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Mechanism for propagation of rate signals through a 10-layer feedforward neuronal network*

Li Jie(李 捷)[a)b)], Yu Wan-Qing(于婉卿)[a)], Xu Ding(徐 定)[a)],
Liu Feng(刘 锋)[a)†], and Wang Wei(王 炜)[a)]

[a)]National Laboratory of Solid State Microstructure and Department of Physics, Nanjing University,
Nanjing 210093, China
[b)]State Key Laboratory of Pharmaceutical Biotechnology and School of Life, Nanjing University,
Nanjing 210093, China

Using numerical simulations, we explore the mechanism for propagation of rate signals through a 10-layer feedforward network composed of Hodgkin–Huxley (HH) neurons with sparse connectivity. When white noise is afferent to the input layer, neuronal firing becomes progressively more synchronous in successive layers and synchrony is well developed in deeper layers owing to the feedforward connections between neighboring layers. The synchrony ensures the successful propagation of rate signals through the network when the synaptic conductance is weak. As the synaptic time constant τ_{syn} varies, coherence resonance is observed in the network activity due to the intrinsic property of HH neurons. This makes the output firing rate single-peaked as a function of τ_{syn}, suggesting that the signal propagation can be modulated by the synaptic time constant. These results are consistent with experimental results and advance our understanding of how information is processed in feedforward networks.

Keywords: feedforward network, synchrony, rate coding, Hodgkin–Huxley model
PACC: 8730, 8710, 8725, 8700

1. Introduction

How the brain extracts important information from sensory inputs is an essential problem in neuroscience. To address this issue, many experimental and theoretical studies have been made on multiple layers of neurons with feedforward connections, i.e., feedforward networks.[1−6] How information is coded in such networks has been hotly debated. It can be carried by precise spike timing (temporal coding) or by firing rates (rate coding). For example, Litavk *et al* theoretically showed that the transmission of rate codes in feedforward networks with a balance between excitation and inhibition is highly unlikely.[5] In contrast, Reyes experimentally found that the rate coding can be realized in a feedforward network and the firing rate in deeper layers is saturated.[4] Similar results were reported by Wang *et al.*[6] Thus, the mechanism for signal propagation through feedforward networks still remains unclear and is worth further exploration.

In the present work, we investigate how rate signals can be propagated through a 10-layer feedforward network composed of Hodgkin–Huxley (HH) neurons with sparse connectivity. Results show that when Gaussian white noise is afferent to the input layer, synchrony can be well developed through layers owing to the feedforward connections between neighboring layers. The synchrony ensures the propagation of rate signals through the network when the synaptic conductance is weak, and the signal propagation can be modulated by the synaptic time constant.

2. Model and method

2.1. A feedforward network

In this work, a 10-layer feedforward network with sparse connectivity is constructed as shown in Fig.1(a). There are 200 neurons in each layer. The connection probability between neighboring layers is $P_{\mathrm{syn}} = 10\%$ unless specified otherwise. That is, each neuron randomly receives synaptic inputs from about 20 neurons in the preceding layer. Note that there are no couplings between neurons within the same layer.

†Corresponding author. E-mail: fliu@nju.edu.cn
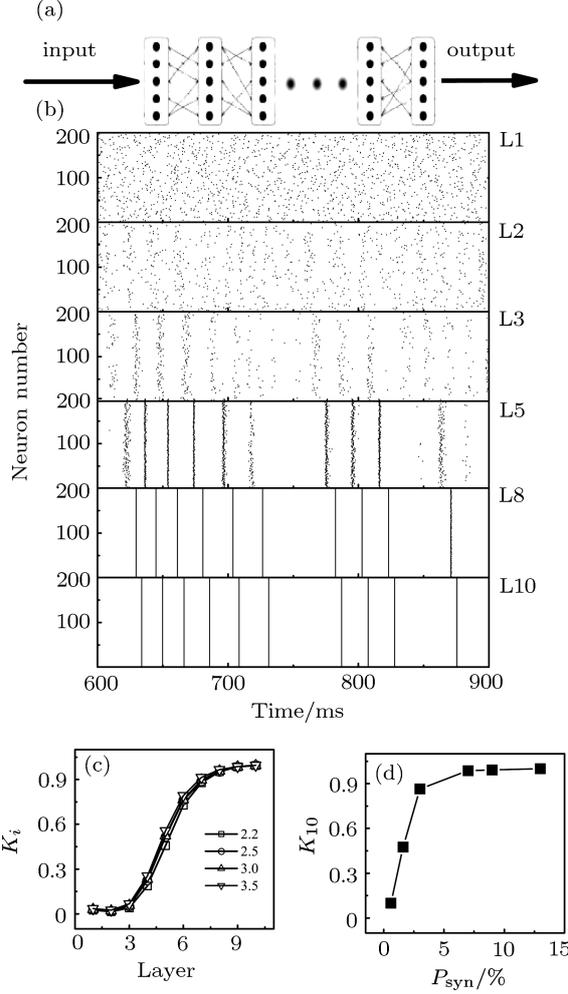
(a)

input

output

(b)

Fig.1. Network structure and network dynamics. (a) Schematic illustration of the feedforward network. The network is composed of 10 layers, each consisting of 200 neurons. Each neuron randomly receives synaptic inputs from about 20 neurons in the preceding layer. (b) Spatiotemporal firing patterns for layer 1, 2, 3, 5, 8 and 10 with $D_0 = 3 \ \mu\mathrm{A}^2\mathrm{ms/cm}^4$. (c) The coherence measure K_i versus layer index with $D_0 = 2.2$, 2.5, 3.0 or 3.5 $\mu\mathrm{A}^2\mathrm{ms/cm}^4$. (d) K_{10} versus the connection probability between neighboring layers, P_{syn}, with $D_0 = 3 \ \mu\mathrm{A}^2\mathrm{ms/cm}^4$.

2.2. Dynamical equations for the network

Each neuron is described by the Hodgkin–Huxley (HH) neuron model. The dynamical equations for the network are described as follows:

$$C_m \frac{\mathrm{d}V_{i,j}}{\mathrm{d}t} = -g_{Na} m_{i,j}^3 h_{i,j}(V_{i,j} - E_{Na}) - g_K n_{i,j}^4 (V_{i,j} - E_K) - g_l(V_{i,j} - E_l) - I_{i,j}^{\mathrm{syn}}(t) + I_i^0 + \delta_{i,1}\eta_j(t),$$

$$\mathrm{d}m_{i,j}/\mathrm{d}t = \alpha_m(V_{i,j})(1 - m_{i,j}) - \beta_m(V_{i,j})m_{i,j},$$

$$\mathrm{d}h_{i,j}/\mathrm{d}t = \alpha_h(V_{i,j})(1 - h_{i,j}) - \beta_h(V_{i,j})h_{i,j},$$

$$\mathrm{d}n_{i,j}/\mathrm{d}t = \alpha_n(V_{i,j})(1 - n_{i,j}) - \beta_n(V_{i,j})n_{i,j},$$

where $V_{i,j}$ denotes the membrane potential of the j-th neuron in layer i. The same functions and parameters are used as in Refs.[6] and [7]. I_i^0 is a constant bias set to 1 $\mu\mathrm{A/cm}^2$. The afferent input to layer 1, $\eta_j(t)$, is Gaussian white noise with $\langle \eta_j(t) \rangle = 0$ and $\langle \eta_j(t_1)\eta_k(t_2) \rangle = 2D_0\delta_{j,k}\delta(t_1 - t_2)$, where $\delta_{j,k}$ equals 1 if $j = k$ and 0 otherwise. Here D_0 is referred to as noise intensity.

The synaptic input is described as $I_{i,j}^{\mathrm{syn}}(t) = N_{i,j}^{-1} \sum_{k=1}^{N_{i,j}} g_{\mathrm{syn}}\alpha(t - t_{i-1,k})(V_{i,j}(t) - E_{\mathrm{syn}})$ with $\alpha(t - t_{i-1,k}) \equiv \alpha(t') = (t'/\tau)\mathrm{e}^{-t'/\tau}$ for $t' > 0$ and 0 otherwise. $N_{i,j}$ is the number of neurons in layer $i - 1$ coupled to the j-th neuron in layer i; $t_{i-1,k}$ is the firing time of the k-th neuron in layer $i - 1$. The synaptic reversal potential E_{syn} is set to 0 mV, implying that all the couplings are excitatory. The synaptic conductance g_{syn} is set to 0.6 ms/cm^2 and the synaptic time constant τ_{syn} is taken to be 3 ms, unless specified otherwise.

2.3. Coherence measure

A coherence measure, K_i, is used to characterize the degree of synchrony between neurons in layer i; it is defined as

$$K_i = \frac{1}{N(N-1)} \sum_{m=1}^{N} \sum_{n=1, n \neq m}^{N} \times \frac{\sum_{l=1}^{k} X_m^i(l) X_n^i(l)}{\sqrt{\sum_{l=1}^{k} X_m^i(l) \sum_{l=1}^{k} X_n^i(l)}}.$$

Here N is the number of neurons in each layer, and $X_j^i(l)$ represents the l-th bin in the spike train of neuron j in layer i when the whole processing time (2 s) is divided into k bins with each bin lasting 1 ms. $X_j^i(l)$ equals one or zero corresponding to one and no spike, respectively. K_i equals 1 when all neurons in layer i fire synchronously.[6]

2.4. Coherence factor

A coherence factor, β_i, is used to quantify the coherence resonance observed in layer i; it is defined as

$$\beta_i = \frac{1}{N} \sum_{j=1}^{N} h_{i,j} f_{i,j}^{\mathrm{peak}} / \Delta f_{i,j}^{\mathrm{peak}}.$$

Here $h_{i,j}$ and $f_{i,j}^{\mathrm{peak}}$ are the height and frequency of the highest peak in the power spectrum density (PSD) for the membrane potential of neuron j in layer i, respectively, and $\Delta f_{i,j}^{\mathrm{peak}}$ is the width of the peak at half height.[8]

3. Result

3.1. The development of synchrony

Figure 1(b) shows the spatiotemporal firing patterns for various layers when Gaussian white noise is afferent to the first layer. Neuronal firing is completely asynchronous in the first layer but becomes progressively more synchronous in successive layers. Synchrony is well developed by layer 8. This process can be characterized by the coherence measure K_i, which rises sigmoidally from 0 to 1 as the layer index increases (Fig.1(c)). This is consistent with the results in Refs.[4] and [6]. Moreover, the K_i curves for distinct noise intensities nearly overlap. This suggests that the buildup of synchrony is independent of noise intensity. Then, what is the intrinsic mechanism for the development of synchrony?

It has been argued that synchrony in such feedforward networks is closely related to the manner in which neighboring layers are connected.[3] When the connection probability between neighboring layers is 10%, neurons in the same layer share about 1% of the synaptic inputs. These common inputs tend to evoke spikes within a restricted time window, leading to partial synchrony between corresponding postsynaptic neurons. In this way this partial synchrony accumulates through layers, resulting in complete synchrony in deeper layers. Thus, the connection probability determines how fast synchrony is developed. The larger the P_{syn} is, the more easily the synchrony is built up. Indeed, K_{10} rises with increasing P_{syn} and is saturated to 1 when $P_{\mathrm{syn}} > 9\%$ (Fig.1(d)). Therefore, the development of synchrony is intrinsic to such feedforward networks with $P_{\mathrm{syn}} > 9\%$.

3.2. Synchrony-dependent propagation of rate signals

Figure 2(a) plots the mean firing rate f_i of each layer, which is calculated by averaging over all neurons within the same layer and over a time window of 2 s. Clearly, f_i first decreases and then increases until saturation occurs as the layer index increases, in agreement with the results in Refs.[4] and [6]. This trend is closely associated with the buildup of synchrony through the network and is preserved for different noise intensities. When white noise is afferent to layer 1, asynchronous spikes are evoked in the first few layers. Therefore, for each postsynaptic neuron, the

presynaptic pulses are relatively difficult to arrive simultaneously within an effective integration time window (~ 10 ms),[9] and thus the resulting excitatory postsynaptic currents (EPSCs) may be insufficient to trigger one spike (see the left panel in Fig.2(b)). This leads to a decrease of f_i in the first few layers. In contrast, when the presynaptic pulses become centralized, the resulting EPSCs within the effective integration time are large enough to evoke spikes (see the right panel in Fig.2(b)). This results in an increase or saturation of f_i. Thus, the development of synchrony can prevent the signal dying out during the propagation.

The above results are based on the fact that synaptic conductance is physiologically weak so that one spike cannot be evoked by only one presynaptic pulse. In contrast, if g_{syn} is unrealistically large, the spikes in layer i will evoke the same or more spikes in layer $i+1$ even in the absence of synchrony. Then f_i increases with layer index (see the curve for $g_{\mathrm{syn}} = 0.85$ in Fig.2(c)) despite weak synchrony (see Fig.2(d)) in the first several layers. Thus, we stress that synchrony ensures the successful propagation of rate signals through the feedforward network when the synaptic conductance is weak.
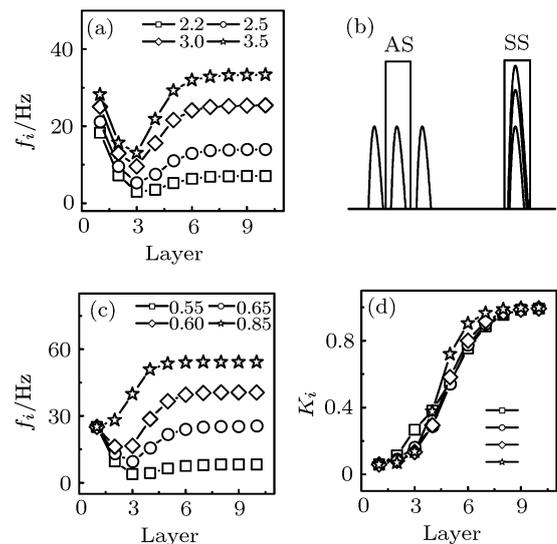

Fig.2. Propagation of rate signals through the network. (a) The average firing rate f_i of each layer versus layer index with $D_0 = 2.2$, 2.5, 3.0 or 3.5 $\mu\mathrm{A}^2\mathrm{ms/cm}^4$. (b) Illustration of how to integrate EPSPs within an effective integration time window for asynchronous spikes (AS) or synchronous spikes (SS). (c) f_i and (d) K_i versus layer index with $D_0 = 3$ $\mu\mathrm{A}^2\mathrm{ms/cm}^4$ and $g_{\mathrm{syn}} = 0.55$, 0.60, 0.65 or 0.85 ms/cm^2.

When D_0 is systematically changed, the average firing rate of each layer varies accordingly. Figure 3 plots the output rate (i.e., f_{10}) versus the input

rate (f_1). Clearly, f_{10} rises monotonically over a wide range of f_1 (marked as A_{code} in Fig.3). This range is also the physiological regime over which neurons perform various functions. As a result, the synchrony-based rate coding can be realized in the feedforward network.
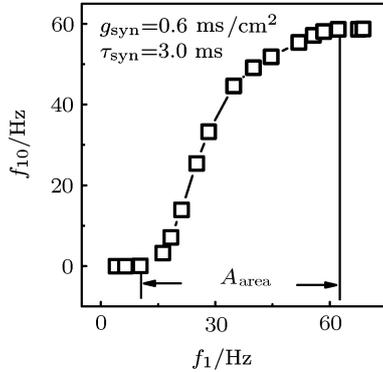

Fig.3. The output rate (f_{10}) versus the input rate (f_1). To plot the curve, the noise intensity D_0 is systematically varied. A_{code} marks the coding area.

3.3. Network activity modulated by the synaptic time constant

It is worth noting that the synaptic time constant, τ_{syn}, remarkably affects the network dynamics. Figure 4(a) shows f_{10} versus τ_{syn} for different noise intensities. The curves are unimodal with a peak at $\tau_{\text{syn}} = 3$ ms. This is related to the special relationship between f_2 and I_2 (I_i is the mean synaptic current to neurons in layer i averaged over the time interval of 2 s), when τ_{syn} is systematically changed. For $D_0 = 3$, for example, the f_2 curve is single-peaked (see Fig.4(b)). Since I_2 rises monotonically with τ_{syn}, the curve of f_2 versus τ_{syn} is also unimodal with a peak at $\tau_{\text{syn}} = 3$ ms. For $i > 2$, however, f_i rises monotonically with increasing I_i (see the inset in Fig.4(b)). Moreover, I_i rises monotonically with increasing f_{i-1}, and thus the curve of f_i versus τ_{syn} is also unimodal (see Fig.4(c)). Thus, f_{10} first rises and then decreases with increasing τ_{syn} with the peak also at $\tau_{\text{syn}} = 3$ ms.
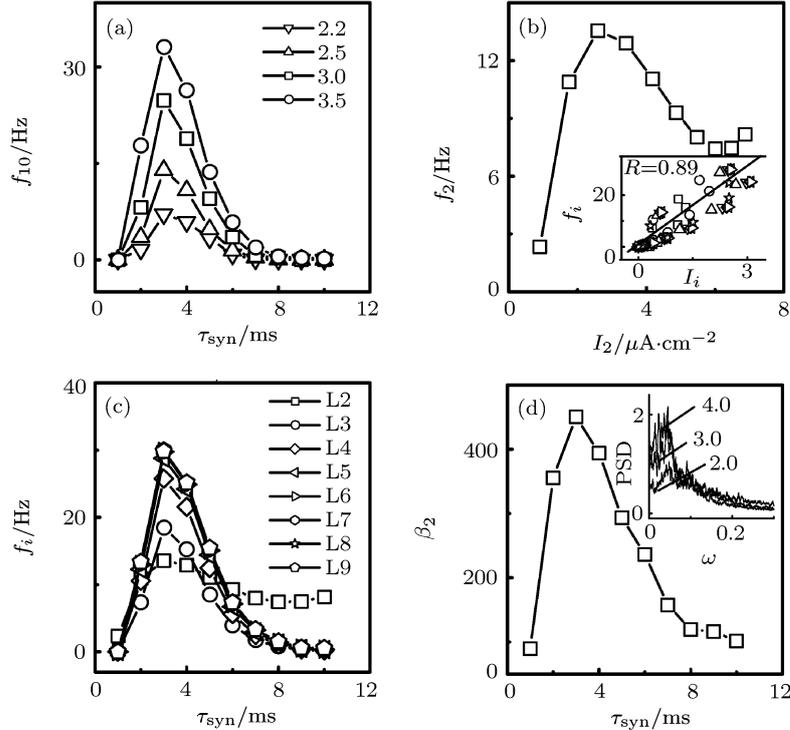

Fig.4. The effect of the synaptic time constant τ_{syn} on signal propagation. f_i represents the averaging firing rate of layer i, and I_i denotes the mean synaptic current to neurons in layer i averaged over the time interval of 2 s. (a) f_{10} versus τ_{syn} with $D_0 = 2.2$, 2.5, 3.0 or 3.5 $\mu\text{A}^2\text{ms/cm}^4$. (b)–(d) $D_0 = 3$ $\mu\text{A}^2\text{ms/cm}^4$. (b) f_2 versus I_2. The inset shows f_i versus I_i for $i > 2$. (c) f_i versus τ_{syn} for $2 \leq i \leq 9$. (d) The coherence factor β_2 versus τ_{syn}. The insert shows the PSD for membrane potential of the 10th neuron in layer 2 with $\tau_{\text{syn}} = 2$, 3 or 4 ms.

We can interpret the above results as follows: The inset of Fig.4(d) shows the PSDs for membrane potential of the 10th neuron in layer 2 with different values of τ_{syn}. Clearly, these curves are single-peaked, suggesting that there exists a frequency preference in neuronal activity. In fact, the HH neuron is of type II and exhibits intrinsic subthreshold oscillations, which is reflected in many phenomena such as coherence resonance.[8] Here, neurons in layer 2 also exhibit such coherence resonance. As a function of τ_{syn}, the coherence factor is single-peaked with a maximum at $\tau_{syn} = 3$ ms (see Fig.4(d)). This causes f_2 to reach its maximum at $\tau_{syn} = 3$ ms. Therefore, the maximal mean firing rate attained at $\tau_{syn} = 3$ ms results from the intrinsic property of the HH neuron itself.

4. Discussion

We have explored the propagation of rate signals through a 10-layer feedforward network composed of HH neurons with sparse connectivity. It is shown that when Gaussian white noise is afferent to the first layer, neuronal firing becomes progressively more synchronous in successive layers and synchrony is well developed in deeper layers. The development of synchrony is mainly due to the feedforward connections between neighboring layers. The larger the connection probability, the more rapidly the synchrony is developed. The output rate changes monotonically over a wide range of input rate; that is, synchrony ensures that rate signals are effectively propagated through the multilayered feedforward network.

It is noted that the synaptic conductance is physiologically weak.[2,4] This easily leads to the failure of signal propagation since fewer spikes are evoked in successive layers.[2] However, synchrony can change this situation. When synchrony is built up during the signal propagation, the synaptic currents within the effective integration time window will be strengthened due to the centralized presynaptic pulses. This will avoid the loss of spikes and keep the signal propagating successfully through the network. This type of signal propagation with the help of synchrony is commonly termed a "synfire chain".[10]

Our results show that when white noise is afferent to the input layer, the rate coding can be realized by the "synfire chain". This seems to be in conflict with the notion that the "synfire chain" can destroy the rate coding.[11] But this is not the case here. In fact, the manner in which input signals are transmitted through a feedforward network depends largely on the properties of signals. When the input signal changes fast temporally, the rate signal may be distorted during propagation. That is, rate coding cannot be accomplished with the "synfire chain" in that case. In contrast, when the input signal varies slowly over time, the input rate can be precisely encoded in the output rate. Thus, rate signals can be propagated with the "synfire chain".[4] When Gaussian white noise is delivered to layer 1, the mean firing rate of layer 1 is nearly constant over time, and thus the network can propagate the rate signal with neurons firing synchronously in deeper layers.

It has been demonstrated that the HH neuron can exhibit coherence resonance in response to noise only.[8] Here, the mean firing rate of layer 2, f_2 is a single-peaked function of τ_{syn}, with a maximum at $\tau_{syn} = 3$ ms. Accordingly, the output rate is also peaked at $\tau_{syn} = 3$ ms, suggesting that the propagation of rate signals can be modulated by the synaptic time constant.

Moreover, compared with Ref.[6], we further confirm that a key reason for synchrony in such feedforward networks is that neurons in any given layer share a large quantity of common synaptic inputs. The optimal network performance acquired at $\tau_{syn} = 3$ ms may be related to the resonance coherence observed in layer 2. These results thus advance our understanding of how information is processed in feedforward networks. Finally, it is worth noting that cortical circuits are endowed with collateral connections between pyramidal cells as well as inhibitory interneurons. Taking that into account will further clarify the underlying mechanism for signal propagation.

In conclusion, in a 10-layer feedforward network with sparse connectivity, neurons fire synchronously in deeper layers due to the feedforward connection between neighboring layers. Synchrony subserves the propagation of rate signals in the case of weak synaptic conductance.

References

[1] Abeles M 1991 *Corticonics* (Cambridge: Cambridge Univ. Press)

[2] Diesmann M, Gewaltig M O and Aertsen A 1999 *Nature* (London) **402** 529

[3] Segev I 2003 *Nat. Neurosci.* **6** 543

[4] Reyes A D 2003 *Nat. Neurosci.* **6** 593

[5] Litvak V, Sompolinsky H, Segev I and Abeles M 2003 *J. Neurosci.* **23** 3006

[6] Wang S, Wang W and Liu F 2006 *Phys. Rev. Lett.* **96** 018103

[7] Hansel D, Mato G and Meunier C 1993 *Europhys. Lett.* **23** 367

[8] Yu Y, Wang W, Wang J and Liu F 2001 *Phys. Rev.* E **63** 021907

[9] König P, Engel A K and Singer W 1996 *Trends Neurosci.* **19** 130

[10] Vogels T P, Rajan K and Abbott L F 2005 *Ann. Rev. Neurosci.* **28** 357

[11] van Rossum M C W, Turrigiano G G and Nelson S B 2002 *J. Neurosci.* **22** 1959