Propagation of Firing Rate in a Feedforward Network With Stochastic Hodgkin-Huxley Neurons

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Abstract. We study firing rate propagation in a feedforward network with multiple layers. Neurons in the network are modeled by using stochastic Hodgkin-Huxley neuronal model, which considers stochastic behaviour of voltage-gated ion channels embedded in neuronal membranes. In the model, ion channel noise due to its stochastic behaviour is related to the cell size in such a way that the noise strength increases with decreasing the cell size, mimicking the actual biophysical conditions. An external additive current noise is also injected into the first layer of the network. Therefore, neurons in the first layer are subject to both internal and external noise while neurons in the subsequent layers are subject to only internal noise. It is shown that the efficient transmission of firing rates requires an appropriate intrinsic noise level in the network if the input firing rate or the external noise strength is higher than a critical value.

1 Introduction

Information processing in the nervous system involves multiple stages of neuronal networks, where neuronal activity progress from one sub-population to another [1,2]. Computational approaches provide useful tools to understand the underlying mechanisms of the activity propagation through multiple processing stages [3]. As neuronal processing often involves multiple synaptic stages, a feedforward network, in which each neuron of a given layer receives multiple synaptic inputs from the previous layer, provides a simple platform for analyzing the propagation of neuronal activity in the nervous system. Within such a network structure, two modes of activity propagation have been proposed depending on the background noise: synfire chain mode and rate mode[1]. In a synfire chain, neurons are either noiseless or subjected to a weak noise current. Neuronal activity is carried by the groups of neurons that fire synchronously, and information is encoded with precise timings of these synchronized events (temporal code). On the other hand, in the rate mode, neurons fire at random times within the same layer, and information is encoded by firing rates (rate code). The rate mode propagation requires appropriate noise level within the layers. A number of computational and experimental studies[4-9] have analyzed these two propagation modes and reported the necessary conditions for stable propagation of activity through the layers. One of the most interesting experimental finding, presented by Reyes [8], suggests the synchrony dependent propagation of firing rates in a multilayer feedforward network constructed in an in-vitro slice preparation of rat cortex using an iterative procedure. Then, Wang et.al [2] and Liu et al. [6] introduced the computational model of this experimental study based on the Hodgkin-Huxley (H-H) [10] neurons. The feedforward network models in [2,6] involve ten-layers, and considered noise as an external additive current. However, an external source of noise may be biologically questionable due to the fact that the source of noisy activity in neuronal dynamics is primarily internal [3,9]. Therefore, Ozer et al. [9] recently extended the model by considering a biophysically more realistic neuronal model for each neuron in the network, where the stochastic behaviour of voltage-gated ion channels is modeled depending on the cell size. In this study, we use the same network model by Ozer et al. [9] and examine the firing rate propagation in the network, where neurons in the first layer are subject to both internal and external noise while neurons in the subsequent layers are subject to only internal noise.

2 Model and Methods

We constructed a 10-layer feedforward network involving 200 neurons in each layer. Each neuron in a given layer receives synaptic inputs from %10 of neurons, randomly chosen, in the previous layer as in the previous studies [2,6,9]. (Fig1).

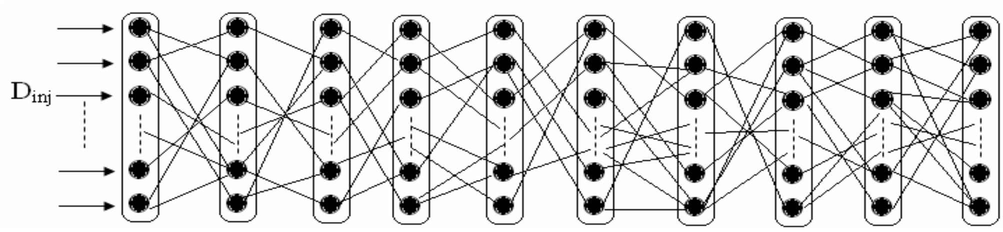


Fig 1. Schematic illustration of the 10-layer feedforward neural network. Columns and lines represent the layers and synaptic connections, respectively.

We consider that each neuron in all layers is subject to internal noise due to the ion channel stochasticity whereas external noise is applied only to neurons in the first layer. The time evolution of the membrane potentials of stochastic H-H neurons in the network is described as follows [2,9]:

$$C_m \frac{dV_{i,j}}{dt} = -g_{Na} m_{i,j}^3 h_{i,j}\left(V_{i,j} - V_{Na}\right) - g_K n_{i,j}^4 \left(V_{i,j} - V_K\right) - g_L (V_{i,j} - V_L) + I_{i,j}^{syn}(t) + D_{inj}\xi_{1,j}(t) \quad (1)$$

where $V_{i,j}$ denotes the membrane potential of neuron $j = 1....N = 200$ at layer $i = 1.....10$. $C_m = 1\mu Fcm^{-2}$ is the membrane capacity, $g_{Na} = 120\ mScm^{-2}$ and $g_K = 36\ mScm^{-2}$ are the maximal sodium and potassium conductance, respectively. The leakage conductance is assumed to be constant, equaling $g_L = 0.3\, mScm^{-2}$. $V_{Na} = 50\, mV$, $V_K = -77\, mV$ and $V_L = -54.4\, mV$ are the reversal potentials for the sodium, potassium and leakage channels, respectively. $\xi_{1,j}$ is the Gaussian white noise with zero mean and a variance of D_{inj}, applied only to neurons in the first layer. $I_{i,j}^{syn}$ denotes the synaptic current and described as follows [2,9]:

$$I_{i,j}^{syn}(t) = \frac{1}{N_{i,j}} \sum_{p=1}^{N_{i,j}} g_{syn}\alpha(t - t_{(i-1)p})(V_{i,j} - V_{syn}) \quad (2)$$

with $\alpha(t) = (t/\tau)e^{-t/\tau}$. $N_{i,j}$ and $t_{(i-1)p}$ are the number of neurons in layer $i-1$ coupled to j-th neuron in layer i and the firing time of the p-th neuron in layer $i-1$, respectively. The rising time of the synaptic current is assumed to be $\tau = 2\, ms$ as in [2,9]. $g_{syn} = 0.6$ is the coupling strength and V_{syn} represents the synaptic reversal potential, equaling 0 mV, indicating that all the couplings in the network are excitatory [2,9]. Finally, $m_{i,j}$ and $h_{i,j}$ denote activation and inactivation variables for the sodium channel, respectively, and the potassium channel includes only an activation variable, $n_{i,j}$.

Stochastic behaviour of the voltage-gated ion channels is modelled by using different computational algorithms. In this study, we use the algorithm presented by Fox [11], which is widely used [12-15] and computationally efficient than the other algorithms. In the Fox's algorithm, the stochastic gating variables are described by the following Langevin generalization [11]:

$$\frac{dx_{i,j}}{dt} = \alpha_x(V_{i,j})(1-x_{i,j}) - \beta_x(V_{i,j})x_{i,j} + \xi_{x_{i,j}}(t), \quad x_{i,j} = m_{i,j}, n_{i,j}, h_{i,j} \tag{3}$$

where α_x and β_x are rate functions for the gating variable $x_{i,j}$. $\xi_{x_{i,j}}(t)$ is an independent zero mean Gaussian white noise whose autocorrelation function described as follows [11]:

$$\left\langle \xi_m(t)\xi_m(t')\right\rangle = \frac{2\alpha_m\beta_m}{N_{Na}(\alpha_m+\beta_m)}\delta(t-t'), \tag{4a}$$

$$\left\langle \xi_h(t)\xi_h(t')\right\rangle = \frac{2\alpha_h\beta_h}{N_{Na}(\alpha_h+\beta_h)}\delta(t-t'), \tag{4b}$$

$$\left\langle \xi_n(t)\xi_n(t')\right\rangle = \frac{2\alpha_n\beta_n}{N_K(\alpha_n+\beta_n)}\delta(t-t'), \tag{4c}$$

where N_{Na} and N_K denote the total number of sodium and potassium channels within the membrane patch, respectively. The channel numbers are calculated through $N_{Na} = \rho_{Na}S$ and $N_K = \rho_K S$, where $\rho_{Na} = 60\mu m^{-2}$ and $\rho_K = 18\mu m^{-2}$ are the sodium and potassium channel densities, respectively. S is the cell membrane area which determines the intensity of intrinsic channel noise.

We computed the firing rates by averaging over all the neurons in a given layer within a long time window of 20 s. Synchronization degree within the neurons in a given layer is quantified by a coherence measure K_i based on the normalized cross-correlations of neuronal pairs in a layer as defined in [2,6]. The simulation duration of T second is divided into small time bins of $\Delta t = 2ms$, and a pair of membrane potential traces for neurons i and j are converted to the binary sequences according to firing or non-firing states as $X(l) = 0$ or 1 and $Y(l) = 0$ or 1 ($l = 1.....T/\Delta t$), respectively. Then the coherence measure of the pairs is determined as follows [2,6]:

$$k_{i,j}(\Delta t) = \frac{\sum_{l=1}^{T/\Delta t} X(l)Y(l)}{\sqrt{\sum_{l=1}^{T/\Delta t} X(l)\sum_{l=1}^{T/\Delta t} Y(l)}} \tag{5}$$

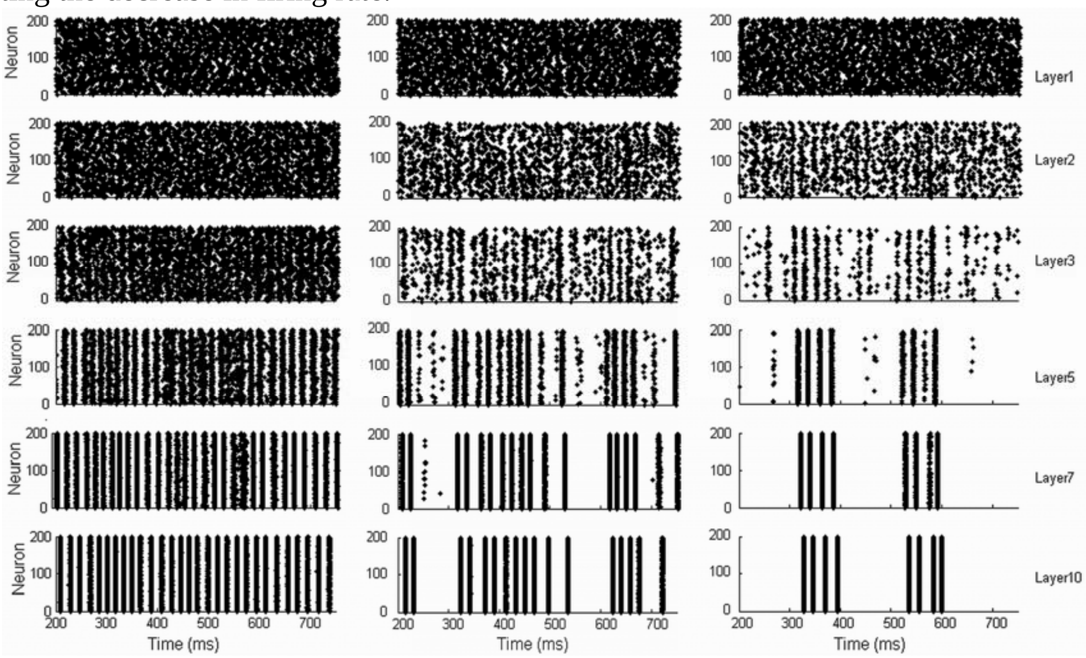
The coherence measure K_i for a given layer is computed over the coherence measure of the pairs in that layer as follows [2,6]:

$$K_i = \frac{1}{N(N-1)} \sum_{i=1}^{N} \sum_{j=1, j \neq i} k_{i,j}(\Delta t) \tag{6}$$

3 Results

We first analyzed the impact of cell size on the propagation of input firing rate. Therefore, we obtained firing patterns of several layers for three different patch sizes with a fixed value of the external noise intensity, $D_{inj} = 10\,\mu A^2/cm^4$ (Fig.2). Fig.2 shows the raster plots of time-varying firings, and provides synchronization degree at a glance for three different patch sizes. Neurons in layer 1 fire irregularly regardless of the cell size. On the other hand, spiking activity tends to become synchronized as the layer index increases [2,6,8,9]. In other words, neuronal firings in the feedforward neuronal networks are asynchronous for the first few layers while they become progressively more synchronous in deeper layers, which is clearly shown with the coherence measure, K_i in Fig.3. Fig.3 also shows that this synchronization becomes more pronounced as the channel noise decreases or the cell size increases.

This synchronization mechanism can be explained as follows: each neuron in a given layer randomly receives synaptic inputs from %10 of neurons in the previous layer meaning that neurons in any given layer share about % 1 of the same (common) synaptic inputs [2,16]. The common synaptic inputs yields partial synchrony between the corresponding postsynaptic neurons. Neurons progressively will tend to 'pick-up' synchronous firings in their common inputs through the next layer downstream and, consequently, they will tend to fire even more synchronously in deeper layers [16]. On the other hand, Fig.2 also shows that the number of spikes in the first several layers decrease due to the filtered sparse firings in the previous layer except for small cell sizes($S = 32\ \mu m^2$), where spontaneous firings occur frequently tolerating the decrease in firing rate.



(a) (b) (c)

Fig 2. Neuronal activity in several layers of the network for three different cell sizes: (a) $S = 32\ \mu m^2$, (b) $S = 200\ \mu m^2$, (c) $S = 10000\ \mu m^2$ ($D_{inj} = 10\,\mu A^2/cm^4$).

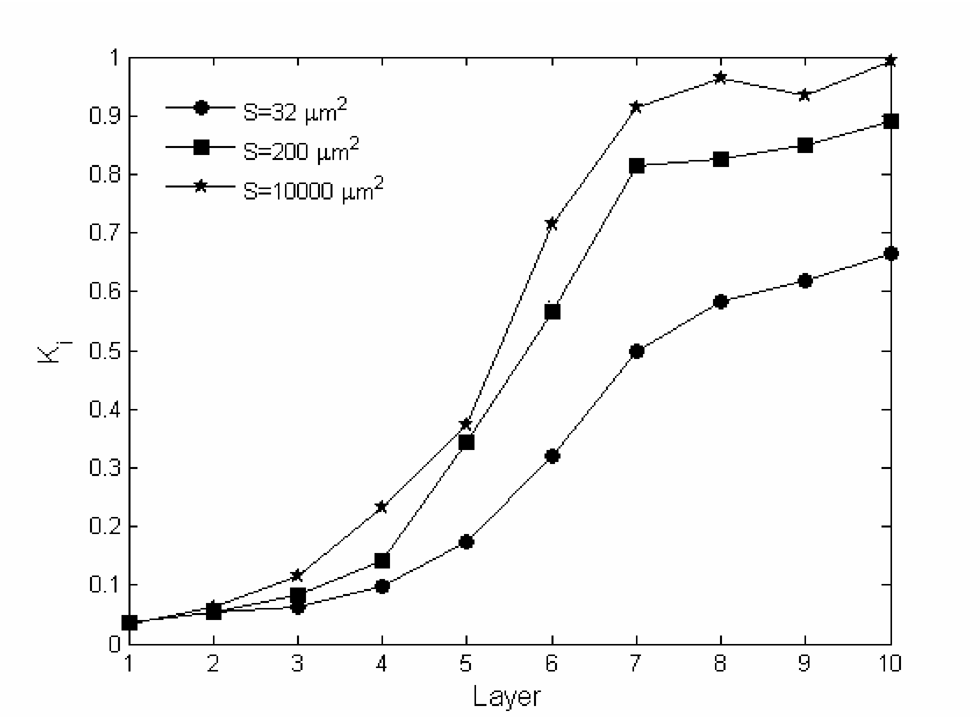


Fig 3. The coherence measure K_i versus layer index ($D_{inj} = 10\,\mu A^2/cm^4$).

To quantify the impact of the cell size or the channel noise strength on the firing rate propagation in a noisy feedforward network, we calculated the average firing rate as a function of layer index for various cell sizes with a fixed value of the external noise intensity, $D_{inj} = 10\,\mu A^2/cm^4$. Results are presented in Fig. 4. For all values of the cell size, firing rates decrease for the first several layers up to the third layer, and then begin to increase, and finally attain to a saturated value in deeper layers. Such a behaviour of firing rate in layers is

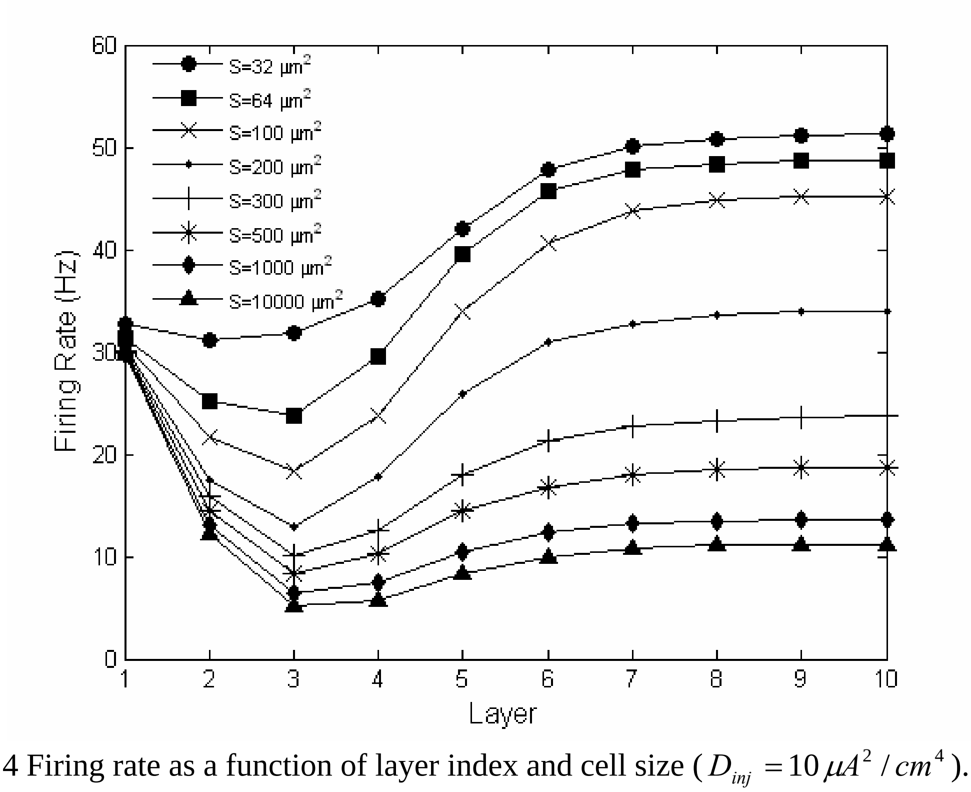


Fig 4 Firing rate as a function of layer index and cell size ($D_{inj} = 10\,\mu A^2/cm^4$).

related to the synchronization mechanism, which was explained above. Sparse firings in the first few layers are filtered resulting a decrease in firing rates. Since the synchronization progressively increases in deeper layers, firing rates increase until layer 8, where the synchronization is well built up.

The output firing rate becomes higher than the input rate for smaller cell sizes because of the intense internal noise strength. On the other hand, output firing rate becomes much lower than the input firing rate for larger the cell size, which means that the firing rate in the first layer transmits very weakly or even die out towards successive, deeper layers when the cell size becomes larger. However, it is seen that the input and output layers have almost same firing rate values between these two boundaries for the cell size, indicating that the firing rate in the first layer is being transmitted efficiently for optimal cell sizes .

Finally, we investigated the dependence of the propagation on the external noise strength for a cell size of $S = 200\ \mu m^2$, which is within the range of optimal cell sizes. Input firing rate was changed, and the firing rates of layers were computed for seven different external noise intensities (Fig.5). It is seen that input firing rate can be transmitted to the output layer for the noise intensities of $D_{inj} > 9\ \mu A^2 / cm^4$, implying that the firing rate in the first layer must be higher than a critical value for an efficient propagation, provided the intensity of intrinsic noise or the cell size is appropriately adjusted.

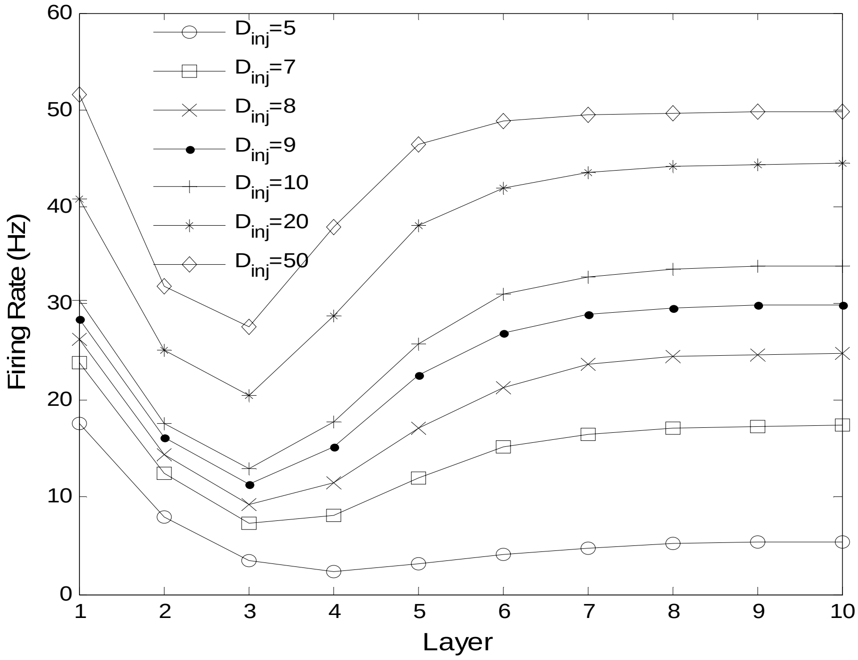


Fig 5. Firing rate versus layer index for different external noise strengths ($S = 200\ \mu m^2$)

4 Conclusions

We studied the propagation of firing rate in a noisy feedforward network. Although all neurons are subject to internal noise, the external noise is applied only to the neurons in the first layer. It is shown that the efficient transmission of firing rates requires an appropriate intrinsic noise level in the network if the input firing rate is higher than a critical value.

5 References

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