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Enhancement of stochastic resonance in a FitzHugh–Nagumo neuronal model driven by colored noise

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Abstract

We investigate the stochastic resonance in a FitzHugh–Nagumo neuronal model driven by colored noise with a $1/f^{\beta}$ spectrum $(0 \leqslant \beta \leqslant 2)$. A numerical simulation shows that the noise intensity needed to maximize the coherence between input and output signals is the smallest when $\beta \approx 1$. We also demonstrate analytically that this phenomenon is never seen in a nondynamical threshold system. © 1998 Elsevier Science B.V.

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1. Introduction

It has recently been recognized that stochastic noise can enhance the response of nonlinear systems to a weak signal [21,27]. Since the response is optimized by a particular level of noise intensity, this phenomenon is called "stochastic resonance (SR)" [21,27]. Originally, SR was proposed as a theoretical explanation why the ice-age occurred periodically [1]. After that, the phenomenon was widely observed for bistable physical systems experimentally and theoretically [18,22,27]. Much attention has also been paid to SR in sensory biology because neural systems have been shown to use SR to detect very weak signals that are otherwise undetectable [3–8,15,16,21,28]. According to Ref. [8], the sensory mechanoreceptors of crayfish can detect a very weak water movement of about 10 nm by adding noise. This surprising experimental result shed light on the possible beneficial role of noise in biological sensory systems.

In the majority of studies on SR, white noise without any time correlation has been used. With the increasing popularity of fractal theory [17], the existence of "colored noise" with a $1/f^{\beta}$ type power spectrum has been reported in many scientific areas. A question thus arises as to whether $1/f^{\beta}$ noise can play any functional role for SR. A partial answer was given by Kiss et al. [13] by showing that $1/f$ noise (i.e., $\beta \approx 1$) could be used as additive noise for SR in a physical system. However, how the color of noise (i.e., β) affects the response of nonlinear systems showing SR has, to our knowledge, never been reported.

In this Letter, we show that physical noise with a $1/f^{\beta}$ type power spectrum $(0 \leqslant \beta \leqslant 2)$ can also increase the response of a mathematical neuronal model to subthreshold signals regardless of the value of β.

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Furthermore, we report a novel finding that the noise intensity optimizing the response of this neuronal system is the smallest when $\beta \approx 1$.

Colored noise with a $1/f^{\beta}$ spectrum ($\beta \approx 1$) has been reported in the output of human nervous control systems including the autonomic nervous system [11,29,30] and the motor nervous system [2,23,24]. In spite of the possibility that $1/f$ noise might be needed in healthy physiological control systems [11], however, the functional significance of $1/f$ noise has not been fully elucidated. The results shown here might provide a novel explanation for why $1/f$ noise would be desirable for physiological control systems.

2. SR in neuronal model driven by colored noise

We consider a FitzHugh–Nagumo neuronal model (FHN model) with an aperiodic input signal added by stochastic noise,

$$\varepsilon \dot{v} = v(v-a)(1-v) - w + A_T - B + S(t) + \xi(t), \tag{1}$$

$$\dot{w} = v - w - b, \tag{2}$$

where $v(t)$ is a "fast" variable representing the membrane voltage of the neuron, $w(t)$ is a "slow" (recovery) variable, and $\varepsilon = 0.005$, $a = 0.5$, $b = 0.15$. The time constant ε determines the speed of the firing process, and the value of 0.005 is a commonly used one [3,4,16]. The A_T is a critical value (≈ 0.11) which makes the neuron fire periodically. The source term $S(t)$ is an aperiodic subthreshold signal with zero mean, and B is the distance between the mean signal level and A_T. The quantity $\xi(t)$ represents Gaussian $1/f^{\beta}$ noise ($0 \leqslant \beta \leqslant 2$) with zero mean and variance σ^2. When β is equal to 0, $\xi(t)$ reduces to the Gaussian white noise frequently used in SR studies. The system is the same as that used in Refs. [3,4] except for the use of $1/f^{\beta}$ noise.

The above system was integrated numerically using the fourth-order Runge–Kutta method ($\Delta t = 0.005$ s, total time 81.92 s, total number of data $(N) = 2^{14}$). The $1/f^{\beta}$ noise was generated by the following procedures [12,25]. The discrete version of $\xi(t)$ can be expressed by a Fourier series,

$$\xi(\mathrm{i}\Delta t) = \sum_{k=1}^{N/2} A_k \cos(2\pi \mathrm{i} k/N + \theta_k), \tag{3}$$

where θ_k is a random phase. The coefficient A_k is related to the power spectrum for wave number k by

$$P(k) = A_k^2/N. \tag{4}$$

We first generated the power spectrum of $\xi(t)$ with the power-law dependence

$$P(k) = k^{-\beta}. \tag{5}$$

Next, by combining Eqs. (4) and (5), the values of A_k were obtained by setting θ_k in Eq. (3) from a uniform random distribution on the interval $(0, 2\pi)$. Finally, the $1/f^{\beta}$ noise was derived using Eq. (3) before being transformed to have zero mean and predetermined variance (σ^2). Note that the physical $1/f^{\beta}$ noise obtained by these procedures is stationary with the upper and the lower limit of frequency (in our case, $1/N\Delta t$–$1/2\Delta t$ (i.e., 0.012–100) Hz).

The aperiodic signal $S(t)$ was obtained by convolving the Gaussian white noise with the Hanning window (window width 6 s). To evaluate the coherence between input and output signals, the cross power and the cross correlation measures were used as follows,

$$C_0 = \overline{S(t)R(t)}, \tag{6}$$

$$C_1 = \frac{C_0}{[\overline{S^2(t)}]^{1/2}\{\overline{[R(t) - \overline{R(t)}]^2}\}^{1/2}}, \tag{7}$$

where $R(t)$ is the mean firing rate of the neuron constructed by applying the unit-area symmetric Hanning window (window width 6 s) to the impulse train of action potentials (an action potential is defined as an event when $v(t)$ crosses 0.5 with positive slope), and the overbar denotes an average over time. In the original SR concept based on the power spectrum of output signals, C_0 corresponds to the cross power between input and output signals. C_1 is related to the signal to noise ratio. Note that C_1 is not proportional to the signal to noise ratio; however, there is an interrelation between them which can be characterized by a monotonic function.

Fig. 1 shows ensemble-averaged values for C_0 and C_1 (500 trials) with different levels of the noise variance σ^2 with $\beta = 0$, 1, and 2. Not only for white noise but also for $1/f$ noise and $1/f^2$ noise, there are

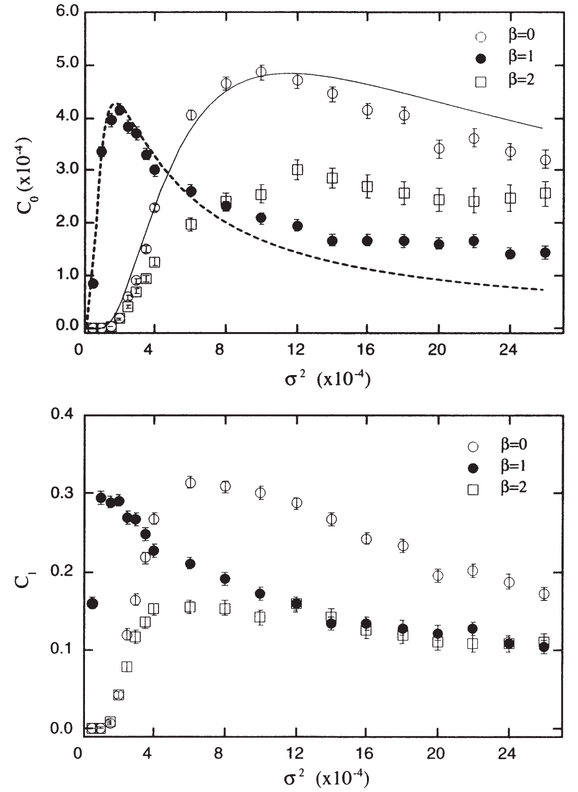

Fig. 1. Ensemble-averaged values and the standard errors for C_0 and C_1 (500 trials) in the FHN model with different levels of noise variance σ^2 (white noise: open circles, $1/f$ noise: filled circles, $1/f^2$ noise: squares). The variance of $S(t)$ was 5.0×10^{-5} and the signal to threshold distance B was 0.07. The solid line is the theoretical prediction for white noise by Ref. [3]. The broken line is a modified version of the theoretical curve for $1/f$ noise (see text).

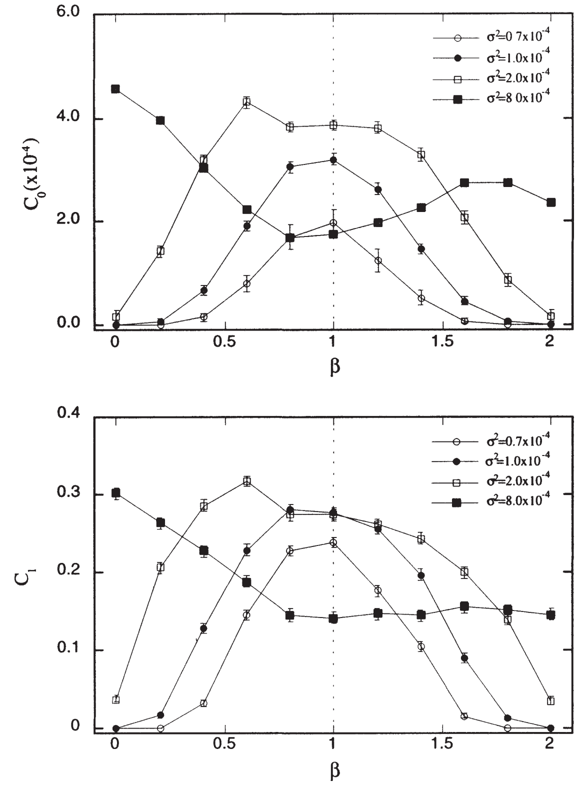

Fig. 2. Ensemble-averaged values and the standard errors for C_0 and C_1 (500 trials) in the FHN model with different levels of β. The values for $\overline{S(t)^2}$ and B are the same as those used in Fig. 1. When σ^2 is sufficiently small, the values for $\langle C_0 \rangle$ and $\langle C_1 \rangle$ are maximal when $\beta \approx 1$.

typical characteristics of SR with an optimal intensity of noise maximizing the coherence between $S(t)$ and $R(t)$. The SR-type behavior was also observed when other values for β, B and $\overline{S(t)^2}$ were used (data not shown). The result that SR is observed for $1/f$ noise is not unexpected because it has already been reported in the Schmidt trigger [13] and in a nondynamical threshold system [9]. What is considered novel here is that the optimal noise intensity for $1/f$ noise is much smaller than that for white noise, and maximal values for $\langle C_0 \rangle$ and $\langle C_1 \rangle$ are similar for the types of noise. For $1/f^2$ noise, however, these values are consistently smaller for the entire range of noise intensity.

The dependence of $\langle C_0 \rangle$ and $\langle C_1 \rangle$ on β is shown in Fig. 2. The values for $\overline{S(t)^2}$ and B are the same as in Fig. 1. When the variance of noise is small ($\sigma^2 = (0.7–1.0) \times 10^{-4}$), the values for $\langle C_0 \rangle$ and $\langle C_1 \rangle$ are maximal when $\beta \approx 1$. This tendency was observed when different values for $\overline{S(t)^2}$ and B were used (data not shown). The level of noise required for the FHN model to detect the subthreshold signal is the smallest when $1/f$ noise is added to the system. On the contrary, as the noise intensity becomes larger, the superiority of $1/f$ noise is diminished, and, finally, the values for $\langle C_0 \rangle$ and $\langle C_1 \rangle$ are the greatest when $\beta \approx 0$ (see the case of $\sigma^2 = 8.0 \times 10^{-4}$ in Fig. 2).

3. Firing rate of FHN model driven by $1/f^\beta$ noise

The FHN model has the two steady states, i.e., resting and firing states. When the value of ε in Eq. (1)

is sufficiently small, the change of $v(t)$ is much faster than that of $w(t)$. In this case, the FHN model can be regarded as a bistable system with the fourth-order potential function (one stable state corresponds to the resting state and the other to the firing state). The degree to which the output of the system is coherent with the input (evaluated by C_0 and/or C_1) is related to the instantaneous firing rate ($\langle R(t)\rangle$) and therefore considered to be governed by the classical theory of Kramers on the escape rate from a potential well [14],

$$\langle R(t)\rangle \propto \exp(-\varepsilon U/D), \tag{8}$$

where U corresponds to the height of the potential barrier of the FHN model and $2D$ is the coefficient of the autocorrelation function for white noise in $\langle \xi(t)\xi(s)\rangle = 2D\delta(t-s)$ ($\langle\ldots\rangle$ represents the ensemble average). In the discrete case, the value of $2D$ relates to the variance of $\xi(t)$ as $2D = \langle \xi(t)^2\rangle \times \Delta t$.

When the time-varying behavior of $S(t)$ is sufficiently slower than the characteristic time of the FHN model, U (as a function of time) can be represented as a function of B and $S(t)$. In Ref. [3], the theoretical curve of $\langle C_0\rangle$ for white noise was given, when $[\overline{S(t)^2}]^{1/2} \ll B$, as

$$\langle C_0\rangle \propto [\overline{S(t)^2}/D]\exp(-\sqrt{3}B^3\varepsilon/D). \tag{9}$$

It follows that the optimal noise intensity where $\langle C_0\rangle$ takes the maximal value is $2D = 2\sqrt{3}B^3\varepsilon$. The theoretical curve for white noise shown in Fig. 1 (solid line) agrees well with our numerical results.

The above scenario holds true only when $\beta = 0$. When $\xi(t)$ has time-correlation, the applicability of Eq. (8) cannot be guaranteed. Thus, we investigate the relationship between $\langle R(t)\rangle$ and D numerically. Eqs. (1) and (2) were integrated without input signals, i.e., by holding U constant. The value of B was the same as Fig. 1.

As shown in Fig. 3, a linear relationship between $\log\langle R(t)\rangle$ and $1/D$ is observed regardless of the value of β. This means that the same type of relationship as Eq. (8) is observed when $\beta > 0$ (this does not mean that the Kramers theory holds true when $\beta > 0$). However, since the slopes of these lines are different from each other, we tentatively modify Eq. (8) to

$$\langle R(t)\rangle \propto \exp[-(\varepsilon U/\alpha)/D], \tag{10}$$

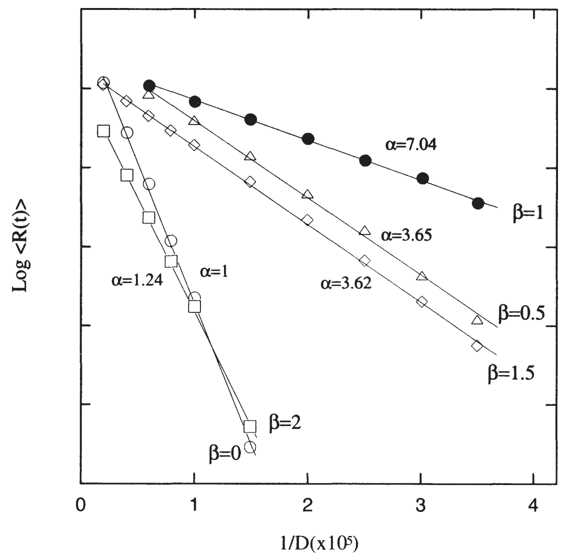

Fig. 3. Relationships between $\log\langle R(t)\rangle$ and $1/D$ in the FHN model. Regardless of the value of β, linear relationships are observed. Each plot is an ensemble-averaged value (500 trials). Note that the slope $(1/\alpha)$ is smallest when $\beta = 1$.

where $1/\alpha$ represents the ratio of the slopes to that for white noise. The slope of the lines is most gradual when $\beta \approx 1$, and for $1/f$ noise, the value of α was calculated to be approximately 7.04 by a least squares regression.

Eq. (10) is obtained simply by replacing D in Eq. (8) by αD. Thus, if Eq. (10) can be used in an approximate sense, we can obtain another equation similar to Eq. (9) by replacing D by αD. The broken line for $1/f$ noise in Fig. 1 was drawn in this way by setting $\alpha = 7.04$, and is also in accord with the numerical results. It follows that the optimal noise intensity for SR is dependent on the value of α as $2D = 2\sqrt{3}B^3\varepsilon/\alpha$. In other words, the larger the value of α, the smaller the optimal noise intensity.

4. SR in nondynamical system driven by colored noise

We next ask whether the superiority of $1/f$ noise for SR in the FHN model could be caused either by the property of $1/f^\beta$ noise itself or the interaction between the noise property and the dynamics of the FHN model. For this purpose, we consider SR in a nondynamical system which has recently been shown with $1/f$ noise theoretically and experimentally [9]. The system adopted in the previous study [9] was a very simple nondynamical threshold system: When the signal plus noise crossed a threshold unidirectionally, a single narrow pulse was generated. We now study whether $1/f^{\beta}$ noise with $\beta \approx 1$ could induce SR with weaker noise intensity in a nondynamical system. If so, it would be possible to conclude that the superiority of $1/f$ noise for SR seen in the FHN model might be due to the noise property.

Fig. 4 shows $\langle C_0 \rangle$ and $\langle C_1 \rangle$, obtained by the same procedures as those for the FHN model, as a function of the variance of noise ($\overline{S(t)^2} = 1.0 \times 10^{-5}$, threshold value 0.03). The maximal values for $\langle C_0 \rangle$ and $\langle C_1 \rangle$ are the largest when $\beta = 0$, and the optimal noise level for $\beta = 0$, 1, and 2 do not seem to be much different. These results clearly indicate that the superiority of $1/f$ noise is not seen in this nondynamical system. The reason can be explained analytically as follows.

The firing frequency ($\langle R(t) \rangle$) of the nondynamical system driven by stochastic noise is equivalent to the frequency at which the noise crosses a certain level and therefore is given by Rice's formula [26],

$$\langle R(t) \rangle \propto \frac{1}{\sqrt{\sigma^2}} \left(\int_{f_l}^{f_h} f^2 P(f)\, \mathrm{d}f \right)^{1/2} \times \exp\left(-\frac{\theta^2}{2\sigma^2} \right), \tag{11}$$

where σ^2 is the variance of noise, $P(f)$ is the power spectrum of $1/f^{\beta}$ noise, f_l and f_h are lower and higher cutoff frequencies, respectively, and θ is a threshold value.

The variance of the noise is represented by the power spectrum as $\sigma^2 \sim \int_{f_l}^{f_h} P(f)\mathrm{d}f$ and $P(f) \propto f^{-\beta}$. Thus, we obtain

$$\langle R(t) \rangle \propto \sqrt{\frac{\int_{f_l}^{f_h} f^{-\beta+2}\mathrm{d}f}{\int_{f_l}^{f_h} f^{-\beta}\mathrm{d}f}} \exp\left(-\frac{\theta^2}{2\sigma^2} \right). \tag{12}$$

When a subthreshold aperiodic signal $S(t)$ is added to the nondynamical system, the signal to threshold distance is modulated as $(\theta - S(t))$. Therefore, when $[\overline{S(t)^2}]^{1/2} \ll \theta$, Eq. (12) can be rewritten as

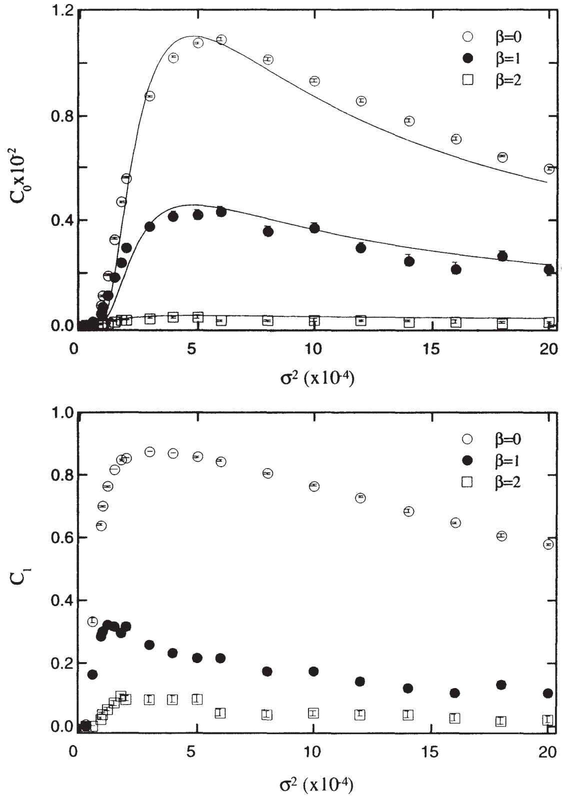

Fig. 4. Ensemble-averaged values and the standard errors for C_0 and C_1 (500 trials) in the nondynamical threshold system with different levels of noise variance σ^2 (white noise: open circles, $1/f$ noise: filled circles, $1/f^2$ noise: squares). The variance of $S(t)$ was 1.0×10^{-5} and the threshold value was 0.03. Both $\langle C_0 \rangle$ and $\langle C_1 \rangle$ for $1/f$ noise and $1/f^2$ noise are lower than those for white noise. Note that the optimal noise levels for $\langle C_0 \rangle$ are approximately the same among three types of noise. The solid lines are the theoretical curves given by Eq. (15).

$$\langle R(t) \rangle \propto g(\beta) \exp\{-[\theta - S(t)]^2/2\sigma^2\} \sim g(\beta) \exp\{-[\theta^2 - 2\theta S(t)]/2\sigma^2\}, \tag{13}$$

where $g(\beta) = (\int_{f_l}^{f_h} f^{-\beta+2}\mathrm{d}f / \int_{f_l}^{f_h} f^{-\beta}\mathrm{d}f)^{1/2}$. Because $S(t)$ is a deterministic signal, the ensemble-averaged value for C_0 is calculated by

$$\langle C_0 \rangle = \langle \overline{S(t)R(t)} \rangle = \overline{S(t)\langle R(t) \rangle}. \tag{14}$$

Substituting Eq. (13) into Eq. (14) and expanding to linear order gives

$$\langle C_0 \rangle \propto \frac{g(\beta)\theta\overline{S(t)^2}}{\sigma^2} \exp\left(-\frac{\theta^2}{2\sigma^2} \right). \tag{15}$$

The solid lines in Fig. 4 are the theoretical curves for $\langle C_0 \rangle$, where only the amplitude for $\beta = 0$ has been adjusted to fit the data, and the amplitudes for $\beta = 1$ and 2 have been scaled by factors of $g(1)/g(0)$ and $g(2)/g(0)$, respectively. These theoretical curves are well in accordance with the numerical results. From Eq. (15), the optimal noise level maximizing $\langle C_0 \rangle$ can be calculated to be $\theta^2/2$ ($0.03^2/2 = 4.5 \times 10^{-4}$) which is independent of the value of β. As the maximal $\langle C_0 \rangle$ is observed at around this level of noise (Fig. 4), this prediction is also confirmed.

These results indicate that the characteristics of SR obtained in the FHN model in this study do not hold true for the nondynamical system. Therefore, the superiority of $1/f$ noise for the FHN model is not due to the property of noise itself. The results for the nondynamical system clearly show that the interaction between the noise property and the dynamics of the FHN model is significant.

5. Conclusions and implications

This study demonstrates that $1/f$ noise is more suitable for SR in the FHN neuronal model (Eqs. (1) and (2)) than conventional white noise, because an even weaker noise intensity is sufficient for the neuron to detect the subthreshold signals. In an actual system the noise is not a sum of delta-functions in a mathematical sense, but it has width and amplitude. So our result means that smaller amplitude noise is sufficient to maximize SR when it has a $1/f$ type power spectrum.

In this Letter, we only examined the responsible mechanism, i.e., the superiority of $1/f$ noise caused by the interaction between the noise property and the dynamics of the FHN model, by comparing the analytical result of the nondynamical threshold system. Further theoretical studies on the mechanism(s) of enhanced SR by $1/f$ noise in the FHN model are needed. Especially, it is considered to be important to study analytically whether Eq. (10) holds true in a strict sense or in an approximate sense.

The concept of SR has recently received attention in the biological and physiological sciences [8,5–7,10,15,20]. On the other hand, although $1/f$ noise is commonly observed in physiological control systems [2,11,23,24,29,30], its functional significance has not been fully elucidated. Our results lead to the interesting hypothesis that intrinsic $1/f$ noise might be operative in a system showing SR. For example, considering our recent finding that $1/f$ noise-like modulation from the supraspinal centers is added to the human stretch-reflex system [24], the $1/f$ noise intrinsic to the human motor nervous system might play a significant role in detecting input proprioceptive signals and controlling the reflex motor nervous system outflow.

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