left( \frac{D \psi_{y,-}}{\psi_{y,-}} + \frac{\psi_{y,-}}{D} \right) \]  \hspace{1cm} (24d)

\[ c_{1,2}^2 = \frac{e^{2i\pi} J_0}{k_1} \left( \frac{\psi_{x,1}'}{D \psi_{x,-}} - \frac{\psi_{x,1}'}{D \psi_{x,-}} \right) \]  \hspace{1cm} (24e)

D. Cumulative firing rate and internal noise

Next, we shift our focus to deriving an analytical representation of the cumulative firing rate of a neuron ensemble, \( R_{X_i}(t) = 1/N \sum R_{x_i, i}(t) \). Here, since we have two modes \( p^2_{x,1} \) and \( p^2_{x,1} \) in the linear response functions, we use the upper right index to denote the mode as \( R_{y, i}^{1, 2}(t) \). The mean cumulative firing rate \( R_{y, i}^{1, 2}(t) \) is computed as

\[ R_{y, i}^{1, 2}(t) = \int_{y_-}^{y_+} \Phi_{y, i}^{1, 2} dy + \int_{y_-}^{y_+} \Phi_{y, i}^{1, 2} dy. \]  \hspace{1cm} (25)

The analytical representation of \( R_{y, i}^{1, 2}(t) \) is computed by expanding Eq. (25) around \( g = 0 \) to first order and applying the following indefinite integrals:

\[ U(\omega, z)e^{\pi\omega z} dz = -\sqrt{\pi} U(\omega + 1, z)e^{\pi\omega z}, \]  \hspace{1cm} (26a)

\[ V(\omega, z)e^{\pi\omega z} dz = [U(\omega + 1, -z) - \sin(\pi\omega)U(\omega + 1, z)] \frac{\pi e^{\pi\omega}}{[\sqrt{\pi} (\omega + 1)]}. \]  \hspace{1cm} (26b)

The time series \( R_{x, i}^{1, 2}(t) \) is represented as

\[ R_{x, i}^{1, 2}(t) = R_0 + c \sum_j s_{x, j}(t)G_{x, j}^{1, 2}(\omega_j) \]  \hspace{1cm} (27)

where \( R_0 \) is the unperturbed cumulative firing rate, \( \eta_i(t) \) is the stationary neuronal noise, and \( G_{x, i}^{1, 2}(\omega) \) is the linear response to the input signal \( s_{x, i}(t) \) as follows:

\[ G_{x, i}^{1}(\omega) = -\sqrt{D}c_{y,2} e^{\pi\omega} \psi_{1+\omega, y, i} \]  \hspace{1cm} (28a)

\[ -\sqrt{D}c_{y,1} e^{\pi\omega} \psi_{1+\omega, y, i} - e^{\pi\omega} \psi_{1+\omega, y, i} \]  \hspace{1cm} (28b)

The linear response function \( G_{x, i}^{1}(\omega) \) takes a finite value in the limit \( \omega \to 0 \), whereas the function \( G_{x, i}^{2}(\omega) \) diverges. In Sec. IV, we show that the function \( G_{x, i}^{1}(\omega) \) corresponds mainly to a signal with a frequency less than 5 Hz, and \( G_{x, i}^{2}(\omega) \) corresponds mainly to a signal with a frequency larger than 5 Hz. Note that \( R_{x, i}^{1, 2}(t) \) consists of both real and imaginary parts unlike the instantaneous firing rate \( r(t) \) that consists of only a real part [see Ref. [30] for a detailed expression for \( r(t) \)].

E. Derivation of \( R_{x, i}^{1, 2}(t) \) and \( C_0 \)

By using the forms of \( R_{x, i}^{1, 2}(t) \) given in Eqs. (27)–(28b), the total firing rate of the \( N \) neuron ensemble, \( R_{x, i}^{1, 2}(t) \), can be
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FIG. 1. (Color online) The correlation coefficient \( C_1 \) of the neuronal ensemble consisting of \( N = 2000 \) neurons with a bias signal \( b = 0.3 \), as a function of the noise intensity \( D_0 \) for (a)–(c) a periodic input signal and (d) a semiperiodic input and several input gains \( g \): \( g = 0.01, 0.05, 0.1, \) and \( 0.2 \) [35]. The theoretical curves of \( C_1 \) are computed using Eq. (37) with \( \sigma^2(D) = R_0 \). The solid curves in (a) are \( \omega = 0.1 \) Hz using the mode \( (G_1^r, A_1^r, A_1^r) \); in (b), \( \omega = 1 \) Hz using \( (G_1^r, A_1^r, A_1^r) \); in (c), \( \omega = 10 \) Hz using \( (G_1^r, A_1^r, A_1^r) \); and in (d), \( \omega_1 = 1 \) and \( \omega_2 = \sqrt{2} \) Hz using \( (G_1^r, A_1^r, A_1^r) \). The theoretical prediction of \( C_1 \) using another signal and linear response mode pair with \( g = 0.01 \) is shown for reference by the dashed lines. The numerical \( C_1 \) values are obtained from 20 trials of a 100 s simulation and are represented by the symbols and error bars for \( g = 0.01 (\bigcirc), 0.05 (\bigotimes), 0.1 (\triangle), \) and \( 0.2 (\triangleleft) \). The theoretical and numerical phase shifts \( \alpha \) are determined such that the result \( C_1 \) is a maximum. In all cases shown here, an increase in \( g \) leads to growth of the SR profiles from bell-shaped curves into trapezoid-shaped curves.

described as

\[
R_1^2(t) = \frac{1}{N} \sum_{i=1}^{N} \left[ R^1_{y_i^r} + \eta_i(t) \right].
\]  

(29)

To compute the ensemble average \( R_1(t) \), we introduce the probability density function \( P(\eta) \), which is based on the assumption that \( \eta(t) \) is equivalent to neuronal random firings in the stationary state. We also assume that the time series of \( \eta(t) \) can be approximated by the zero-mean Gaussian process with a variance of \( \sigma^2(D^2) = R_0 \). Then, \( P(\eta) \) is defined as

\[
P(\eta) = \frac{1}{\sqrt{2\pi\sigma(D)^2}} e^{-\frac{\eta^2}{2\sigma^2(D^2)}}.
\]  

(30)

By using this function, the total firing rate of the neuron ensemble, \( R_\Sigma \), can be described as

\[
R_\Sigma(t) = \int_{-\infty}^{\infty} P(\eta) R_\Sigma(t) d\eta.
\]  

(31)

The time averages of the ensemble averages of \( R_\Sigma \) and \( R_\Sigma^2 \) can be computed as

\[
\langle R_\Sigma \rangle = \lim_{T \to \infty} \frac{1}{T} \int_0^T \int_{-\infty}^{\infty} P(\eta) R_\Sigma(t) d\eta dt,
\]  

(32)

\[
\langle R_\Sigma^2 \rangle = \lim_{T \to \infty} \frac{1}{T} \int_0^T \int_{-\infty}^{\infty} P(\eta) R_\Sigma(t) d\eta dt.
\]  

(33)

The analytical form of \( \langle C_0 \rangle \), i.e., the ensemble average of the cross-correlation between the cumulative mean firing rate \( R_\Sigma(t) \) and the input signal \( s_0(t) \), is computed as

\[
\langle C_0 \rangle = \lim_{T \to \infty} \frac{1}{T} \int_0^T s_0(t + \alpha) R_\Sigma(t) dt.
\]  

(35)

Note that all aperiodic components corresponding to \( \lambda_m \) vanish from \( \langle R_\Sigma \rangle \), \( \langle R_\Sigma^2 \rangle \), \( \langle C_0 \rangle \), and \( \langle C_1 \rangle \) as a result of the \( \lim_{T \to \infty} \) operation. Likewise, the interaction terms of the different linear response functions \( G_i(\omega_i) \) and \( G_j(\omega_j) \), i.e., \( G_i(\omega_i)G_j(\omega_j) \), where \( i \neq j \), also vanish from the resulting expressions. The expression for \( \langle C_0 \rangle \) then reduces to

\[
\langle C_0 \rangle = g^2 \sum_{j=1}^{N_1} \left[ e^{i\alpha_i} A(\omega_i) A(\omega_j^*) G_j(\omega_j) \right.
\]  

\[+ e^{i\alpha_j} A(\omega_j) A(\omega_i^*) G_i(\omega_i) \].

(36)
FIG. 2. (Color online) The coefficient $\langle C_1 \rangle$ in the mode $G_1^1, A_0^0, A_1^1$ in response to the periodic input signal of $\omega = 1$ Hz as a function of noise intensity $D_0$ with bias intensities of (a) $b = -1$, (b) $b = 0$, (c) $b = 1$, and (d) $b = 2$ [35]. Note that biases $b = -1$ and 0 correspond to the excitable regime and that biases $b = 1$ and 2 correspond to the excitation-blocked regime. Numerically obtained $\langle C_1 \rangle$ are represented by the symbols and error bars as used in Fig. 1. The size of the neuron ensemble is $N = 500$. For large negative and positive values of $b$, i.e., $b = -1$ and 2, the value of the theoretical $\langle C_1 \rangle$ increases rapidly with an increase in $D_0$, whereas the numerical data implicate a very slow increase in $\langle C_1 \rangle$. For a relatively small $b$ value, i.e., $0 \leq b \leq 1$, or for relatively large $D_0$ values, the theory matches the numerical data. It is clear that the growth of SR occurs also in the excitatory and the excitation-blocked firing regimes.

where $A_0(\omega_j)$ takes the form $A_0^0(\omega_j)$ or $A_0^1(\omega_j)$, $A(\omega_j)$ takes the form $A_1^1(\omega_j)$ or $A_1^1(\omega_j)$, and $G_1(\omega)$ takes the form $G_1^1(\omega)$ or $G_1^2(\omega)$. Substituting Eqs. (33), (34), and (36) into Eq. (2) yields the analytical form of $\langle C_1 \rangle$, the ensemble average of the correlation coefficient between $R_{2}(t)$ and $s_{0}(t)$, as follows:

$$\langle C_1 \rangle = \frac{\sum_{j=1}^{N} A(\omega_j) A_0(\omega_j) e^{\omega_j \sigma} G_1^1(\omega_j) + A(\omega_j) A_0(\omega_j) e^{\omega_j \sigma} G_1^2(\omega_j) + 2 A(\omega_j) A_0(\omega_j) G_1(\omega_j) G_1(\omega_j) + \frac{\sigma \epsilon \Delta t}{N \sigma}}{\sum_{j=1}^{N} A(\omega_j) A_0(\omega_j) e^{\omega_j \sigma} G_1^1(\omega_j) + A(\omega_j) A_0(\omega_j) e^{\omega_j \sigma} G_1^2(\omega_j) + 2 A(\omega_j) A_0(\omega_j) G_1(\omega_j) G_1(\omega_j) + \frac{\sigma \epsilon \Delta t}{N \sigma}}.$$  (37)

IV. GROWTH OF STOCHASTIC RESONANCE

The behavior of the theoretical $\langle C_1 \rangle$ and numerically computed $\langle C_1 \rangle$ are shown in Fig. 1. The theoretical $\langle C_1 \rangle$ curves are computed using Eqs. (15), (16), (28), and (37), whereas the numerical $C_1$ of the FHN model neuron is computed by integrating Eq. (6) using the Euler method [36] with $\epsilon = 0.005$ and a step size of $\Delta t = 0.0001$.

The computation of the theoretical $\langle C_1 \rangle$ requires a determination of the signal-driving modes, either $A_0^1$ and $A_1^1$ or $A_0^1$ and $A_1^1$, and the linear response mode, either $G_1^1$ or $G_2^1$. In this article, we determine these in an arbitrary manner. Furthermore, because the theoretical $\langle C_1 \rangle$ also contains an imaginary part, we use only $\text{Re}(\langle C_1 \rangle)$ for the theoretical estimations.

The growth of SR with the signal intensity is clearly demonstrated in Fig. 1 by the increase in the signal gain $g$; the $\langle C_1 \rangle$ curve grows from a bell-shaped curve to a plateau and leads to the manifestation of SR without the need for tuning. The growth of SR with the signal intensity is observable even if the signal is semiperiodic [Fig. 1(d)]. Furthermore, the growth of SR is not limited by the neuronal firing regime and is observable using arbitrary bias signal values as demonstrated in Fig. 2. Note that $\langle C_1 \rangle$ is sensitive to the neuronal firing regime only for a small noise intensity as shown in Fig. 3; the difference in the neuronal firing regimes only becomes dominant for small noise intensities $D < 0.1$.

The emergence of SR without tuning by an increase in the signal intensity is accounted for by Eq. (37). The signal
The growth of SR, i.e., the SR peak dependence on the signal intensity, is fairly well accounted for by our theory. The estimation of $\langle C_1 \rangle$ using the linear response theory and piecewise linearization technique match the numerical data for signal frequencies of $\omega = 0.1–10$ Hz and a bias signal of approximately $0 \leq b \leq 1$. Furthermore, our theory also accounts for the $\langle C_1 \rangle$ behavior for the semiperiodic signals. However, the difference between the theoretical $\langle C_1 \rangle$ estimation and the numerical data cannot be neglected for large bias signals, i.e., $b \leq -1$ or $b \gg 1$, as shown in Figs. 2(a) and 2(d), particularly for the small $D$ values. This implies that the piecewise linearization of the cubic null cline in the FHN neuron is an oversimplification; a FHN neuron rarely fires with bias signals of $b \leq -1$ or $b \gg 1$ due to the cubic null cline, although a plFHN neuron fires frequently.

A difference in the theoretical estimation of $\langle C_1 \rangle$ and the numerical data is also observed for a signal frequency of around $\omega = 5$ Hz, as shown in Fig. 4. At this frequency, we cannot identify the signal driving mode and linear response mode pair that matches the numerical result. It will likely be necessary to consider a mixture of different signal modes, $A^I$ and $A^H$, and linear response modes, $G^I_y$ and $G^H_y$, by developing a distribution function of the modes. However, since $A^I$ and $A^H$ correspond to different plFHN models and different Fokker-Planck equations, it would be necessary to introduce a new condition to mix and normalize different Fokker-Planck equations.

Note that the theoretical curves of $\langle C_1 \rangle$ for $\omega = 10$ Hz depicted in Fig. 1 involve rapid jittering. Although we cannot reject possible errors in the numerical evaluations because evaluating the parabolic cylinder function $D_0(x)$ against
large values of $\omega$ is a very difficult technical issue, the rapid jittering may imply intrinsic fluctuations of the time-averaged cumulative firing rate against changes in the noise intensity $D$.

There are three main conclusions from these results. First, the linear response function of an FHN neuron involves, in the piecewise linear perspective, at least two different modes $G_i^0$ and $A_i^0$ in addition to the two different signal driving modes $A_i^1$ and $A_i^2$. This means that the FHN model neuron may take four modes in responding to the input signal. To analyze the FHN model neuron in more detail, it would be necessary to develop distribution functions of these four modes. Second, the cumulative firing rate $R_{c,i}(t)$ may involve intrinsic internal noise that jitters rapidly against changes in the noise intensity $D$ due to the instability of the parabolic cylinder function $D_{\omega}(z/\sqrt{D})$. Third, because the signal intensity $g$ plays exactly the same role as the neuron ensemble size $N$, SR profiles grow from bell-shaped curves to plateaus with an increase in the input signal intensity, and thus SR without tuning is realized.

Previous research on SR without tuning has focused on the role of the neuron ensemble size, i.e., SR without tuning emerges only if the ensemble contains a vast amount of neurons [2,4–6,28]. In this article, we have demonstrated that SR without tuning emerges based on an increase in the input signal intensity, and thus SR without tuning is realized. The size of the neuron ensemble is $N = 2000$.

FIG. 4. (Color online) The coefficient $\langle C_i \rangle$ in response to a periodic input signal of $\omega = 5$ Hz and bias $b = 0.3$ as a function of the noise intensity $D_0$ [35]. The theoretical estimation of $\langle C_i \rangle$ in response to a signal frequency $\omega = 5$ Hz using the mode $G_i^0$, $A_i^0$, and $A_i^0$ with $g = 0.01, 0.05, 1$, and $0.2$ is shown by the solid lines; that using the mode $G_i^1$, $A_i^0$, and $A_i^0$ with $g = 0.01$ is shown by the dashed line; and that using the mode $G_i^1$, $A_i^1$, and $A_i^1$ with $g = 0.01$ is shown by the long dashed line. The theoretical $\langle C_i \rangle$ using the $G_i^1$, $A_i^1$, and $A_i^2$ mode is not shown as it falls well below the dashed line. Around the input frequency $\omega = 5$ Hz, no single mode matches the numerical result. Numerically obtained $\langle C_1 \rangle$ are represented by the same symbols and error bars as used in Figs. 1 and 2. The size of the neuron ensemble is $N = 2000$.

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APPENDIX: DERIVATION OF THE plFHN MODEL

The signal term $s_0(t)$ in the FHN model neuron in Eq. (1) can drive the system in two different ways, i.e., either by directly coupling with the variable $W_i$ (mode I) or not (mode II). Here, we derive two different plFHN neuron models corresponding to the two different signal-driving modes by using the input signal term $s_0(t) = g_0 \sum_{i=0}^{N-1} e^{i\omega t}$.

1. Derivation of the plFHN model in driving mode I

First, we present the mode I plFHN model where the signal $s_0(t)$ is directly coupled with the variable $W_i$. Here, we change the variables $V$ and $W$ such that $V = \frac{1}{\sqrt{3}} (\bar{v} + \sqrt{3} \gamma) + \sqrt{3} \gamma D_0 \tilde{\xi}(\tilde{t})/\sqrt{\tau}$ and $W = \frac{1}{\sqrt{3} \gamma} (\bar{w} - \sqrt{3} \gamma \tilde{\omega})$. Furthermore, we rescale the time variable $t$ such that $\tilde{t} = 7 \tau \times t$. Then, we have

\[
\tilde{v}_i(\tilde{t}) = \frac{1}{6} f(v_i) - \frac{\gamma}{6} w_i + 2\sqrt{3} \left( b - \frac{1}{2} \right), \tag{A1a}
\]

\[
\tau \dot{w}_i(\tilde{t}) = \frac{6}{\gamma} v_i - \frac{1}{7} w_i + \frac{12}{\gamma} \sum_{j}^{N} \left( 1 + \tilde{\omega}_j \right) e^{i\omega_0 t} \gamma + \frac{12\sqrt{3}}{\gamma} \tau \sqrt{2D_0 \tilde{\xi}(\tilde{t})}/\tau, \tag{A1b}
\]

where and $\tilde{\omega} = \omega_0/(7\tau)$.

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By applying the piecewise linearization of $f(v)$ to $F(v)$ and the limit $\tilde{\epsilon} \tilde{v}_i \rightarrow 0$, we have the following equations:

\[ \gamma w_i = F(v_i) + 12\sqrt{3}\left(b - \frac{1}{2}\right), \quad (A2a) \]

\[ \tau \dot{w}_i = -w_i + \frac{12}{7\gamma} \sigma_i + 12\sqrt{3} g_0 \sum_j N_j (1 + \tilde{\omega}) e^{\tilde{\omega}^2 i} \]
\[ - \frac{12\sqrt{3}}{7\gamma} \sqrt{2D_0 \xi_i(t)} \tau, \quad (A2b) \]

\[ F(v) = 2\sigma - v, \quad \sigma = \begin{cases} +1, & v \geq 1, \\ -1, & v \leq 1, \end{cases} \quad (A2c) \]

where we neglected the neuron behavior in the middle branch $-1 < v_i < 1$.

By considering the following variable transformations:

\[ x_i(\tilde{t}) = w_i(\tilde{t}) + \frac{12}{7\gamma} + \frac{12\sqrt{3}}{7\gamma} \left(b - \frac{1}{2}\right) - g_0 \sum_j N_j A_0^i(\tilde{\omega}_j) e^{\tilde{\omega}_j \tilde{t}}, \quad (A3a) \]

\[ y_i(\tilde{t}) = w_i(\tilde{t}) - \frac{12}{7\gamma} + \frac{12\sqrt{3}}{7\gamma} \left(b - \frac{1}{2}\right) - g_0 \sum_j N_j A_0^i(\tilde{\omega}_j) e^{\tilde{\omega}_j \tilde{t}}, \quad (A3b) \]

\[ A_0^i(\tilde{\omega}) = \frac{72\sqrt{3}(1 + \tau \tilde{\omega})}{7\gamma(1 + \tau \tilde{\omega})}, \quad (A3c) \]

we obtain the following two-state Langevin equations with the effective noise intensity $D = \left(\frac{12\sqrt{3}}{7\gamma}\right)^2 D_0$:

\[ \tau \dot{x}_i(\tilde{t}) = -x_i(\tilde{t}) + \sqrt{2D_0 \xi_i(\tilde{t})}, \quad (A4a) \]

\[ \tau \dot{y}_i(\tilde{t}) = -y_i(\tilde{t}) + \sqrt{2D_0 \xi_i(\tilde{t})}, \quad (A4b) \]

The source points $X_+$ and $Y_+$ and the sink points $X_-$ and $Y_-$ are described as

\[ X_\pm = x_\pm - g_0 \sum_j N_j A_0^i(\tilde{\omega}_j) e^{\tilde{\omega}_j \tilde{t}}, \quad (A5a) \]

\[ Y_\pm = y_\pm - g_0 \sum_j N_j A_0^i(\tilde{\omega}_j) e^{\tilde{\omega}_j \tilde{t}}, \quad (A5b) \]

\[ A_0^i(\tilde{\omega}) = \frac{72\sqrt{3}(1 + \tau \tilde{\omega})}{7\gamma(1 + \tau \tilde{\omega})}, \quad (A5c) \]

where $x_\pm = \frac{12\pm7-6\sqrt{3}+12\sqrt{3}b}{7\gamma}$ and $y_\pm = \frac{-12\pm7-6\sqrt{3}+12\sqrt{3}b}{7\gamma}$. Note that in the mode I pIFHN model neuron, the effective signal amplitudes $A_0^i(\omega)$ and $A^i(\omega)$ are identical.

### 2. Derivation of the pIFHN model in driving mode II

Similarly to the mode I pIFHN model, we change the variable $V$ and $W$ in Eq. (1) such that $V = \frac{1}{2\sqrt{3}} v + \frac{1}{2}$ and

\[ W = \frac{1}{2} + \frac{V}{12\sqrt{3}} \tilde{\omega}. \] Furthermore, we rescale the time variable $t$ into $\tilde{t}$ such that $\tilde{t} = (7\tau) t$. Then, we have

\[ \dot{\tilde{v}}_i = -\frac{1}{2} f(v_i) - \frac{V}{6} w_i + 2\sqrt{3}\left(b + g_0 \sum_j N_j e^{\tilde{\omega}_j \tilde{t}} - \frac{1}{2}\right), \quad (A6a) \]

\[ \tau \dot{w}_i = \frac{6}{7\gamma} - \frac{1}{7\gamma} - \frac{12\sqrt{3}}{7\gamma} \sqrt{2D_0 \xi_i(\tilde{t})} \tau, \quad (A6b) \]

where $\tilde{\epsilon} = 7\tau \epsilon, f(v) = -1/2\tau(v - \sqrt{3}(v + \sqrt{3})), \tilde{\omega} = \omega/(7\tau)$. Note that we assume that $\xi_i(\tilde{t}) = \xi_i(\tilde{t})\tau$.

By applying the limit of $\tilde{\epsilon}, \dot{\tilde{v}} \rightarrow 0$ and the piecewise linearization of $f(v)$ to $F(v)$, we have the following equations:

\[ \gamma w_i = F(v_i) + 12\sqrt{3}\left(b + g_0 \sum_j N_j e^{\tilde{\omega}_j \tilde{t}} - \frac{1}{2}\right), \quad (A7a) \]

\[ \tau \dot{w}_i = \frac{6}{7\gamma} - \frac{1}{7\gamma} - \frac{12\sqrt{3}}{7\gamma} \sqrt{2D_0 \xi_i(\tilde{t})} \tau. \quad (A7b) \]

By substituting Eq. (A7a) into Eq. (A7b), we have the following one-dimensional differential equation with respect to $w$:

\[ v_i = 2\sigma - \gamma w_i + 12\sqrt{3}\left(g + g_0 \sum_j N_j e^{\tilde{\omega}_j \tilde{t}} - \frac{1}{2}\right), \quad (A8a) \]

\[ \tau \dot{w}_i = -w_i + \frac{12}{7\gamma} \sigma_i + \frac{12\sqrt{3}}{7\gamma} \left(b - \frac{1}{2} + g_0 \sum_j N_j e^{\tilde{\omega}_j \tilde{t}}\right) \]
\[ - \frac{12\sqrt{3}}{7\gamma} \sqrt{2D_0 \xi_i(\tilde{t})} \tau. \quad (A8b) \]

To have the simple two-state Langevin equations, we use the following variable transformations:

\[ x_i(\tilde{t}) = w_i(\tilde{t}) + \frac{12}{7\gamma} + \frac{12\sqrt{3}}{7\gamma} \left(b - \frac{1}{2}\right) - g_0 \sum_j N_j A_0^i(\tilde{\omega}_j) e^{\tilde{\omega}_j \tilde{t}}, \quad (A9a) \]

\[ y_i(\tilde{t}) = w_i(\tilde{t}) - \frac{12}{7\gamma} + \frac{12\sqrt{3}}{7\gamma} \left(b - \frac{1}{2}\right) - g_0 \sum_j N_j A_0^i(\tilde{\omega}_j) e^{\tilde{\omega}_j \tilde{t}}, \quad (A9b) \]

\[ A_0^i(\tilde{\omega}) = \frac{72\sqrt{3}}{7\gamma(1 + \tau \tilde{\omega})}. \quad (A9c) \]

By using the above variable transformations, we obtain

\[ \tau \dot{x}_i(\tilde{t}) = -x_i(\tilde{t}) + \sqrt{2D_0 \xi_i(\tilde{t})}, \quad (A10a) \]

\[ \tau \dot{y}_i(\tilde{t}) = -y_i(\tilde{t}) + \sqrt{2D_0 \xi_i(\tilde{t})}, \quad (A10b) \]

where the effective noise intensity $D$ is $D = \left(\frac{12\sqrt{3}}{7\gamma}\right)^2 D_0$. The source points $X_+$ and $Y_+$ and the sink points $X_-$ and $Y_-$ are described as

\[ X_\pm = x_\pm - g_0 \sum_j N_j A_0^i(\tilde{\omega}_j) e^{\tilde{\omega}_j \tilde{t}}, \quad (A11a) \]

\[ Y_\pm = y_\pm - g_0 \sum_j N_j A_0^i(\tilde{\omega}_j) e^{\tilde{\omega}_j \tilde{t}}. \quad (A11b) \]
\[ A^H(\tilde{\omega}) = \frac{12\sqrt{3}(1 + 7\tau\tilde{\omega})}{7\gamma(1 + \tau\tilde{\omega})}, \]  

where \( x_\parallel = \frac{12\tilde{\omega}T - 6\gamma T + 12\sqrt{\gamma T}}{7\gamma} \) and \( y_\parallel = \frac{-12\tilde{\omega}T - 6\gamma T + 12\sqrt{\gamma T}}{7\gamma} \). Note that the effective signal amplitudes \( A^H_0 \) and \( A^H \) are not identical, unlike those of mode \( I \).