

Possible roles of electrical synapse in temporal information processing: A computational study

Xu-Long Wang, Xiao-Dong Jiang and Pei-Ji Liang*

Abstract—Temporal information processing in the range of tens to hundreds of milliseconds is critical in many forms of sensory and motor tasks. However, little has been known about the neural mechanisms of temporal information processing. In the present study, we explore the possible roles of electrical synapses in processing the duration information of external stimuli in the neural system by constructing neural networks. Our results suggest that neural networks with electrical synapses functioning together with chemical synapses can effectively work for the temporal-to-spatial transformation of neuronal activities, and the spatially distributed sequential neural activities can potentially represent temporal information.

Index Terms—model, neural network, electrical synapse, duration, temporal information processing.

I. INTRODUCTION

Biological neural systems are endowed with the ability to process temporal information given the inherent temporal nature of sensory environments and motor tasks. Temporal information processing in the neural system can be roughly categorized into four different time scales: microseconds, milliseconds, seconds and circadian rhythm, which serve for different physiological functions and rely on different neural mechanisms. The process within the scale of millisecond is perhaps the most sophisticated and the least well understood one among these categories. Behavioral tasks with temporal information processing falling within this scale include speech discrimination in the auditory system, motion information processing in the visual systems, and movement coordination in the motor system [1], [2], [3]

Physiological observations indicate that neurons in the sensory levels do not respond selectively to the temporal properties of external stimuli. Temporal information is thus suggested to be contained in the temporal structures of neuronal activities in the sensory layer. On the other hand, neurons which show selective response to specific temporal properties, especially the duration content, have been reported in the cortex of many species [4], [5], [6], [7], [8]. Temporal information is therefore suggested to be transformed into the spatially distributed neuronal activities in the cortex and neural mechanisms which contribute to the temporal-to-spatial transformation of neuronal activities are required.

Electrical synapse is widely distributed in the neural systems in addition to chemical synapse [9], [10]. Functional role

Asterisk indicates corresponding author.

X.-L. Wang and X.-D. Jiang are with the Department of Biomedical Engineering, Shanghai Jiao Tong University, Shanghai 200240, China

*Prof. P.-J. Liang is with the Department of Biomedical Engineering, Shanghai Jiao Tong University, Shanghai 200240, China e-mail: pjliang@sjtu.edu.cn

of electrical synapse has been identified in fine motor coordination which requires temporal information processing in milliseconds scale [11]. In the present work, we try to explore possible mechanisms of electrical synapse in processing the duration content of external stimuli within millisecond scale via computational approach. We construct neural networks containing both electrical and chemical synapses, which are activated by stimuli with various durations. The computational results show that electrical synapse can substantially contribute to the temporal-to-spatial transformation of neuronal activities, and the neuronal activities in such networks can potentially represent information about stimulus durations.

II. MODELS AND METHODS

A. Model structure

Two types of computational models are constructed. One is a small-scale neural network which contains only tens of neurons. Another is a large-scale one which is more biologically realistic. We use the simple model to clarify the basic properties of neural networks with electrical synapses functioning together with chemical synapse in temporal information processing. The overall behavior is further tested in the large-scale model. The schematic structures of the small- and large-scale neural networks are illustrated in Figure 1, A and B, respectively.

The input neuron is connected to some of the ten excitatory neurons (E) in the small-scale model (Figure 1A). Electrical synapses are presented among assigned neurons. The large-scale neural network model contains 400 excitatory neurons and 100 inhibitory neurons (Figure 1B) [12]. The neural network is further divided into 100 subgroups with each subgroup consisting of 4 excitatory neurons and 1 inhibitory neuron. Excitatory and inhibitory neurons in each individual subgroup are connected recurrently. Input neuron is connected to excitatory and inhibitory neurons on a random basis. All excitatory neurons are further connected with each other probabilistically in a recurrent way, and the synaptic strengths are variables which follow normal distributions.

B. Mathematical description of neurons and synapses

1) *Description of integrate-and-fire neuron*: Neurons are described in an integrate-and-fire manner (I-F neuron) [13]. Membrane potential of the input neuron (V_S), excitatory neuron (V_{Ex}), and inhibitory neuron (V_{In}) can be determined

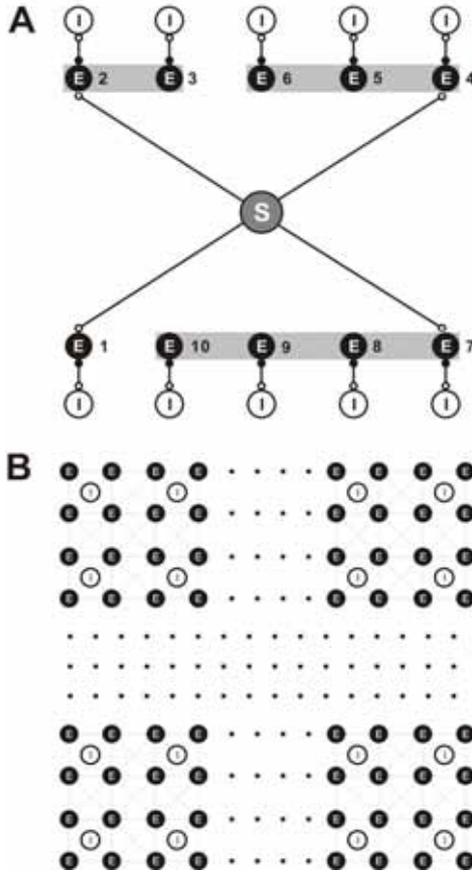


Fig. 1. A. Schematic structure of the small-scale neural network model. The input neuron (S) is connected to 4 of the 10 the excitatory neurons (E). All excitatory neurons are connected to each other in a recurrent way and each excitatory neuron is coupled with an inhibitory neuron (I). Excitatory and inhibitory synapses are represented by open and solid circles, respectively. Neurons in grey shadow are electrically coupled together recurrently. B. Schematic structure of the large-scale neural network model. Input neuron is connected to excitatory (E) and inhibitory (I) neurons in the network on a random basis. All excitatory neurons are further connected with each other probabilistically in a recurrent way. Electrical synapses are formed between some of the excitatory neurons randomly.

as follows:

$$C \cdot \frac{dV_S}{dt} = g_{leak} \cdot (V_{eq} - V_S) + I_S \quad (1)$$

$$C \cdot \frac{dV_{Ex}}{dt} = g_{leak} \cdot (V_{eq} - V_{Ex}) + [g_{ex}(t) \cdot (E_{ex} - V_{Ex}) + g_{in} \cdot (E_{in} - V_{Ex})] + I_{esyn} \quad (2)$$

$$C \cdot \frac{dV_{In}}{dt} = g_{leak} \cdot (V_{eq} - V_{In}) + [g_{ex}(t) \cdot (E_{ex} - V_{In}) + g_{in} \cdot (E_{in} - V_{In})] + I_{esyn} \quad (3)$$

In addition, when the membrane potential reaches a threshold (V_{th}), the neuron fires an action potential, and the membrane potential is immediately reset to the equilibrium potential (V_{eq}) after a firing lasting time (T_{fire}).

2) *Description of synaptic current:* The chemical synapses are modeled as follows [14], [15]:

$$I_{csyn} = g_{csyn} \cdot g(t) \cdot (E - V_{post}) \quad (4)$$

where $g_{ex}(t)$ and $g_{in}(t)$ in eqns (2) and (3) are presented by $g_{csyn}(t) \cdot g(t)$ here, with g_{csyn} representing synaptic strength which is modified by a factor of $g(t)$:

$$\frac{dg(t)}{dt} = \frac{1}{\tau_{syn}} \cdot [f(t) - g(t)] \quad (5)$$

where

$$\frac{df(t)}{dt} = \frac{1}{\tau_{syn}} \cdot [\Theta(V_{pre} - E_{thr}) - f(t)] \quad (6)$$

in which $\Theta(u)$ follows a step function:

$$\Theta(u) = \begin{cases} 0 & u \leq 0 \\ 1 & u > 0 \end{cases} \quad (7)$$

The electrical synapses are described as follows:

$$I_{esyn} = g_{esyn} \cdot (V_{pre} - V_{post}) \quad (8)$$

where g_{esyn} represents the synaptic strength [16].

III. RESULTS

A. Performance of the small-scale neural network model

The injected current is first transformed into a spike train of the input neuron. A sustained current elicits periodic spikes from the input neuron and the duration of the spike train is determined by the stimulus duration. The input neuron is connected to four of the ten excitatory neurons in the network where three neuronal groups are electrically coupled together which contain 2, 3 and 4 neurons, respectively. Raster plots of the firing performances of the model neurons in absence and presence of electrical synapses are compared with stimulus duration being 50 ms (Fig. 2A&B) and 100 ms (Fig. 2C&D), respectively.

Results given in Figure 2B&D suggest that electrical synapses in a neural network can effectively transform the temporal domain spike train of the input neuron into the spatial-temporal firing pattern of a group of neurons. Each activated neuron in the group fires within a specific time window, which is determined by the configuration of the synaptic connection of the neural network. Furthermore, stimulus with longer duration can evoke spikes from more neurons and therefore the stimulus durations can be represented by the spatial and temporal structure of the sequential neuronal activities.

B. Performance of the large-scale neural network model

In real neural network, the synaptic strengths as well as the electrical coupling configuration are variable and situations are much more complex compared with our schematic small-scale model. We use a large-scale model which is more biologically realistic to further test our hypothesis.

Representative firing patterns of the large-scale model in absence and presence of electrical synapses are shown in Figure 3A and B, respectively. The stimulus duration time is

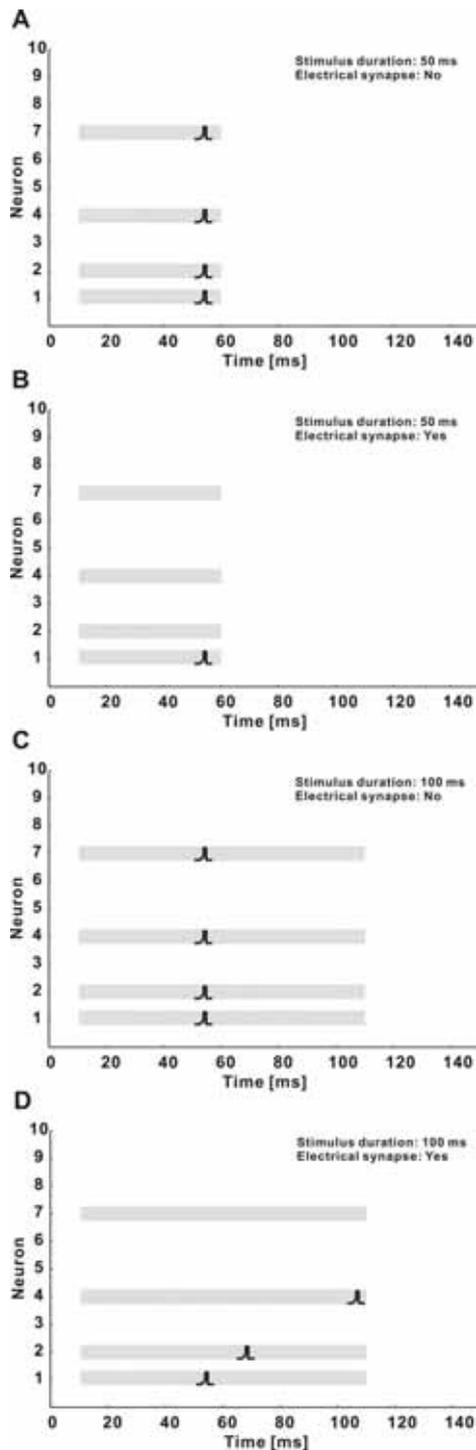


Fig. 2. Raster plots for neuronal activities of the small-scale model elicited by 50 and 100 ms stimulus durations. Stimuli are indicated by grey shadows. A, 50 ms duration, without electrical synapses; B, 50 ms duration, with electrical synapses; C, 100 ms duration, without electrical synapses; D, 100 ms, with electrical synapses.

100 ms. The inset graphs represent the recruitment process of the neuronal spiking activities. It is clear that the presence of electrical synapses results in a broader temporal distribution of the sequential spike activities of the neurons, while the neuronal firing activities are limited within a narrow temporal

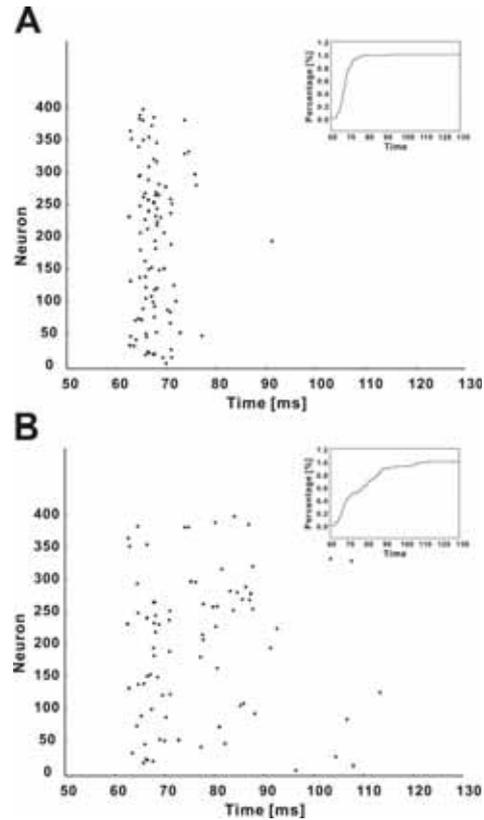


Fig. 3. A and B are representative raster plots of the neuronal activities of the large-scale model in absence and presence of electrical synapses, respectively. The stimulus duration is 100 ms. Inset graphs represent the processes of spike activity recruitment.

window in the absence of electrical coupling.

The firing patterns of the large-scale model in response to stimuli with various durations are further tested. Stimuli with durations varying from 50 ms to 100 ms are applied to the network, with steps being 10 ms. Our results revealed that the model neurons fire in a sequential pattern, with more neurons being sequentially recruited in response to longer duration. The recruitment process in response to different durations is averaged based on ten independent trials and the result is shown in Figure 4A. The model can effectively represent durations in other ranges while relevant parameters are changed. These parameters include the capacitance value of the I-F neuron, the time constant for chemical synaptic strength, the synaptic strengths from input neuron to the network et al. Stimuli with durations ranging from 100 ms to 200 ms are applied to the network, in which the mean value of synaptic strength from input neuron to the neural network are changed (from $0.055 \mu\text{S}$ to $0.038 \mu\text{S}$). The performance of the model (averaged across ten independent trials) is plotted in Figure 4B.

IV. DISCUSSION

In the present study, computational results demonstrate that electrical synapses could effectively contribute to the formation of a spatio-temporal firing pattern of neuronal ensembles while each neuron within the ensemble fires within different

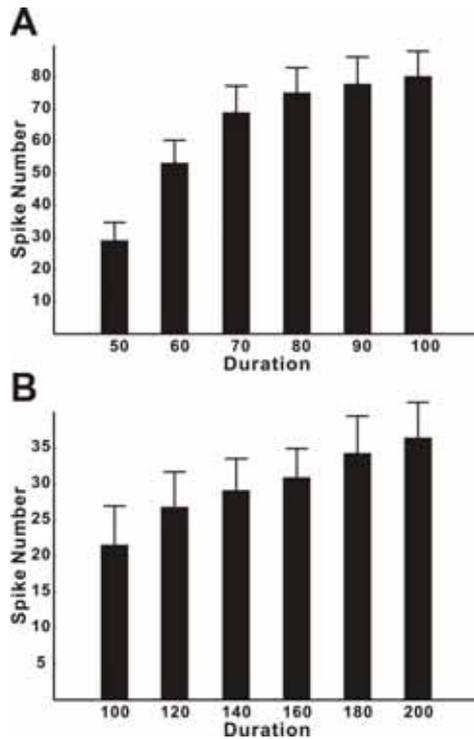


Fig. 4. Recruitment of neuronal activities (activated numbers) for the large-scale model in response to stimuli with durations ranging from 50 to 100 ms (A, step 10 ms) and 100 to 200 ms (B, step 20 ms). The mean values of synaptic strength from input to excitatory neurons are 0.055 and 0.038 μ S for results in figure A and B, respectively.

time windows, and the spatio-temporal pattern of the neuronal activities is capable of representing stimulus duration in the form of sequential firing activities of the spatially distributed neurons. Although specific roles of electrical synapse for temporal information processing are proposed in our model. It is necessary to mention that other factors can also contribute to this process. For example, membrane capacitance of specific neurons can be variable because of variation in surface area as well as the membrane capacitance value per unit area [17], [18], [19], [20]. We suppose that these mechanisms can function in parallel to electrical synapses in influencing the sequential firing patterns of neuronal ensembles.

Neurons in the present work are modeled following the classic I-F neuron fashion without any specific properties for temporal information processing. These neurons can be tuned to respond to any non-temporal properties of natural stimulus and thereby function for the corresponding behavioral tasks. For example, these neurons could be tone selective neuron which function for auditory behavior, or mechanosensory neurons which function for mechanosensation. While both electrical and chemical synapses are universal in the central nervous system, the model results suggest that both the spatial and temporal neuronal activities produced at the sensory layer of neural system could be processed together by sharing the same neural circuit. Temporal content of external stimulus could be read out from spike patterns of neuronal ensembles in the brain.

ACKNOWLEDGMENT

The authors would like to thank Dr. Shi-Yong Huang for helpful discussion. This work was supported by grants from the Hi-Tech Research and Development Program of China (No. 2006AA01Z125).

REFERENCES

- [1] D. V. Buonomano and U. R. Karmarkar, "How do we tell time?," *Neuroscientist*, vol. 8, pp. 42–51, 2002.
- [2] M. D. Mauk and D. V. Buonomano, "The neural basis of temporal processing," *Annu Rev Neurosci*, vol. 27, pp. 307–340, 2004.
- [3] R. B. Ivry and R. M. Spencer, "The neural representation of time," *Curr Opin Neurobiol*, vol. 14, pp. 225–232, 2004.
- [4] J. H. Casseday, D. Ehrlich, and E. Covey, "Neural tuning for sound duration: role of inhibitory mechanisms in the inferior colliculus," *Science*, vol. 264, pp. 847–850, 1994.
- [5] A. V. Galazyuk and A. S. Feng, "Encoding of sound duration by neurons in the auditory cortex of the little brown bat, *Myotis lucifugus*," *J Comp Physiol*, vol. 180, pp. 301–311, 1997.
- [6] J. He, T. Hashikawa, H. Ojima, and Y. Kinouchi, "Temporal integration and duration tuning in the dorsal zone of cat auditory cortex," *J Neurosci*, vol. 17, pp. 2615–2625, 1997.
- [7] D. Ehrlich, J. H. Casseday, and E. Covey, "Neural tuning to sound duration in the inferior colliculus of the big brown bat, *Eptesicus fuscus*," *J Neurophysiol*, vol. 77, pp. 2360–2372, 1997.
- [8] T. Fremouw, P. A. Faure, J. H. Casseday, and E. Covey, "Duration selectivity of neurons in the inferior colliculus of the big brown bat: tolerance to changes in sound level," *J Neurophysiol*, vol. 94, pp. 1869–1878, 2005.
- [9] B. W. Connors and M. A. Long, "Electrical synapses in the mammalian brain," *Annu Rev Neurosci*, vol. 27, pp. 393–418, 2004.
- [10] G. Sohl, S. Maxeiner, and K. Willecke, "Expression and functions of neuronal gap junctions," *Nat Rev Neurosci*, vol. 6, pp. 191–200, 2005.
- [11] D. G. Placantonakis, A. A. Bukovsky, X. H. Zeng, H. P. Kiem, and J. P. Welsh, "Fundamental role of inferior olive connexin 36 in muscle coherence during tremor," *Proc Natl Acad Sci U S A*, vol. 101, pp. 7164–7169, 2004.
- [12] C. Beaulieu, Z. Kisvarday, P. Somogyi, M. Cynader, and A. Cowey, "Quantitative distribution of GABA-immunopositive and -immunonegative neurons and synapses in the monkey striate cortex (area 17)," *Cereb Cortex*, vol. 2, pp. 295–309, 1992.
- [13] P. Dayan and L. F. Abbott, *Theoretical Neuroscience*. MIT Press, 2001.
- [14] W. Rall, "Distinguishing theoretical synaptic potentials computed for different soma-dendritic distributions of synaptic input," *J Neurophysiol*, vol. 30, pp. 1138–1168, 1967.
- [15] T. Nowotny, M. I. Rabinovich, and H. D. Abarbanel, "Spatial representation of temporal information through spike-timing-dependent-plasticity," *Phys Rev E Stat Nonlin Soft Matter Phys*, vol. 68, p. 011908, 2003.
- [16] N. Kopell and B. Ermentrout, "Chemical and electrical synapses perform complementary roles in the synchronization of interneuronal networks," *Proc Natl Acad Sci U S A*, vol. 101, pp. 15482–15487, 2004.
- [17] R. A. Chitwood, A. Hubbard, and D. B. Jaffe, "Passive electrotonic properties of rat hippocampal CA3 interneurons," *J Physiol*, vol. 515, pp. 743–756, 1999.
- [18] L. J. Gentet, G. J. Stuart, and J. D. Clements, "Direct measurement of specific membrane capacitance in neurons," *Biophys J*, vol. 79, pp. 314–320, 2000.
- [19] G. Major, A. U. Larkman, P. Jonas, B. Sakmann, and J. J. Jack, "Detailed passive cable models of whole-cell recorded CA3 pyramidal neurons in rat hippocampal slices," *J Neurosci*, vol. 14, pp. 4613–4638, 1994.
- [20] D. Thurbon, H. R. Luscher, T. Hofstetter, and S. J. Redman, "Passive electrical properties of ventral horn neurons in rat spinal cord slices," *J Neurophysiol*, vol. 80, pp. 2485–2502, 1998.