

Mutual-Information Noise Benefits in Brownian Models of Continuous and Spiking Neurons

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Abstract—The Ito calculus shows that noise benefits can occur in common models of continuous neurons and in random spiking neurons cast as stochastic differential equations. Additive Gaussian noise perturbs the neural dynamical systems as additive Brownian diffusions. The first of two theorems uses a global Lipschitz continuity condition to characterize a stochastic resonance (SR) noise benefit in models of continuous neurons that receive random subthreshold inputs. Brownian diffusions produce an SR noise benefit in the sense that they increase the neuron’s mutual information or bit count if the noise mean falls within an interval that depends on model parameters. The second theorem extends an earlier SR result for the random spiking FitzHugh-Nagumo neuron model by replacing a firing-rate approximation with exact stochastic dynamics. This gives an interval-based sufficient condition for an SR noise benefit.

I. STOCHASTIC RESONANCE IN BROWNIAN NEURAL MODELS

Stochastic resonance (SR) occurs in a nonlinear system when injected noise benefits the system’s performance. Several researchers have demonstrated SR effects in many neuron models [2], [3], [5], [8], [12], [23], [24], [25], [27], [28], [29], [30], [33], [38], [39]. Figure 1 shows an SR noise benefit in a bistable neuron whose noisy input activation defines a scaled Brownian diffusion process. The input is a random bipolar Bernoulli sequence. The output is the neuron’s thresholded activation potential. The right amount of noise makes the neurons output cohere with or approximately match the Bernoulli input.

We recently showed [33] that most models of random spiking retinal neurons benefit from some level of noise for all possible finite-variance noise and for the wide class of infinite-variance stable noise [16], [23], [25], [35], [36]. That paper in turn extended the recent ‘forbidden interval’ theorems for SR in [24], [25]. These theorems state that an SR noise benefit occurs in simple threshold neurons if and only if the noise mean $E(n)$ or location parameter does not lie in the interval $(T - A, T + A)$ where $-A < A < T$ for bipolar subthreshold signal $\pm A$ and threshold T . The proof strategy shows that a noise benefit occurs if the positive mutual information goes to zero as the noise variance or dispersion goes to zero. We apply that strategy again here using the Ito stochastic calculus for more sophisticated neural dynamics.

We consider the noisy dynamical neuron models of the

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general form

$$\dot{x} = -x(t) + f(x(t)) + s(t) + n(t) \quad (1)$$

$$y(t) = g(x(t)) \quad (2)$$

with initial condition $x(t_0) = x_0$. Here $s(t)$ is the additive forcing input signal—either s_1 or s_2 , $n(t)$ is the additive Gaussian white noise of the neuron, g is a static (usually threshold) transformation function, and $y(t)$ is the neuron’s output. The neuron feeds its activation or membrane potential signal $x(t)$ back to itself through $-x(t) + f(x(t))$ and emits the thresholded signal $y(t)$ as output. We can rewrite (1)-(2) as the formal Ito stochastic differential equations [9]

$$dX_t = b(t, X_t)dt + \sigma(t, X_t)dB_t \quad (3)$$

$$Y_t = g(X_t) \quad (4)$$

for initial condition $X_{t_0} = X_0$ where $b(t, X_t) = -X_t + f(X_t) + S_t$ is a global or local Lipschitz drift term and where $\sigma(t, X_t)$ is a constant diffusion term. B_t is the standard Wiener process or Brownian motion such that the stochastic differential dB_t corresponds to additive white Gaussian noise $n(t)$. The solution X_t of (3) is a stochastic process and its distribution derivation can be complicated. We exploit the pathwise uniqueness property [9] of X_t to prove Lemma 1 and Lemma 2. We then use these two lemmas to prove Theorem 1 and Theorem 2 respectively.

II. SR IN NOISY CONTINUOUS NEURON MODELS

We will prove that an SR noise benefit holds for many types of noisy continuous neurons by using a limiting argument and the stochastic calculus. The results hold for the additive continuous neuron model (1)-(2) with a neuronal signal function $f(x)$ of quite general form that can include the following common signal functions:

- *Logistic*. The logistic signal function [22] is sigmoidal and strictly increasing

$$f(x) = \frac{1}{1 + e^{-cx}} \quad (5)$$

for scaling constant $c > 0$. This signal function gives a bistable additive neuron model.

- *Hyperbolic Tangent*. This signal function is also sigmoidal and gives a bistable additive neuron model. [1], [2], [4], [18], [19], [22]

$$f(x) = 2 \tanh x \quad (6)$$

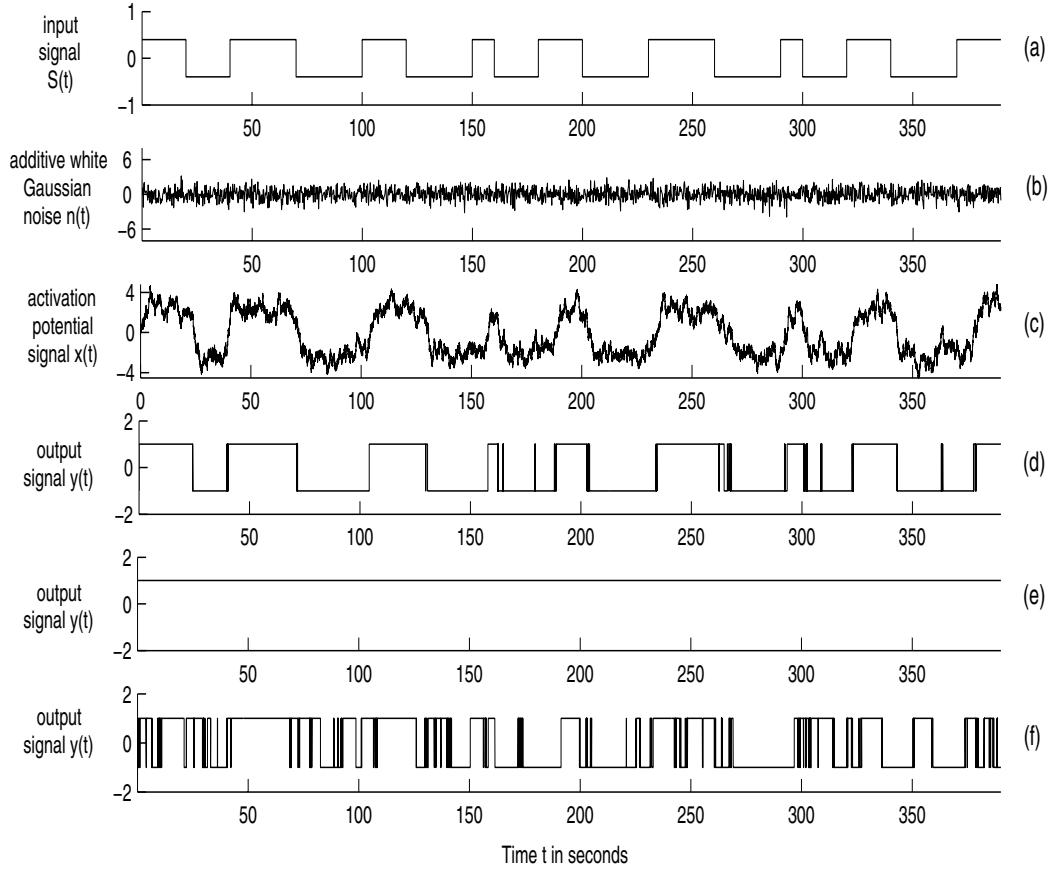


Fig. 1. Stochastic resonance in a Brownian bistable neuron (3)-(4) and (6). The output of the neuron should cohere with the input signal. (a) Bernoulli input signal S as a function of time t . (b) Additive Gaussian white noise $n(t)$ with variance $\sigma^2 = 1$. (c) Noisy Brownian membrane potential of the neuron. (d) SR effect: The neuron's thresholded output approximately matches the Bernoulli input signal. (e) Output signal in the absence of noise. (f) Too much noise distorts the output signal.

• *Linear Threshold.* This linear-threshold signal has the form [22]:

$$f(x) = \begin{cases} cx & |cx| < 1 \\ 1 & cx > 1 \\ -1 & cx < -1 \end{cases} \quad (7)$$

for constant $c > 0$.

• *Exponential.* This signal function is asymmetric and has the form [22]

$$f(x) = \begin{cases} 1 - \exp\{-cx\} & \text{if } x > 0 \\ 0 & \text{else} \end{cases} \quad (8)$$

for constant $c > 0$.

• *Gaussian.* The Gaussian or “radial basis” signal function [22] differs from the other signal functions above because it is nonmonotonic:

$$f(x) = \exp\{-cx^2\} \quad (9)$$

for constant $c > 0$.

The above neuron models can have one-to-three fixed points depending on the input signal and the model parameters. The input signal is subthreshold in the sense that switching it from s_1 to s_2 or vice versa does not change the output Y_t of (4). There exist θ_1 and θ_2 such that the input S is subthreshold whenever $\theta_1 \leq s_1 < s_2 \leq \theta_2$. The values of θ_1 and θ_2 depend on the model parameters. Consider the bistable potential neuron model (1)-(2) and (6). A simple calculation shows that if the input signal $S \in \{s_1, s_2\}$ satisfies $-0.5329 < s_1 < s_2 < 0.5329$ then the bistable potential neuron has two stable fixed points (one positive and the other negative) and has one unstable fixed point between them. Then the input is subthreshold because switching it from s_1 to s_2 or vice versa does not change the output Y_t .

A. Mutual Information and SR

Mutual information [7] can measure the stochastic resonance (SR) effect [3], [8], [15], [21], [26], [34], [37]. The Shannon mutual information of the discrete input random variable S and the output random variable Y is the difference

between its unconditional and conditional entropy:

$$I(S, Y) = H(Y) - H(Y|S) \quad (10)$$

$$= -\sum_y P_Y(y) \log P_Y(y) + \sum_s \sum_y P_{SY}(s, y) \log P_{Y|S}(y|s) \quad (11)$$

$$= -\sum_y P_Y(y) \log P_Y(y) + \sum_s P(s) \sum_y P(y|s) \log P(y|s) \quad (12)$$

$$= \sum_{s,y} P_{SY}(s, y) \log \frac{P_{SY}(s, y)}{P_S(s)P_Y(y)} \quad (13)$$

We can view the mutual information as the expectation of the random variable $\log \frac{P_{SY}(s, y)}{P_S(s)P_Y(y)}$:

$$I(S, Y) = E \left[\log \frac{P_{SY}(s, y)}{P_S(s)P_Y(y)} \right] \quad (14)$$

Here $P_S(s)$ is the probability density of the input S , $P_Y(y)$ is the probability density of the output Y , $P_{Y|S}(y|s)$ is the conditional density of the output Y given the input S , and $P_{SY}(s, y)$ is joint density of the input S and the output Y . Jensen's inequality implies that $I(S, Y) \geq 0$ [7]. Random variables S and Y are statistically independent if and only if $I(S, Y) = 0$. Hence $I(S, Y) > 0$ implies some degree of dependence. This implies that the system exhibits the SR noise benefit if $I(S, Y) > 0$ for some noise intensity σ and $I(S, Y) \rightarrow 0$ as $\sigma \rightarrow 0$.

We will use the following technical lemma to prove the mutual information-based SR result for the continuous neuron models (3)-(4) and (5)-(9). The proof is lengthy and we omit it for space reasons.

Lemma 1: Let $b : \mathbf{R}^+ \times \mathbf{R}^n \rightarrow \mathbf{R}^n$ and $\sigma : \mathbf{R}^n \times \mathbf{R}^m \rightarrow \mathbf{R}^n$ in (3) be measurable functions that satisfy

$$\sum_{i=1}^n \{2x_i b_i(t, x) + a_{ii}(t, x)\} \leq K(1 + \|x\|^2) \quad (15)$$

for every $x \in \mathbf{R}^n$ and a global Lipschitz condition

$$\|\sigma(t, x) - \sigma(t, y)\| + \|b(t, x) - b(t, y)\| \leq D\|x - y\| \quad (16)$$

for all $x, y \in \mathbf{R}^n$ for some constant $D > 0$. Here $a = \sigma\sigma^T$ and $\|x\|^2 = x^T x$.

$$\text{Suppose } dX_t = b(t, X_t)dt + \sigma dB_t \quad (17)$$

$$d\hat{X}_t = b(t, \hat{X}_t)dt. \quad (18)$$

Then for every $T \in \mathbf{R}^+$ and for every $\varepsilon > 0$:

$$E \left[\sup_{0 \leq t \leq T} \|X_t - \hat{X}_t\| > \varepsilon \right] \rightarrow 0 \quad \text{as } \sigma \rightarrow 0$$

and hence

$$P \left[\sup_{0 \leq t \leq T} \|X_t - \hat{X}_t\| > \varepsilon \right] \rightarrow 0 \quad \text{as } \sigma \rightarrow 0. \quad (19)$$

Lemma 1 holds for any continuous neuron model that has a neuronal signal function $f(x)$ of the form (5)-(9) because its respective drift term $b(t, X_t)$ in (3) is globally Lipschitz in accord with (15)-(16). For example:

$$b(t, X_t) = -X_t + 2 \tanh(X_t) + S_t \quad (20)$$

for the bistable potential neuron. Then $b'(t, X_t) = -1 + 2 \tanh^2(X_t)$ and so $b(t, X_t)$ is $C^1(\mathbf{R})$. Now $Z_t > Y_t$ holds without loss of generality. Then the mean-value theorem gives $|b(t, Z_t) - b(t, Y_t)| = |b'(\xi_t)||Z_t - Y_t|$ for some $\xi_t \in (Y_t, Z_t)$. Thus $b(t, X_t)$ satisfies the global Lipschitz condition because $b'(X_t)$ is bounded on \mathbf{R} . The linear-threshold neuron model gives

$$b(t, X_t) = -X_t + f(X_t) + S_t \quad (21)$$

where

$$f(X_t) = \begin{cases} cX_t & |cX_t| < 1 \\ 1 & cX_t > 1 \\ -1 & cX_t < -1 \end{cases} \quad (22)$$

for constant $c > 0$. Then $|b(t, Z_t) - b(t, Y_t)| \leq (1+c)|Z_t - Y_t|$ for all $Z_t, Y_t \in \mathbf{R}$. Thus $b(t, X_t)$ satisfies the global Lipschitz condition.

We now use Lemma 1 to prove a sufficient interval condition for the SR effect in the continuous neuron models (3)-(4) and (5)-(9). Lack of a necessary condition broadens rather than lessens the scope of potential SR effects in the neurons. The proof structure follows that of the 'forbidden interval' theorems [24], [25], [33]. The proof strategy is that *what goes down must go up*. The proof assumes that the nonnegative mutual information is positive for some level of input-output correlation. Then the mutual information goes to zero as the noise variance goes to zero. Hence the mutual information must increase as the noise variance or standard deviation increases from zero—and thus a noise benefit must occur.

Theorem 1: Suppose that continuous neuron models (3)-(4) and (5)-(9) have additive Gaussian white noise with mean $E(n)$ and variance σ^2 and that the input signal $S(t) \in \{s_1, s_2\}$ is subthreshold: $\theta_1 \leq s_1 < s_2 \leq \theta_2$. Suppose that there is some statistical dependence between the input random variable S and the output random variable Y so that $I(S, Y) > 0$. Then the neuron models (3)-(4) and (5)-(9) exhibit the nonmonotone SR effect in the sense that $I(S, Y) \rightarrow 0$ as $\sigma \rightarrow 0$ if $\theta_1 - s_1 \leq E(n) \leq \theta_2 - s_2$.

Proof: Let $\sigma_1, \sigma_2, \dots$ be any decreasing sequence of noise standard deviations such that $\lim_{n \rightarrow \infty} \sigma_n = 0$. Define X_t^n and Y_t^n as solution processes of the equations (3)-(4) with noise standard deviation σ_n instead of σ .

Suppose that $E(n) \neq 0$. We can absorb $E(n)$ into the input signal S because the noise n is additive in the neuron models (3)-(4). Then the new input signal $S' = S + E(n)$ and S' is subthreshold ($\theta_1 \leq S' \leq \theta_2$) if and only if $\theta_1 - s_1 \leq E(n) \leq \theta_2 - s_2$. So we can let $S \in \{s_1, s_2\}$ be subthreshold without loss of generality.

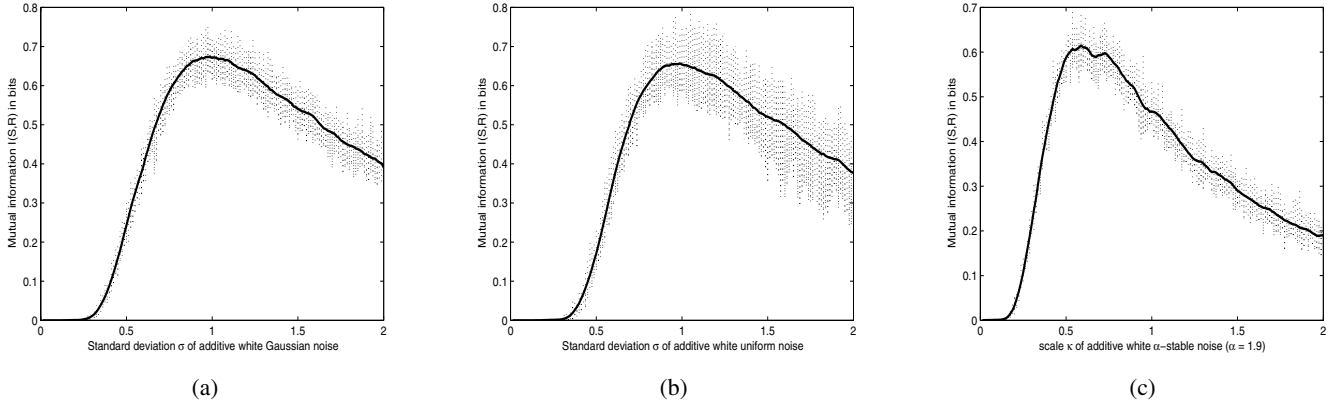


Fig. 2. SR Noise benefits in noisy continuous neurons: finite-variance and infinite-variance cases. Noise increases the mutual information of the bistable potential neuron (1)-(2) and (6). The graphs show the nonmonotonic signatures of SR for the bipolar input signal $s_t = \pm 0.35$. The additive noise are (a) Gaussian, (b) uniform, and (c) symmetric α -stable noise with $\alpha = 1.9$ (thick-tailed bell curve with infinite-variance [16]). The dashed vertical lines show the total min-max deviations of the mutual information in 100 simulation trials.

Let the symbol ‘0’ denote the input signal $S = s_1$ and the output signal $Y = -1$. Let the symbol ‘1’ denote the input signal $S = s_2$ and the output signal $Y = 1$. Assume that $0 < P_S(s) < 1$ to avoid triviality when $P_S(s) = 0$ or 1. We show that S and Y are asymptotically independent: $I(S, Y) = 0$ if and only if S and Y are statistically independent [7]. So we need to show only that $P_{SY}(s, y) = P_S(s)P_Y(y)$ or $P_{Y|S}(y|s) = P_Y(y)$ as $\sigma \rightarrow 0$ for signal symbols $s \in S$ and $y \in Y$. The two symbol alphabet set S gives

$$\begin{aligned}
 P_Y(y) &= \sum_s P_{Y|S}(y|s)P_S(s) \\
 &= P_{Y|S}(y|0)P_S(0) + P_{Y|S}(y|1)P_S(1) \\
 &= P_{Y|S}(y|0)P_S(0) + P_{Y|S}(y|1)(1 - P_S(0)) \\
 &= (P_{Y|S}(y|0) - P_{Y|S}(y|1))P_S(0) + P_{Y|S}(y|1)
 \end{aligned}$$

So we need to show only that $P_{Y|S}(y|0) - P_{Y|S}(y|1) = 0$ as $\sigma \rightarrow 0$. This condition implies that $P_Y(y) = P_{Y|S}(y|1)$ and $P_Y(y) = P_{Y|S}(y|0)$. We prove the case for $y = 0$ only: $\lim_{\sigma \rightarrow 0} \{P_{Y|S}(0|0) - P_{Y|S}(0|1)\} = 0$ since the proof for $y = 1$ is similar. Note that

$$\begin{aligned}
 &\lim_{\sigma \rightarrow 0} \{P_{Y|S}(0|0) - P_{Y|S}(0|1)\} \\
 &= \lim_{n \rightarrow \infty} \{P_{Y^n|S}(0|0) - P_{Y^n|S}(0|1)\} \\
 &= \lim_{n \rightarrow \infty} P_{Y^n|S}(0|0) - \lim_{n \rightarrow \infty} P_{Y^n|S}(0|1) \\
 &= \lim_{n \rightarrow \infty} P[Y^n = 0|S = 0] - \lim_{n \rightarrow \infty} P[Y^n = 0|S = 1] \\
 &= \lim_{n \rightarrow \infty} P[X_t^n < 0|S = 0] \\
 &\quad - \lim_{n \rightarrow \infty} P[X_t^n < 0|S = 1] \text{ for } t \gg 0 \\
 &= \lim_{n \rightarrow \infty} \{P[X_t^n < 0, \hat{X}_t < 0|S = 0] \\
 &\quad + P[X_t^n < 0, \hat{X}_t > 0|S = 0]\} \\
 &\quad - \lim_{n \rightarrow \infty} \{P[X_t^n > 0, \hat{X}_t < 0|S = 1] \\
 &\quad - P[X_t^n > 0, \hat{X}_t > 0|S = 1]\} \\
 &\quad \text{for large values of } t
 \end{aligned}$$

$$\begin{aligned}
 &= \lim_{n \rightarrow \infty} \{P[X_t^n < 0|\hat{X}_t < 0, S = 0]P[\hat{X}_t < 0|S = 0] \\
 &\quad + P[X_t^n < 0|\hat{X}_t > 0, S = 0]P[\hat{X}_t > 0|S = 0]\} \\
 &\quad - \lim_{n \rightarrow \infty} \{P[X_t^n > 0|\hat{X}_t < 0, S = 1]P[\hat{X}_t < 0|S = 1] \\
 &\quad - P[X_t^n > 0|\hat{X}_t > 0, S = 1]P[\hat{X}_t > 0|S = 1]\} \\
 &\quad \text{for large values of } t \\
 &= \{1 \cdot \frac{1}{2} + 0 \cdot \frac{1}{2}\} - \{0 \cdot \frac{1}{2} + 1 \cdot \frac{1}{2}\} \\
 &\quad \text{by Lemma 1 and the assumption that} \\
 &\quad P[\hat{X}_t < 0|S = s_i] = P[\hat{X}_t > 0|S = s_i] \\
 &\quad = 1/2 \text{ for } i = 1, 2. \\
 &= 0
 \end{aligned}$$

Q.E.D.

Figure 2(a) shows a simulation instance of Theorem 1 for additive white Gaussian noise. Small amounts of additive noise in a bistable potential neuron model produce the SR effect in terms of the noise-enhanced Shannon mutual information $I(S, Y)$ between realizations of a random (Bernoulli) bipolar input signal S and the neuron’s thresholded output random variable Y . The SR effects in Figure 2 (b) and (c) lie beyond the scope of Theorem 1 because they show that the SR effect still occurs for other finite-variance non-Gaussian noise such as uniform noise and for infinite-variance alpha-stable noise [16], [23], [25], [35], [36].

III. STOCHASTIC RESONANCE IN FHN SPIKING NEURONS

We first review the dynamics of the FitzHugh-Nagumo (FHN) neuron model for subthreshold input signals. We then use Lemma 2 to prove Theorem 2. This direct proof avoids the firing-rate approximation that we used in an earlier version of the theorem [33]. Theorem 2 gives only a sufficient interval condition for the SR noise benefit in the FHN neuron.

So SR can still occur when the noise mean violates the interval condition.

The FHN neuron model [5], [11], [14], [32] is a two-dimensional simplification of the Hodgkin and Huxley neuron model [17]. It describes the response of a so-called Type II excitable system [14], [27] that undergoes a Hopf bifurcation. The system first resides in the stable rest state for subthreshold inputs as do multistable systems. Then the system leaves the stable state in response to a strong input but returns to it after passing through firing and refractory states in a manner quite unlike the behavior of multistable systems. The FHN neuron model is a limit-cycle oscillator of the form

$$\epsilon \dot{x} = -x(x^2 - \frac{1}{4}) - w + A + s(t) + n(t) \quad (23)$$

$$\dot{w} = x - w \quad (24)$$

where $x(t)$ is a fast (voltage) variable, $w(t)$ is slow (recovery) variable, A is a constant (tonic) activation signal, and $\epsilon = 0.005$. $n(t)$ is Gaussian white noise and $s(t)$ is a subthreshold input signal—either s_1 or s_2 . We measure the neuron's response to the input signal $s(t)$ in terms of the transition (firing) rate $r(t)$.

The intersection of the cubic nullcline $w = x(x^2 - 1/4) + A + s(t)$ with a linear nullcline $w = x$ gives the location of the system's fixed-point attractor because $\dot{w} = 0$ and $\dot{x} = 0$ at the fixed point. The (x, w) -phase plane shows that the FHN neuron model performs relaxation oscillations when the fixed point lies between the first minimum and the first maximum of the cubic nullcline. So the threshold occurs when the linear nullcline intersects the cubic nullcline at the minimum. The cubic nullcline has a minimum at $x = -1/(2\sqrt{3})$ and so it does not depend on $A + s(t)$. The term $A + s(t)$ shifts the cubic nullcline in the vertical direction and hence it controls the location of the fixed point. The fixed point occurs at the minimum of the cubic nullcline if $A + s(t) = -5/(12\sqrt{3}) \equiv A_T$. So the fixed point occurs between the first minimum and maximum of the cubic nullcline when $A + s(t) > A_T$. Then the FHN model exhibits relaxation oscillations.

We can rewrite (23)-(24) as

$$\epsilon \dot{x} = -x(x^2 - \frac{1}{4}) - w + A_T - (B - s(t)) + n(t) \quad (25)$$

$$\dot{w} = x - w \quad (26)$$

where B is a positive constant parameter that corresponds to the distance that the input signal $s(t)$ must overcome to cross the threshold. Then $B - s(t)$ is the signal-to-threshold distance and so $s(t)$ is subthreshold when $B - s(t) > 0$. We chose $B = 0.007$ in simulations and hence $A = -(5/(12\sqrt{3} + 0.007))$.

Let $x_i = H_{F_i}$ denote the stable fixed point that corresponds to the subthreshold signal s_i . Then x_i is a solution of $x(x^2 - \frac{1}{4}) - w + A_T - (B - s_i) = 0$ and it depends on s_i . Note that x is a fast variable and w is a slow variable for $\epsilon \ll 1$. So we assume $\dot{w} \sim 0$ and $w \sim x = x_i$. Then the escape from

the fixed-point x_i is "quasi" one-dimensional along x and (25) reduces to the double-well barrier-escape problem [5]. The corresponding double-well potential function has three roots x_i, u_i , and v_i . If the system state is at x_i then it needs to surmount u_i to get to v_i . Once it reaches the state v_i then it returns to x_i through the w degree of freedom.

The deterministic FHN model ($n(t) \equiv 0$ in (25)) performs relaxation oscillations and its action potential $x(t)$ is bounded between 0.6 and -0.6. The system emits a spike whenever $x(t)$ crosses the threshold value $\theta = 0$. We use a lowpass-filtered version of $x(t)$ to avoid false spike detections due to the additive noise.

We measure the mutual information between the input signal $s(t)$ and the FHN system response in terms of the output spike-rate random variable R :

$$R = \frac{N(t_1, t_2]}{t_2 - t_1} \quad (27)$$

for sufficiently large values of t_1 and t_2 . Here $N(t_1, t_2]$ is the number of spikes in the time interval $(t_1, t_2]$.

We rewrite equations (23)-(24) as

$$\dot{z}_1 = -\frac{z_1}{\epsilon}(z_1^2 - \frac{1}{4}) - \frac{z_2}{\epsilon} + \frac{A}{\epsilon} + \frac{s(t)}{\epsilon} + \frac{n(t)}{\epsilon} \quad (28)$$

$$\dot{z}_2 = z_1 - z_2. \quad (29)$$

Here $z_1 = x$ and $z_2 = w$. The corresponding matrix Ito stochastic differential equation is

$$dZ_t = b(t, Z_t)dt + \sigma dB_t \quad (30)$$

where $Z_t = (z_{1,t}, z_{2,t})^T$, $B_t = (B_{1,t}, B_{2,t})^T$,

$$b(t, Z_t) = \begin{bmatrix} b_1(z_{1,t}, z_{2,t}) \\ b_2(z_{1,t}, z_{2,t}) \end{bmatrix} \\ = \begin{bmatrix} \frac{z_{1,t}}{\epsilon}(z_{1,t} - \frac{1}{4}) - \frac{z_{2,t}}{\epsilon} + \frac{A}{\epsilon} + \frac{s_t}{\epsilon} \\ z_{1,t} - z_{2,t} \end{bmatrix}, \\ Z_t = \begin{bmatrix} z_{1,t} \\ z_{2,t} \end{bmatrix}, \text{ and } \sigma = \begin{bmatrix} \frac{\sigma}{\epsilon} & 0 \\ 0 & 0 \end{bmatrix}.$$

The drift term $b(t, Z_t)$ in (30) is locally Lipschitz but not globally Lipschitz. So Lemma 1 does *not* apply to the FHN neuron. But Lemma 2 extends the conclusion of Lemma 1 to the locally Lipschitz drift term $b(t, Z_t)$.

Lemma 2: Let $b : \mathbf{R}^+ \times \mathbf{R}^n \rightarrow \mathbf{R}^n$ and $\sigma : \mathbf{R}^n \times \mathbf{R}^m \rightarrow \mathbf{R}^n$ in (3) be measurable functions that satisfy

$$\sum_{i=1}^n \{2x_i b_i(t, x) + a_{ii}(t, x)\} \leq K(1 + \|x\|^2) \quad (31)$$

for every $x \in \mathbf{R}^n$ and a local Lipschitz condition

$$\|\sigma_{ij}(t, x) - \sigma_{ij}(t, y)\| \leq G_r \|x - y\|, \quad (32)$$

$$\|b_i(t, x) - b_i(t, y)\| \leq D_r \|x - y\| \quad (33)$$

when $\|x\|, \|y\| \leq r$. Here $a = \sigma\sigma^T$ and $\|x\|^2 = x^T x$.

Suppose $dX_t = b(t, X_t)dt + \sigma dB_t \quad (34)$

$$d\hat{X}_t = b(t, \hat{X}_t)dt \quad (35)$$

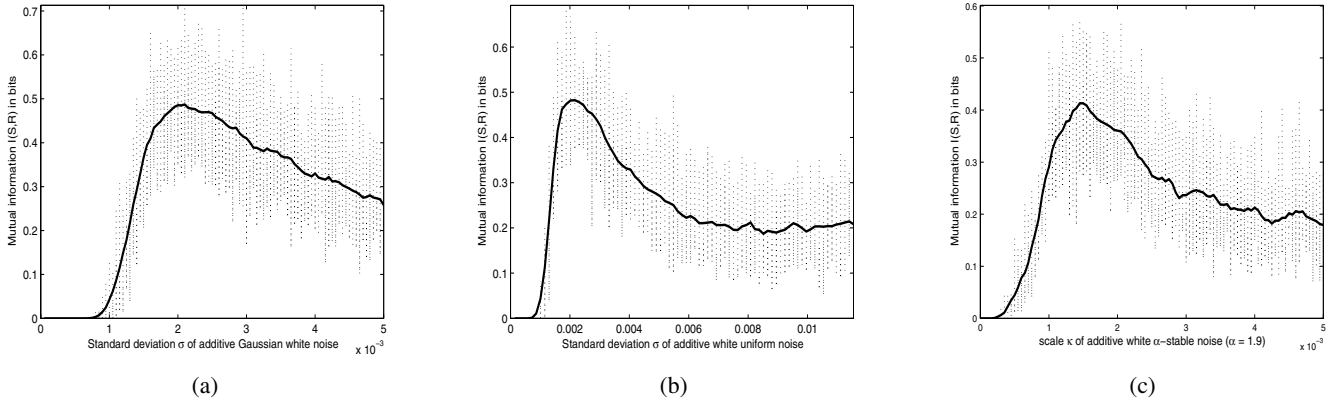


Fig. 3. SR Stochastic resonance in the FHN spiking neuron model (25)-(26). The additive noise are (a) Gaussian, (b) uniform, and (c) symmetric α -stable noise with $\alpha = 1.9$ (thick-tailed bell curve with infinite-variance [16]).

Then for every $T \in \mathbf{R}^+$ and for every $\varepsilon > 0$:

$$E[\sup_{0 \leq t \leq T} \|X_t - \hat{X}_t\| > \varepsilon] \rightarrow 0 \quad \text{as } \sigma \rightarrow 0$$

and hence

$$P[\sup_{0 \leq t \leq T} \|X_t - \hat{X}_t\| > \varepsilon] \rightarrow 0 \quad \text{as } \sigma \rightarrow 0. \quad (36)$$

We can now state and prove Theorem 2.

Theorem 2: Suppose that the FHN neuron system (30) has an additive Gaussian white noise $n(t)$ with mean $E(n)$ and that the input signal $S(t) \in \{s_1, s_2\}$ is subthreshold: $S(t) < B$. Suppose that there is some statistical dependence between the input random variable S and the output spike-rate random variable R so that $I(S, R) > 0$. Then the FHN neuron model (30) exhibits the nonmonotone SR effect in the sense that $I(S, R) \rightarrow 0$ as $\sigma \rightarrow 0$ if $E(n) < B - s_2$.

Proof: Let $\sigma_1, \sigma_2, \dots$ be any decreasing sequence of noise standard deviations such that $\lim_{n \rightarrow \infty} \sigma_n = 0$. Define Z_t^n as a solution process of (37) with noise standard deviation σ_n instead of σ and let R^n be the corresponding output spike-rate random variable.

We can absorb $E(n)$ into the input signal $S(t)$ because the noise n is additive in the spiking neuron model. Then the new input signal is $S' = S + E(n)$ and S' is subthreshold ($S' < B$) because $E(n) < B - s_2$ where $s_2 = \max\{s_1, s_2\}$. So we can assume that $E(n) = 0$ holds without loss of generality.

Recall that $I(S, R) = 0$ if and only if S and R are statistically independent [7]. So we need to show only that $f_{SR}(s, r) = P_S(s)f_R(r)$ or $f_{R|S}(r|s) = f_R(r)$ as $\sigma \rightarrow 0$ for signal symbols $s \in \{s_1, s_2\}$ and for all $r \geq 0$ where f_{SR} is the joint probability density function and $f_{S|R}$ is the conditional density function. This is logically equivalent to $F_{R|S} = F_R$ as $\sigma \rightarrow 0$ where $F_{R|S}$ is the conditional distribution function [10]. The elementary theorem on total

probability and the two-symbol alphabet set $\{s_1, s_2\}$ give

$$\begin{aligned} F_R(r) &= \sum_s F_{R|S}(r|s)P_S(s) \\ &= F_{R|S}(r|s_1)P_S(s_1) + F_{R|S}(r|s_2)P_S(s_2) \\ &= F_{R|S}(r|s_1)P_S(s_1) + F_{R|S}(r|s_2)(1 - P_S(s_1)) \\ &= (F_{R|S}(r|s_1) - F_{R|S}(r|s_2))P_S(s_1) + F_{R|S}(r|s_2) \end{aligned}$$

So we need to show that for all $r \geq 0$:

$$F_{R|S}(r|s_1) - F_{R|S}(r|s_2) \rightarrow 0 \quad \text{as } \sigma \rightarrow 0.$$

This holds if and only if

$$P[R > r|S = s_2] - P[R > r|S = s_1] \rightarrow 0 \quad \text{as } \sigma \rightarrow 0.$$

We prove that $\lim_{\sigma \rightarrow 0} P[R > r|S = s_i] = 0$ for $i = 1$ and 2. Note that if $r > 0$ for (30) then $Z_{1,t}^n$ must cross the firing or spike threshold θ . Then

$$P[R^n > r|S = s_i] \leq P[\sup_{t_1 \leq t \leq t_2} Z_{1,t}^n > \theta|S = s_i]$$

and hence

$$\begin{aligned} \lim_{\sigma \rightarrow 0} P[R > r|S = s_i] &= \lim_{n \rightarrow \infty} P[R^n > r|S = s_2] \\ &\leq \lim_{n \rightarrow \infty} P[\sup_{t_1 \leq t \leq t_2} Z_{1,t}^n > \theta|S = s_i] \\ &= \lim_{n \rightarrow \infty} P[\sup_{t_1 \leq t \leq t_2} Z_{1,t}^n > \theta, \hat{Z}_{1,t} < \theta|S = s_i] \\ &\quad \text{because } \hat{Z}_{1,t} \text{ converges to the FHN} \\ &\quad \text{fixed-point } H_{F_i} < \theta \text{ for large } t \\ &= 0 \quad \text{by Lemma 2.} \end{aligned}$$

Q.E.D.

Figure 3 (a) shows a simulation instance of the SR effect in Theorem 2 for the FHN neuron model (25)-(26) with additive white Gaussian noise. The model parameters are $A_T = -5/12(\sqrt{3})$, $B = 0.07$, and $S = \pm 0.004$. The solid curve shows the smoothed average mutual information. The dashed vertical lines show the total min-max deviations

of the mutual information in 100 simulation trials. The mutual-information plot shows the predicted nonmonotonic signature of SR. Theorem 2 applies to additive white Gaussian noise although Figure 3 (b) and (c) confirm a comparable noise benefit for uniform noise and impulsive infinite-variance α -stable noise.

Simulations of the continuous-time dynamical systems require a suitable time-discretization method. We used the Euler-Maruyama scheme [13], [20] to obtain the discrete stochastic form:

$$\begin{aligned}x_{t+1} &= x_t + \Delta T \left(f(x_t) + s_t \right) + \sigma \sqrt{\Delta T} w_t \\ y_t &= g(x_t)\end{aligned}$$

for $t = 0, 1, 2, \dots$ and initial condition x_0 . The input sample s_t equalled the signal $s(t\Delta T)$ at time step t . The zero-mean white Gaussian noise sequence w_t had unit variance $\sigma_w^2 = 1$ and σ was the standard deviation of the additive white Gaussian noise $n(t)$ in (1). The term $\sqrt{\Delta T}$ scales w_t so that $\sqrt{\Delta T}w_t$ conforms with the Wiener increment [13], [20], [31]. The output sample y_t is some transformation g of the system's state x_t . This algorithm gives fairly accurate results for several nonlinear systems [13], [20], [28], [31].

IV. CONCLUSION

We have shown that our earlier sufficient conditions for noise benefits in neuron models persist for continuous neuron models cast as formal stochastic differential equations. A sufficient condition also holds for the FHN spiking neuron model and does not require the earlier firing-rate approximation [33]. But a severe restriction of the Ito model is that the additive noise is Gaussian. The earlier theorems hold for much broader classes of noise both with arbitrary finite-variance noise and with infinite-variance impulsive noise from the general class of stable distributions [16], [23], [25], [35], [36]. Simulation evidence suggests that some form of Theorems 1 and 2 should hold for (stable) Levy processes and other types of non-Gaussian noise.

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