Stochastic Resonance with a Mixture of Sub- and Supra-threshold Stimuli in a Population of Neuron Models

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Abstract—This paper presents a novel type of stochastic resonance (SR) with a mixture of sub- and supra-threshold stimuli in a population of neuron models beyond regular SR and Supra-threshold SR (SSR) phenomena. We investigate through computer simulations if the novel type of SR can be observed or not, using the mutual information (MI) estimated from a population of neural spike trains as an index of information transmission. Computer simulations showed that the MI had a typical type of SR curves, even when the balance between suband supra-threshold stimuli was varied, suggesting the novel type of SR. Moreover, the peak of MI increased as the balance of supra-threshold stimuli got stronger, i.e., as the situation was getting close to the SSR from the regular SR. This finding could accelerate our understanding about how fluctuations play a role in processing information carried by a mixture of suband supra-threshold stimuli.

Index Terms—Action Potential, Fluctuations, Hodgkin-Huxley Model, Homogeneous Poisson Process, Neural Spike Trains, Mutual Information, Numerical Method, Monte Carlo Simulation

I. INTRODUCTION

Stochastic resonance (SR) is a phenomenon described as an increase in detection of sub-threshold signal generated by uncorrelated noise added to the input signal of a single nonlinear element, observed originally in a bistable system[1], later observed in the sensory nervous system[2][3][4], and the central nervous system[5][6][7]. SR in an array of elements is known as array-enhanced SR (AESR), and depends on added noise as well as number of each element in an array [8][7]. This type of SR is called a regular SR in this paper. The regular SR has been shown to improve encoding of randomly generated sub-threshold stimuli in a single hippocampal neuron model[9] and a population of hippocampal neuron models[10]. Furthermore, it has also been shown that uncorrelated fluctuations can enhance information transmission of supra-threshold stimuli (Supra-threshold SR; SSR) in a population of static and dynamic non-linear systems possessing threshold values [11][12][13][14]. Here, we note that the stimuli applying to all neuron models are assumed to be sub-threshold in the regular SR, whereas they are assumed

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Fig. 1. A population of multi-compartment neuron models[9] (N = 20) in which the balance between sub- and supra-threshold stimuli was set at symmetry. The supra-threshold stimuli were applied to the 1st to 10th neuron models, while the sub-threshold stimuli were applied to the 11th to 20th neuron models. The synaptic current, $I_{signal}(t)$, applied the distal portion of the apical, was presented simultaneously among neurons but the amplitudes were set at sub-threshold or supra-threshold. The uncorrelated fluctuations, $I_{noise}^{[k]}(t)$, was applied to the middle position of the basal dendrite. The transmembrane potentials, $V_{soma}^{[k]}(t)$ were recorded at each soma to detect spike timings, and to generate a binary sequence of spike timings in each neuron. Then, the binary sequence on the neuron network.

to be supra-threshold in the SSR. However, up to now, it has been unclear whether uncorrelated fluctuations can enhance information carried by a mixture of sub- and supra-threshold stimuli with a novel type of SR or not. This assumption is physiologically supposable since neuron receives synaptic inputs with a variable amplitude despite the nearby neurons have similar thresholds in the neuronal network. In the present article, computer simulations were carried out to see if the novel type of SR could be observed or not, when the balance between sub- and supra-threshold stimuli (see Figure 1) was varied, using the mutual information.

II. METHODS

A population of N neurons represented by a multicompartment model and previously obtained [5][9] was implemented as shown in Figure 1 (N = 20). The transmembrane potentials for each neuron were numerically calculated by solving a diffusive partial differential equation with the Crank-Nicholson method at a sampling step of 20 μs .



Fig. 2. Regular SR. (a-c) Stimulating currents and outputs in neurons network : the case of entirely sub-threshold stimuli (RSL = 0; See text for definition of RSL). Top : Input synaptic current, $I_{signal}(t)$, generated by a homogeneous Poisson shot noise with an intensity of 5 Hz and with $a_{signal}^{sub} = 0.6 nA$, Middle : Raster plots where each dot indicates the spike firing time, Bottom : The firing rate of the population sequence, $\tilde{r}(t)$. The amplitude of uncorrelated fluctuations, a_{noise} , was set at 0.1 nA in (a), 0.25 nA in (b), and 0.35 nA in (c). (d) The MI estimated from the neural population as a function of fluctuations amplitude a_{noise} . The regular SR could be observed.

The input signal, $I_{signal}(t)$, was applied simultaneously and the uncorrelated fluctuations, $I_{noise}^{[k]}(t)$, was generated independently on the other stimuli (Figure 1). Both synaptic stimulating currents were generated by a homogeneous Poisson process as follows :

$$I(t) = \int_{-\infty}^{t} h(\tau) dN(t-\tau)$$
(1)

$$h(t) = ae^{-\alpha t} \qquad (t \ge 0) \tag{2}$$

where $\alpha = 1000 \ 1/s$ in all the stimuli. In the signal source, $I_{signal}(t)$, the intensity, λ_s , of the counting process $N_{signal}(t)$



Fig. 3. A novel type of SR. (a-c) Half the neurons receive the supra-threshold stimuli $(a_{signal}^{sup}=3.0 \ nA$, applied to $1^{st}-10^{th}$ neuron (see the raster plots), and the other neurons receive sub-threshold stimuli (RSL = 0.5). Top : Input synaptic current, $I_{signal}(t)$. Middle : Raster plots, Bottom : The firing rate of the population sequence, $\tilde{r}(t)$. The amplitude of noise, a_{noise} , was set at 0 nA in (a), 0.15 nA in (b) and 0.25 nA in (c). (d) The MI as a function of uncorrelated fluctuation amplitude. A novel type of SR could be observed.

was set at 5 Hz. The neuron received the signal with the amplitude of either sub- $(a_{signal}^{sub} = 0.6 \ nA)$ or supra-threshold $(a_{signal}^{sup} = 3.0 \ nA)$ stimuli into the distal position (see Figure 1). The balance between sub- and supra-threshold stimuli was defined to be a coefficient $RSL = N_{supra}/N$ (relative supra-threshold level) where N_{supra} stands for the number of neurons receiving the supra-threshold stimuli. Figure 1 shows an example of RSL = 10/N, indicating a symmetrical mixture of sub- and supra-threshold stimuli. In the uncorrelated fluctuation source, $I_{noise}^{[k]}(t)$ the intensity, λ_N , was set at 100 1/s and the amplitude, a_{noise} was varied to observe the effect of the fluctuations on spike firing time. In the computer simulation, the uncorrelated fluctuation current $I_{noise}^{[k]}(t)$ was



Fig. 4. SSR. (a-c) Stimulating currents and outputs in 20 neurons network : the case of supra-threshold stimuli. (RSL = 1.0) Top : Input synaptic current, $I_{signal}(t)$, with $a_{signal}^{sup}=3.0 \ nA$, Middle : Raster plots, Bottom : The firing rate of the population sequence, $\tilde{r}(t)$. The amplitude of noise, a_{noise} , was set at 0 nA in (a), 0.15 nA in (b), and 0.25 nA in (c). (d) The MI as a function of uncorrelated fluctuation amplitude. Information transmission of the supra-threshold stimuli could be improved by a specific amplitude of noise, implying SSR.

applied to the midpoint in the basal tree in the k^{th} neuron (see Figure 1).

The transmembrane potentials were recorded at each soma $(V_{soma}^{[k]}(t))$ to detect spike timings, and then digitized with a temporal window of 1 *ms* in k^{th} neuron. The firing rate of the population sequence, $\tilde{r}(t)$ was generated by summing up this binary sequences[11]. The population of spike trains, r(t), is generated by smoothing $\tilde{r}(t)$ [11], and then evaluated by mutual information calculated by subtracting the noise entropy [15], [16], [11], [12], [10] :

$$I_{mutual}(I_{signal}(t), r) = H_{total}(r) - H_{noise}(r|I_{signal}(t))$$
(3)

These entropies, H_{total} and H_{noise} were obtained from entire



Fig. 5. Effect of the balance between sub- and supra-threshold stimuli (*RSL*) on the MI. Any type of SR's could be observed as mutual information reached a maximum value at specific noise level in a mixture of sub- and supra-threshold signals. The peak of MI tended to increased as the balance of supra-threshold stimuli got stronger, i.e., as phenomena were getting close to the SSR from the regular SR.

100 trials.

All computer simulations were performed on an IBM compatible PC with a Core 2 Quad Q6600 CPU.

III. RESULTS

The computer simulation was first performed in which all the neurons receive sub-threshold stimuli (RSL = 0.0). Figure 2 shows the input synaptic signal current, $I_{signal}(t)$, generated by a homogeneous Poisson shot noise with an intensity of 5 Hz and an amplitude of a_{signal}^{sub} =0.6 nA (top), the Raster plots where the dot indicates spike firing time (middle), and the firing rate $\tilde{r}(t)$ (bottom). The fluctuation source, amplitude of a_{noise} was set to 0.1 nA in (a), 0.25 nA in (b) and 0.35 nA in (c). With small level of fluctuations, the signals did not generate any spikes since the stimuli (both the signal and the noise) were sub-threshold (Figure 2a). The noise induced spike activity increased with increasing noise amplitude (Figure 2a-c). With a middle fluctuation level, the sub-threshold stimuli were detected (Figure 2b), whereas additional spikes were induced at high noise level (Figure 2c). Then, similar experiments were carried out by the duration was extended at 30 s. The mutual information estimated from the entropies were calculated and summarized as a function of uncorrelated fluctuation amplitude, a_{noise} , shown in Figure 2(d). The MI reached the maximum value for a specific noise amplitude, implying the regular SR.

Next, the simulations were carried out in which the number of neurons receiving the supra-threshold stimuli were modified. First half the neurons (1st-10th neurons) received the supra-threshold stimuli (RSL = 0.5) and the other (secondary) half neurons received the sub-threshold stimuli. Figure 3 (a-c) shows the results as raw data : The signal current , $I_{signal}(t)$, (top), the raster plots (middle) and the firing rate of the population (bottom) (Note that Figure 6 (Top)

does not indicate the amplitude) with the noise amplitude of $a_{noise} = 0$ nA in (a), 0.15 nA in (b) and 0.25 nA in (c). Without fluctuations, the first half neurons could generate spikes simultaneously since these neurons received the suprathreshold stimuli, whereas the other neurons did not generate any spikes since they received the sub-threshold stimuli (Figure 3a). When the uncorrelated fluctuation current with the amplitude of $a_{noise} = 0.15$ was applied, the suprathreshold stimuli could be detected and the spike timings had jitter (Figure 3b). This fluctuation current decreased the redundancy shown in the result of noise-free (Figure 3a). With higher noise amplitude, the spikes uncorrelated to the stimuli was generated (Figure 3c) like shown in Figure 2c. The mutual information as a function of uncorrelated fluctuation amplitude is shown in Figure 3d, summarizing Figure 3a-c. Also, a novel type of SR could be observed since the MI was maximized at a specific amplitude of noise current. However, we note that this phenomenon is different from that of the regular SR (Figure 2d) since applied stimuli were mixed with sub- and supra-threshold ones.

The simulation was then performed with that entirely supra-threshold stimuli were applied into all 20 neurons network (RSL = 1). The input-output characteristics are shown in Figure 4. In the noise source, amplitude of a_{noise} was set at 0 nA in (a), 0.15 nA in (b) and 0.25 nA in (c), respectively. The stimuli were detected without fluctuations in all the neurons (Figure 4(a)). When the middle level of noise was applied, spikes still followed the stimuli with jitter (Figure 4(c)), while a high level fluctuation generated noisy spike trains (Figure 4(c)). Figure 4d shows the MI as a function of noise amplitude. The fluctuation with around $a_{noise} = 0.1$ maximized the MI. This phenomenon described as SSR could be observed, since an optimal amplitude of fluctuations decreased the redundancy[11].

Similar results were obtained in different *RSL*'s and those are summarized in Figure 5, suggesting that any type of SR could be observed even when the balance between suband supra-threshold stimuli, *RSL*, was varied, Moreover, the maximal peak gradually increased as the number of neurons receiving supra-threshold stimuli (*RSL*) increased, i.e., as the situation was getting close to the SSR from the regular SR.

IV. CONCLUDING REMARKS

In this article we have shown through computer simulations that the novel type of SR could be observed in which the balance between sub- and supra-threshold stimuli was varied. Likewise, we have shown as well that the peak of MI tended to increased as the balance of supra-threshold stimuli *RSL*'s increased, i.e., as the situation was getting close to the SSR from the regular SR. These results may indicate that the novel type of SR is more secure in information transmission than the regular SR, and that a smaller fluctuation is preferred to maximize the MI in the novel type of SR than that in the regular SR. The novel type of SR may emerge a new framework beyond the regular SR and SSR phenomena in the research area of stochastic resonance. This finding could accelerate our understanding about how fluctuations play a role in processing information carried by a mixture of suband supra-threshold stimuli.

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