

## Effects of Colored Noise on Stochastic Resonance in Sensory Neurons

Daichi Nozaki,<sup>1</sup> Douglas J. Mar,<sup>1</sup> Peter Grigg,<sup>2</sup> and James J. Collins<sup>1</sup>

<sup>1</sup>Center for BioDynamics and Department of Biomedical Engineering,  
Boston University, 44 Cummington Street, Boston, Massachusetts 02215

<sup>2</sup>Department of Physiology, University of Massachusetts Medical Center, Worcester, Massachusetts 01655  
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Noise can assist neurons in the detection of weak signals via a mechanism known as stochastic resonance (SR). We demonstrate experimentally that SR-type effects can be obtained in rat sensory neurons with white noise,  $1/f$  noise, or  $1/f^2$  noise. For low-frequency input noise, we show that the optimal noise intensity is the lowest and the output signal-to-noise ratio the highest for conventional white noise. We also show that under certain circumstances,  $1/f$  noise can be better than white noise for enhancing the response of a neuron to a weak signal. We present a theory to account for these results and discuss the biological implications of  $1/f$  noise. [S0031-9007(99)08727-X]

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It has recently been recognized that noise can enhance the response of nonlinear systems to weak signals. With this phenomenon, which is known as stochastic resonance (SR), the flow of information through a system is maximized when the input noise intensity is set to a certain value [1]. This concept is particularly interesting for neurobiological systems, because SR may provide a mechanism for such systems to detect and process weak signals [2].

In the majority of SR studies, the additive noise is spectrally flat (i.e., white) with either zero or weak (short) time correlations. However, colored noise with a  $1/f^\beta$  power spectrum has been observed in many biological systems [3]. In several cases, the value of  $\beta$  was found to be nearly equal to 1. Although there are various mechanisms proposed for the origin of this type of noise [4], its functional significance in biological systems remains unclear. A natural question arises as to whether  $1/f^\beta$  noise can play a significant role in the context of SR. In previous works, we have shown that  $1/f^\beta$  noise can induce SR in a FitzHugh-Nagumo (FHN) model neuron and that the optimal noise variance depends on the value of  $\beta$  [5,6].

In this Letter, we investigate whether or not  $1/f^\beta$  noise can be used for SR in an *in vitro* neuronal sensory system, and we examine how the value of  $\beta$  affects the SR profile. Specifically, we show that the spectral type of noise can affect the peak value of the output signal-to-noise ratio (SNR) and the location of the optimal noise variance. We also describe a theory, using the linearized FHN model introduced in Ref. [5], to account for these effects.

Studies were conducted on cutaneous afferents in rat skin using the experimental setup (Fig. 1) from Ref. [7]. A section of hairy skin was excised from the medial aspect of the upper thigh of a rat; its sensory innervation, a branch of the saphenous nerve, was kept intact. We recorded the occurrence times of the action potentials of the nerve while the patch was subjected to uniaxial stretch

stimuli using a linear actuator operated under position control. The stretch stimuli consisted of the sum of a sine wave (3 Hz) and noise of varying intensity and spectral type. Three different types of noise were applied: white noise ( $\beta = 0$ ),  $1/f$  noise ( $\beta = 1$ ), and  $1/f^2$  noise ( $\beta = 2$ ) [8]. The actuator is limited to frequencies below approximately 80 Hz, and the noise bandwidth is taken to be 0.02–40 Hz. The duration of each stimulus trial was at least 50 s and the intertrial time was 70 s.

For each neuron, we first confirmed that the noise-free sine wave was a subthreshold stimulus. Signals with additive noise were then applied to the skin and the resulting neuronal response was recorded. The order of trials was randomized to mitigate adaptation effects.

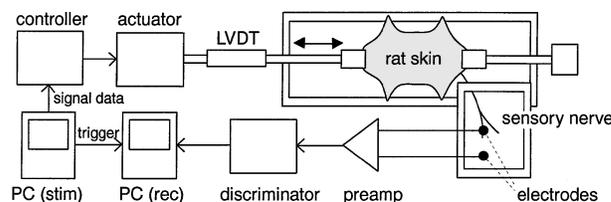


FIG. 1. Schematic diagram of the experimental setup. A 5 mm  $\times$  20 mm specimen of hairy skin from the hindlimb of an adult rat, depilated using Nair, was removed with its sensory innervation, a branch of the saphenous nerve, intact. The specimen was positioned in a Lucite chamber filled with gassed (95% O<sub>2</sub>, 5% CO<sub>2</sub>) rat interstitial fluid at room temperature. The skin was held by two 5-mm-wide clamps, through which the stretch stimuli were applied. One clamp was fixed while the other was coupled to a Ling 203 linear actuator via a linear variable differential transformer. The actuator was position controlled through a feedback system. Control signals were generated on a computer. The nerve was positioned in an adjoining oil-filled chamber. Extracellular signals from the nerve were recorded via fine gold-wire electrodes and amplified using a PAR113 preamplifier. Action potential responses were discriminated using a template-matching algorithm (Signal Processing Systems, Prospect, Australia) and their firing times were recorded.

By repeating the noise-free sine-wave input stimulus at regular intervals, we confirmed that the periodic input to each neuron was maintained at a subthreshold level throughout the course of the experiment [9]. Data were obtained from 12 neurons from four different animals. Figure 2 shows a typical time series of the input stimuli and the resulting neuronal spike train. We calculated the power spectral density (PSD) of each spike train and computed the output SNR as the ratio of the peak amplitude of the PSD at 3 Hz (the input signal frequency) to the level of the background noise at that frequency (Fig. 2).

The SR profiles—output SNR versus input noise variance  $\sigma_N^2$ —for four neurons are shown in Fig. 3. For all 12 neurons tested, we observed a maximum in the output SNR curve for both conventional white noise and  $1/f$  noise. For  $1/f^2$  noise, we found an increase in the output SNR with the addition of noise, but a clear peak in the output SNR was not discernible, with the exception of one neuron. For all 12 neurons tested, we also found that the maximal output SNR value was larger and the corresponding noise level was smaller for white noise than for  $1/f$  noise and  $1/f^2$  noise (see Fig. 3). However, as shown for neurons #2–#4 in Fig. 3, there can be a range of noise variance for which the output SNR for  $1/f$  noise is significantly larger than that for white noise of corresponding intensity. For  $1/f^2$  noise, the output SNR was much smaller than that for white noise and  $1/f$  noise, respectively, over the entire range of noise variances used.

Although the optimal noise variance for  $1/f^2$  noise is not shown in Fig. 3, the data suggest that it may be located at a value larger than those shown in Fig. 3. Hence, as the value of  $\beta$  increases, the optimal noise

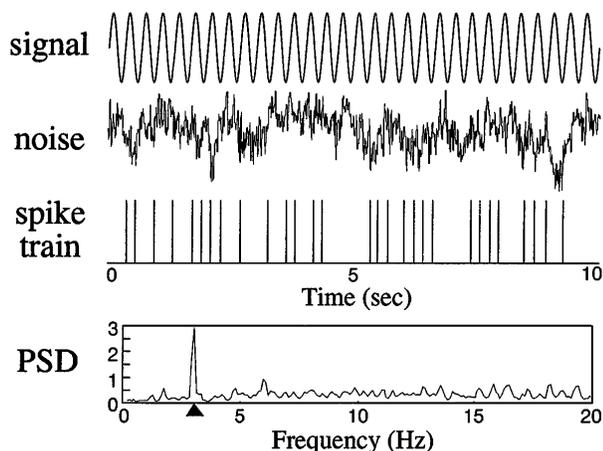


FIG. 2. Typical time traces of the input periodic signal and noise stimuli ( $1/f$  noise) and the corresponding spike train from a sensory neuron. The PSD of the spike train is calculated and the output SNR is computed as the ratio of the peak amplitude of the PSD at the input signal frequency (marked by the solid triangle on the frequency axis) to the level of the background noise at that frequency.

variance may shift to larger values. In previous work [6], the optimal noise variance was shown to be independent of the value of  $\beta$  in nondynamical systems, where a characteristic firing event is generated when the sum of noise and signal crosses a threshold value. Our observation that the optimal noise variance varies with  $\beta$  suggests a dynamical origin.

In Ref. [5], we derived the theoretical SR profile of the cross-power measure between a slowly varying aperiodic input signal and the output firing response of a linearized FHN model neuron. Here we extend the theory to estimate the effect of  $\beta$  on the SR profile of the SNR. The linearized FHN model has dynamics represented by [5],

$$\varepsilon \dot{v} = -\gamma v - w + A \sin(2\pi f_0 t) + \xi(t), \quad (1)$$

$$\dot{w} = v - w, \quad (2)$$

where  $v$  is a fast variable representing the neuron membrane voltage,  $w$  is a slow variable,  $\xi(t)$  is a noise term,  $\varepsilon$  is a constant ( $\varepsilon \ll 1$ ), and the sinusoidal term represents the weak input signal. In this system, the cubic term in the original FHN model is approximated as  $-\gamma v$  by linearization at the fixed points. This model describes only the subthreshold dynamics of the membrane voltage and does not have any mechanism for generating action potentials. Hence, we assume that the model generates an action potential whenever  $v$  increases past a threshold  $\theta$ . Both  $v$  and  $w$ , respectively, are then reset to some arbitrary values. This reset event leads to a refractory period of duration  $T_R$ .

Since the linearized FHN model has essentially linear dynamics, one can easily calculate the frequency response function  $\chi_v \xi(\omega)$ . When the input is taken to be  $\xi(t)$  (with

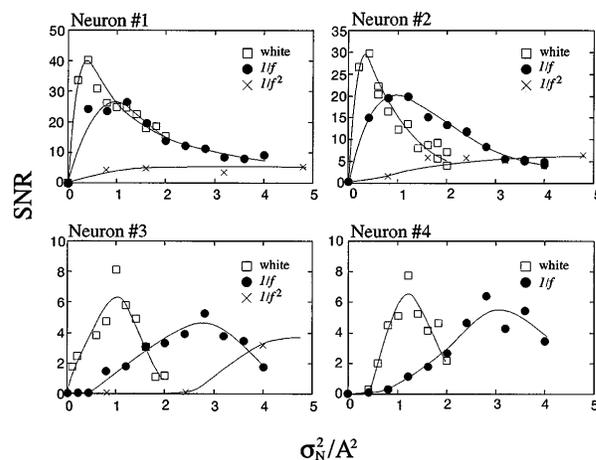


FIG. 3. Plots of output SNR versus input noise variance  $\sigma_N^2$  for white noise,  $1/f$  noise, and  $1/f^2$  noise, as measured for four different neurons. The noise variance  $\sigma_N^2$  is presented in units of the squared amplitude  $A^2$  of the input sine wave. Trials with  $1/f^2$  noise were not conducted for neuron #4. Solid lines are drawn to guide the eye.

no periodic input signal, i.e.,  $A = 0$ ) and the output is taken to be  $v$ , then

$$|\chi_{v\xi}(\omega)|^2 = \frac{(\omega^2 + 1)^2}{[\gamma(\omega^2 + 1) + 1]^2 + \omega^2[\varepsilon(\omega^2 + 1) - 1]^2}, \quad (3)$$

where  $\omega = 2\pi f$ . This function is used to derive the following expression for the zero-input firing rate  $R_0$ :

$$R_0 = 2r_0/(1 + 2T_R r_0), \quad (4)$$

where  $r_0$  represents the frequency that  $v$  crosses  $\theta$ , when the resetting events are not considered [5]. The rate  $r_0$  is obtained from Rice's theory [10] as

$$r_0 = g(\beta) \exp\{-\theta^2/[2h(\beta)\sigma_N^2]\}, \quad (5)$$

where  $g(\beta) = (\int_{f_l}^{f_h} f^{-\beta+2} |\chi_{v\xi}(\omega)|^2 df / \int_{f_l}^{f_h} f^{-\beta} \times |\chi_{v\xi}(\omega)|^2 df)^{1/2}$  and  $h(\beta) = \int_{f_l}^{f_h} f^{-\beta} |\chi_{v\xi}(\omega)|^2 df / \int_{f_l}^{f_h} f^{-\beta} df$ , where  $f_l$  and  $f_h$ , respectively, are the lower and upper limits of the noise bandwidth. Here  $g(\beta)$  is related to the power of the time derivative of  $v$  [10], and  $h(\beta)$  represents the ratio of the power transmitted from the noise to  $v$  [5].

Next, we apply the theory from Ref. [11] which was used to estimate the output SNR in nondynamical systems driven by colored noise. When the input sine wave is slower than the characteristic time of the system,  $\theta$  in Eq. (5) is modulated as  $\theta - [A \sin(2\pi f_0 t)/(1 + \gamma)]$ . Substituting this expression into Eq. (4) and expanding it in a Taylor series in  $A \sin(2\pi f_0 t)$  gives the time-dependent firing rate  $R(t)$ . When  $A/(1 + \gamma) \ll \theta$ , retaining only the lowest order term gives

$$R(t) \approx \frac{2r_0}{1 + 2T_R r_0} \left[ 1 + \frac{\theta A_\gamma \sin(2\pi f_0 t)}{\sigma_v^2 (1 + 2T_R r_0)} \right], \quad (6)$$

where  $\sigma_v^2 = h(\beta)\sigma_N^2$  and  $A_\gamma = A/(1 + \gamma)$ . The time-averaged value of the output pulse train  $U_{av}(t)$  is

$$U_{av}(t) = KR(t) = R(t), \quad (7)$$

where  $K$  is the area under an individual pulse which we set to unity without loss of generality. From Eqs. (6) and (7), we obtain the signal power at the input drive frequency  $f_0$  as

$$S = \frac{4A_\gamma^2 \theta^2 r_0^2}{\sigma_v^4 (1 + 2T_R r_0)^4}. \quad (8)$$

Assuming roughly that the sequence of pulses is more or less random [12], the PSD in the absence of a signal can be obtained using Campbell's theory [13] as  $N = K^2 R_0 = R_0$ . Hence, the  $\text{SNR} = S/N$  is

$$\text{SNR} = \frac{2A_\gamma^2 \theta^2 r_0}{h^2(\beta)\sigma_N^4 (1 + 2T_R r_0)^3}. \quad (9)$$

Figure 4 shows theoretical predictions of the SR profile given by Eq. (9). Figure 4(a) is similar to the

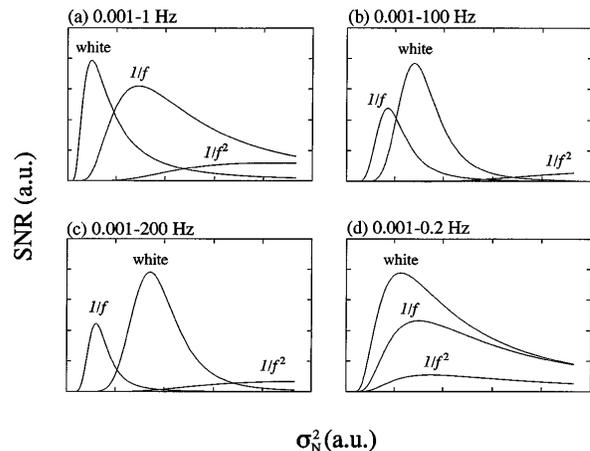


FIG. 4. Theoretical predictions of output SNR versus input noise variance as given by Eq. (9) for the linearized FHN model (with  $\varepsilon = 0.005$ ,  $\gamma = 0.3$ ,  $\theta = 0.03$ , and  $T_R = 0.67$ ). The values of  $g(\beta)$  and  $h(\beta)$  are calculated numerically. The two axes in each plot have arbitrary units. The bandwidth of the noise is 0.001–1 Hz (a), 0.001–100 Hz (b), 0.001–200 Hz (c), and 0.001–0.2 Hz (d). Note that the frequencies in the theory do not correspond quantitatively to those in the experiments.

experimental results in Fig. 3 (neurons #1 and #2, in particular) [14]. The theory can account qualitatively for the dependence of the optimal noise variance on the value of  $\beta$  and the relative peak values of the output SNR. Namely, as  $\beta$  increases so that the noise has stronger time correlations, the peak SNR decreases and the optimal noise intensity shifts toward higher values. A similar result has been previously reported in SR driven by Ornstein-Uhlenbeck processes [15], although the definition of noise intensity differs from ours. In Figs. 4(b) and 4(c), we see that  $1/f$  noise can be better (in the sense of requiring a smaller noise variance to achieve the peak output SNR) than white noise when the upper limit  $f_h$  of the noise bandwidth is sufficiently large. Figure 4(b) shows the theoretical prediction when  $f_h$  is increased to 100 Hz. In this case, the optimal noise variance is smaller for  $1/f$  noise, and  $1/f$  noise can realize a higher output SNR than white noise for small noise variance. As  $f_h$  is increased further, this effect becomes more prominent [see Fig. 4(c)]. Note, however, that the peak output SNR for white noise is always larger than that for  $1/f$  noise. Unfortunately, in our current experimental setup, situations such as those in Figs. 4(b) and 4(c) cannot be realized due to the limited bandwidth of the actuator. Finally, note that when  $f_h$  is small [Fig. 4(d)], the differences between the optimal noise variance become ambiguous and the output SNR for  $1/f$  noise is smaller than that for white noise over the entire range of noise variance.

In this Letter, we have shown that the input noise spectrum can dramatically affect the output SNR curve. Optimizing for various performance criteria, such as the peak output SNR value over a wide noise range, may

be achieved by different colors or types of noise. The optimal noise characteristics, including its spectrum, will depend critically on the dynamics of the system.

For the neurons in our experiment, one might consider white noise to be “better” than  $1/f$  noise for SR because the peak output SNR for white noise is larger and the optimal noise variance is smaller. However, our theory predicts that  $1/f$  noise may be better than white noise when the upper frequency limit of the noise is relatively high, because in that regime  $1/f$  noise can be used to detect subthreshold signals with a smaller noise level. Even when this is not the case, there still may be ranges of noise variance over which the output SNR is significantly greater for  $1/f$  noise than for white noise. Moreover, as shown in the experimental data of Fig. 3 and the theory in Fig. 4(a), such ranges may be significantly larger than the range over which white noise is superior.

The functional significance of  $1/f$  noise has not been fully elucidated in spite of its common occurrence in biological systems. Our experimental result that  $1/f$  noise can induce SR in neuronal systems *in vitro* suggests that this type of noise could be operative in neuronal systems *in vivo*. Our theoretical result that  $1/f$  noise can be better for SR when the noise bandwidth is sufficiently large may provide a novel explanation as to why  $1/f$  noise would be desirable for biological systems.

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