

Stochastic Resonance Can Enhance Information Transmission of Supra-threshold Neural Signals

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Abstract—Stochastic resonance (SR) has been shown to improve detection of sub-threshold signals with additive uncorrelated background noise, not only in a single hippocampal CA1 neuron model, but in a population of hippocampal CA1 neuron models (Array-Enhanced Stochastic Resonance; AESR). However, most of the information in the CNS is transmitted through supra-threshold signals and the effect of stochastic resonance in neurons on these signals is unknown. Therefore, we investigate through computer simulations whether information transmission of supra-threshold input signal can be improved by uncorrelated noise in a population of hippocampal CA1 neuron models by supra-threshold stochastic resonance (SSR). The mutual information was estimated as an index of information transmission via total and noise entropies from the inter-spike interval (ISI) histograms of the spike trains generated by gathering each of spike trains in a population of hippocampal CA1 neuron models at $N=1, 2, 4, 10, 20$ and 50 . It was shown that the mutual information was maximized at a specific amplitude of uncorrelated noise, i.e., a typical curve of SR was observed when the number of neurons was greater than 10 with SSR. However, SSR did not affect the information transfer with a small number of neurons. In conclusion, SSR may play an important role in processing information such as memory formation in a population of hippocampal neurons.

Index Terms—Action Potential, Supra-threshold Stochastic Resonance, Hodgkin-Huxley model, Homogeneous Poisson Process, Synaptic Noise, Information-Theoretic Analysis, 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 non linear element. This phenomenon has been described originally in a bistable system[1], later observed in the sensory nervous system[2], [3], [4], and the central nervous system[6],[7], [8]. SR in an array of elements is known as array-enhanced SR (AESR), and depends on added noise as well as coupling between each element [8]. Further investigations have shown that uncorrelated noise can enhance information transmission of supra-threshold input signal with supra-threshold stochastic resonance (SSR) not only in a population of static non-linear systems possessing

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multilevel threshold values [15],[16], but also in a population of dynamical non-linear systems with single level threshold values, like an array of neurons [17],[18]. However, it is yet unclear if and how uncorrelated noise can enhance information transmission of supra-threshold signals in neural networks in the central nervous systems.

In the present article, we test the hypothesis through computer simulations that information transmission of supra-threshold input signal can be improved by uncorrelated noise in a population of hippocampal CA1 neuron models with SSR. In computer simulations, the amplitude of uncorrelated noise was varied and the spike trains was reconstructed by spike firing times from each of the transmembrane potentials recorded at the soma in order to evaluate information transmission, i.e., the mutual information estimated from the total and noise entropies of the inter-spike interval histogram (ISIH) of the spike trains.

II. METHODS

A population of hippocampal CA1 neurons represented by a multi-compartment model [14] and previously obtained [6] was implemented as shown in figure 1. Each neuron model had 5 cylinders representing the dendritic tree : 5 compartments in the basal tree, one compartment in the soma, and 20 compartments in the apical branches. The soma at each neuron contained a sodium, a calcium, and five potassium channels in which conductances and transition rates were adapted from those in [13]. 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 $20 \mu s$.

In the computer simulation, the signal, $I_{signal}(t)$, was applied simultaneously and the noise, $I_{noise}^{[k]}(t)$, was independent of all other stimuli (figure 1b).

The synaptic stimulating currents defined to be $I_{signal}(t)$ as signal and $I_{noise}^{[k]}(t)$ as noise were modeled by a homogeneous Poisson process filtered as follows :

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

where the impulse response function is described as :

$$h(t) = ae^{-\alpha t} \quad (t \geq 0) \quad (2)$$

where $\alpha = 1000$ 1/s in all the stimulus. In the signal source, $I_{signal}(t)$, the intensity, λ_S , of the counting process $N_{signal}(t)$ was set at 5 1/s, the amplitude, $a_{signal} = 3.0$ nA. This signal was applied to all neuron models simultaneously at

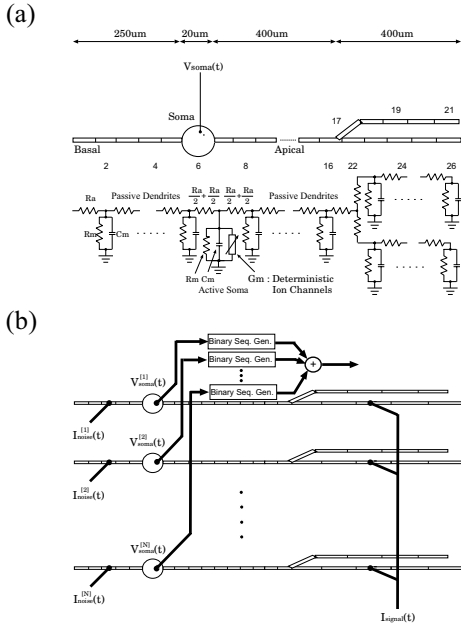


Fig. 1. (a) An hippocampal CA1 neuron was represented as a 5 cylinder multi-compartment model possessing 26 compartments. The equivalent electric circuit was shown in which the dendrites were composed of the passive resistances and capacitance, and in which the soma has the activation channels. (b) A population of hippocampal CA1 neuron models (N neurons). The supra-threshold synaptic current, $I_{signal}(t)$, was presented at the distal position of the apical dendrite (the 24th compartment) and the uncorrelated noise, $I_{noise}^k(t)$, was applied to the middle position of the basal dendrite (the 3rd compartment). The transmembrane potentials were recorded at each soma (6th compartment) to detect spike timings, and to generate a binary sequence of spike timings (“1” or “0”) in each neuron. Then, the binary sequence in each neuron was summed up to evaluate how much information carries on the CA1 neuron network.

the distal position (24th compartment). The noise, $I_{noise}^k(t)$ was also modeled by a homogeneous Poisson process where the intensity, λ_N , was set at 100 1/s and the amplitude, a_{noise} was varied to analyze the effect of the noise on spike firing time. In the computer simulation, the noise current $I_{noise}^k(t)$ was applied to the middle in the basal tree in the k^{th} neuron (see figure 1b).

The spike firing times of the individual neurons were detected by determining at which time the transmembrane potential at the soma, $V_{soma}(t)$, reached the peak amplitude and was greater than 50 mV. The population of neural spikes was defined as the binary data which was generated by summing up the spiking sequence of all neurons in the array, estimated by the mutual information of the inter-spike intervals (ISIs).

The inter-spike interval histogram (ISIH) was generated from spike firing times with an optimal bin width [12] :

$$bw = 3.49 \times \sigma_{ISI} \times N_{ISI}^{-1/3} \quad (3)$$

where σ_{ISI} and N_{ISI} are the standard deviation and the number of the ISI data respectively. This expression is optimal for Gaussian distributed ISI.

Then, from ISI histograms the mutual information *bits* was calculated, assuming that the ISIs were independent, i.e.,

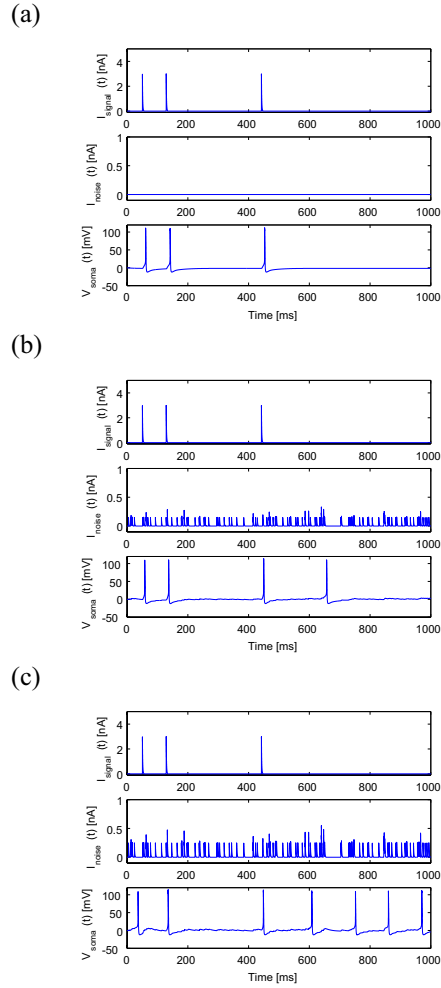


Fig. 2. Stimulating currents and recorded transmembrane potentials in a single neuron. Top : Input synaptic current, $I_{signal}(t)$, generated by a homogeneous Poisson shot noise with an intensity of 5 Hz and $a_{signal}=3.0$ nA, Middle : Background noise uncorrelated to the signal, $I_{noise}(t)$, also generated by homogeneous Poisson shot noise with an intensity of 100 Hz and a variable amplitude (a_{noise}), Bottom : Transmembrane potentials recorded at the soma, $V_{soma}(t)$ relative to the resting potential $E_{rest} = -66mV$. The amplitude of noise, a_{noise} , was set at 0 nA in (a), 0.15 nA in (b), and 0.25 nA in (c).

renewal point process, as follows [9], [10], [11] :

$$I_{mutual}(I_{signal}(t), T) = H_{total}(T) - H_{noise}(T|I_{signal}(t)) \quad (4)$$

$$H_{total}(T) = -\sum_{i=0}^{\infty} p(T_i) \log_2 p(T_i) \quad (5)$$

$$H_{noise}(T|I_{signal}(t)) = -E\left[\sum_{i=0}^{\infty} p(T_i|I_{signal}(t)) \log_2 p(T_i|I_{signal}(t))\right] \quad (6)$$

in which T and R respectively stand for the ISIs, and the spike firing rate, and $E[\]$ denotes the expectation operation.

All computer simulations were performed on an IBM compatible PC with a Pentium 4 CPU.

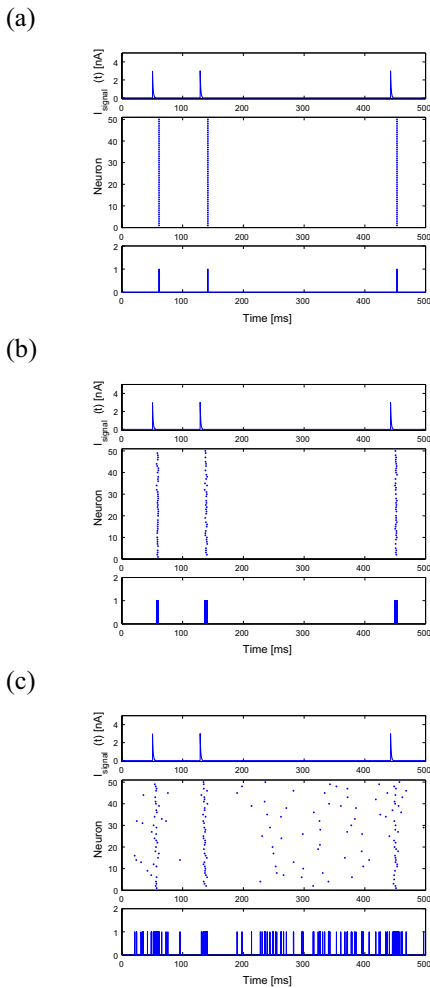


Fig. 3. Signals recorded in an array of 50 neurons. Top : Input synaptic current, $I_{signal}(t)$, applied simultaneously to 50 neurons, Middle : Raster plots in which the dot indicates the action potential, Bottom : Binary sequence for evaluation. The noise amplitude, a_{noise} was set at $0 nA$ in (a), $0.1 nA$ in (b), and $0.25 nA$ in (c).

III. RESULTS

The analysis was first applied to a neural network consisting of a single cell. Figure 2 shows the input signal current, $I_{signal}(t)$ (top), the background uncorrelated noise, $I_{noise}(t)$ (middle), and the transmembrane potentials (bottom) at the soma in one neuron. The noise source, amplitude of a_{noise} was set to $0 nA$ in (a), $0.15 nA$ in (b) and $0.25 nA$ in (c). The noise induced spike activity increased with increasing noise amplitude (a-c). The action potentials in the neurons follow the input indicating that the signal is indeed supra-threshold. At high noise levels, additional action potentials are induced.

Similar experiments in an array of 50 neurons were then carried to analyze the effect of SSR in neural networks. Figure 3 shows the input signal current, $I_{signal}(t)$ (top), the raster plots of 50 neurons (middle) and the binary data (bottom) of the neural spike trains gathered (See Figure 1 (b)). The amplitude a_{noise} was varied as $0 nA$ in (a), $0.1 nA$ in (b) and $0.25 nA$ in (c). Although this result and figure 2 show similar trends, the population of 50 neurons (the

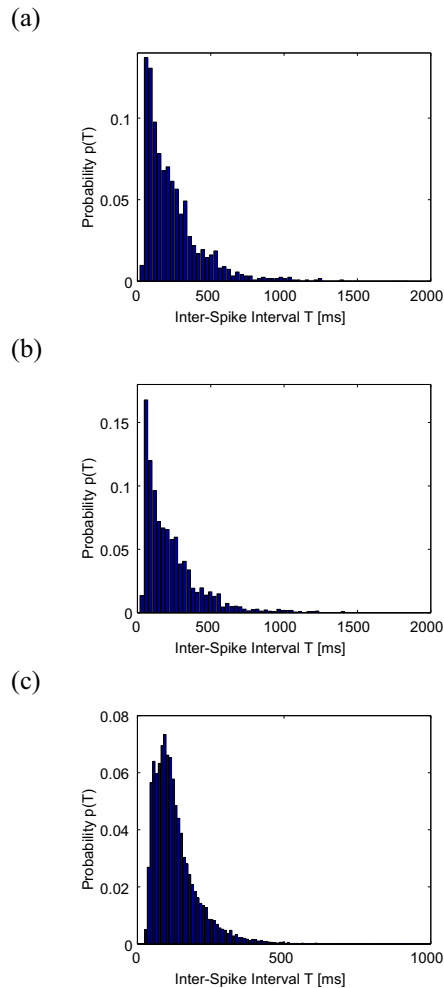


Fig. 4. The inter-spike interval histograms (ISIHS) generated by 100 trials of the simulation of 30s. These ISIHS were from spiking activities of 1 neuron. Noise intensity was varied to be $0 nA$ in (a), $0.1 nA$ in (b), $0.25 nA$ in (c). From the figure, the total entropy was calculated that is needed to estimate the mutual information.

raster plot) displays an additional property : variability at the spiking time along the input signal with the moderate level of noise amplitude (see figure 3b). The spike timing was estimated by the binary sequence.

The experiment similar to that has been shown in figure 2 but the duration was extended to 30 s and repeated 100 trials was performed. It was needed to quantify the information content of population statistically. Figure 4 shows the inter-spike interval histograms (ISIHS). These ISIHS were obtained from the simulation of 1 neuron. The amplitude of noise, a_{noise} was set at $0 nA$ in (a), $0.1 nA$ in (b) and $0.25 nA$ in (c). The probability, $p(T)$ is shown and gives the total entropy. Thus, the mutual information was estimated to be $0.2442 bits$ in (a), $0.2390 bits$ in (b) and $0.0547 bits$ in (c).

The mutual information is plotted as a function of the noise amplitude in figure 5. The mutual information reached a maximum value for the specific amplitude of noise in larger number of neurons (10, 20 and 50 neurons), while networks of smaller size do not display any SSR effect. The results

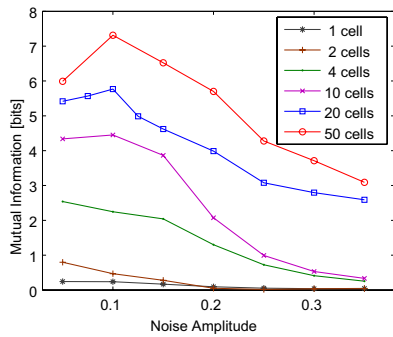


Fig. 5. Effect of the number of neurons on the mutual information. Mutual information reached a maximum value at specific noise level for arrays with 10, 20 and 50 neurons, whereas noise decreases the mutual information in the case of 1, 2 and 4 neurons.

indicate that the maximum mutual information increased when the number of neurons was increased, suggesting that the number of neurons plays an important role in information processing of the central nervous systems.

IV. DISCUSSION AND CONCLUSION

The role of noise in signal processing has already been shown to be important to neuronal function. Previous studies have focused on sub-threshold signals but information in the brain can also be supra-threshold. Therefore an analysis of the role of noise in supra-threshold information transfer is crucial to the determination of the effect of noise in neural networks. The results of this study, have shown that uncorrelated noise can synergistically increase information transmission of supra-threshold input signal in a network of neuron suggesting a mechanism different that the one used to explain sub-threshold stochastic resonance.

Without noise, the firing time of each neuron with supra-threshold signals is the same since the system is deterministic. Therefore, since single element fires spikes at the same time, there is no additional information contained even when the number of elements increases, i.e., greater redundancy. When noise is added optimally to each of element, each neuron becomes more independent from its neighbor, and therefore noise randomizes the spike firing times, reducing redundancy or increasing information content. This is because optimally added noise can generate fluctuations of membrane potentials, transition rates of sodium channels, and threshold values in individual neurons. At high noise amplitude the noise induces random spiking activity and decreases information content. Therefore, mutual information is observed to reach a maximum value with increasing noise amplitude suggesting the presence of SSR[17].

The effect is observed to improve with larger neuronal networks. Since hippocampal neurons receive large numbers of inputs and are made up of large number of neurons. SSR could play an important role as an amplifier of the the mutual information transfer across the hippocampus.

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