

Transmission of neural activity in a feedforward network

Sentao Wang and Wei Wang^{CA}

National Laboratory of Solid State Microstructure and Department of Physics, Nanjing University, Nanjing 210093, China

^{CA}Corresponding Author: wangwei@nju.edu.cn

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In this work, the enhancement of coherence resonance of firings in a 10-layer feedforward neuronal network with sparse couplings is found when there is noise input to each layer. Periodic signals with frequency 30–80 Hz are found to be well transmitted through the network, and such a frequency sensitivity can be modulated by the noise intensity and is different in different layers. When a random

pulse-like signal is input to the neurons of the first layer, the signal can be well read out from the population rates in an optimal range of noise intensity. This ability decreases as the layer index increases. *NeuroReport* 16:807–811 © 2005 Lippincott Williams & Wilkins.

Key words: Coherence resonance; Frequency sensitivity; Population rate; Synchronization

INTRODUCTION

Neurons can fire spikes when the total input crosses a threshold. Information is contained in these activities. In a classical view, the firing rate, namely the number of firing events in a time bin, is used to carry and transform information [1]. In this hypothesis, the exact timing of spikes only reflects the noisy environment. Recently, a temporal coding scheme, in which the precise location of spikes plays a central role in coding information, has been developed [2,3]. Many groups of neurons, called functional cell assemblies, are always involved in computing information. The information is transferred from one subpopulation to another. Therefore, to study the information processing in nervous systems, it is reasonable to consider a multilayer feedforward network. For such a topological structure, it is shown that synchronous activities can propagate in a stable manner under appropriate conditions [4]. Thus, it is possible that firing rate can be transmitted in the feedforward network because of synchronous firings. This possibility has been approved by an experiment [5]. We have confirmed it theoretically by modeling studies. It is found that synchronization can develop gradually in the network and firing rate can be transmitted when there is noise input to only the first layer (i.e. layer 1). When the neurons are only subject to noise input, it has been shown that spikes are discharged around a main frequency, which is called coherence resonance (CR) [6]. How does the CR appear in the feedforward network? Such a question is crucial for the transmission of neural activity.

In the architecture with multiple layers, when there exists a signal input to layer 1 and small noise current in each layer, the network operates in the synfire mode, that is, the temporal code [7]. For the intermediate noise intensity, the mode is changed to rate mode transmission, in which the stimulus can be encoded by the firing rate [7]. Because synchronous activities can survive and develop in the network, can the rate code be changed to the synchronous

code in the process of signal transmission? It is also found that there exists a frequency range of 30–80 Hz in which the periodic signal can be detected and transduced more efficiently [8,9]. When a periodic signal is injected to all the neurons of layer 1, how is the signal transmitted in the feedforward network? Although it is well known that synchronous activities can guarantee synaptic transmission, what role does synchronization play in signal transmission? Obviously, these questions are of importance for information processing in nervous systems.

MODEL AND METHODS

To address these questions clearly, we constructed a feedforward network containing 10 layers. Each layer consists of $N=200$ Hodgkin–Huxley (HH) neurons. The neurons in the network are sparsely coupled: the probability that a given neuron is connected with another neuron in the previous layer is set to 0.1. No coupling exists between the neurons within the same layer. The dynamical equations for the network are presented as follows:

$$C_m \frac{dV_{ij}}{dt} = -g_{Na} m_{ij}^3 h_{ij} (V_{ij} - V_{Na}) - g_K n_{ij}^4 (V_{ij} - V_K) - g_l (V_{ij} - V_l) + I_0 + I_{ij}^{syn}(t) + \eta_{ij}(t), \quad (1)$$

$$\frac{dm_{ij}}{dt} = \alpha_m (V_{ij})(1 - m_{ij}) - \beta_m (V_{ij}) m_{ij}, \quad (2)$$

$$\frac{dh_{ij}}{dt} = \alpha_h (V_{ij})(1 - h_{ij}) - \beta_h (V_{ij}) h_{ij}, \quad (3)$$

$$\frac{dn_{ij}}{dt} = \alpha_n (V_{ij})(1 - n_{ij}) - \beta_n (V_{ij}) n_{ij}. \quad (4)$$

Here, C_m is the capacity of the membrane. V , m , h and n are the membrane potential, the activation and inactivation of the sodium current, and the activation of the potassium

current, respectively. V_{Na} , V_K , V_l are the reversal potentials of the sodium, potassium and leakage currents. g_{Na} , g_K , g_l are the corresponding maximum values of conductance. The layer indices are $i=1, \dots, 10$, and the neuron indices are $j=1, \dots, 200$. All the functions and the parameter values are set as $C_m=1 \mu\text{F}/\text{cm}^2$, $V_{Na}=50 \text{ mV}$, $V_K=-77 \text{ mV}$, $V_l=-54.4 \text{ mV}$, $g_{Na}=120 \text{ mS}/\text{cm}^2$, $g_K=36 \text{ mS}/\text{cm}^2$, $g_l=0.3 \text{ mS}/\text{cm}^2$, and $\alpha_h(V)=0.07e^{-(V+65)/20}$, $\beta_h(V)=1/(1+e^{-(V+35)/10})$, $\alpha_m(V)=0.1(V+40)/(1-e^{-(V+40)/10})$, $\beta_m(V)=4e^{-(V+65)/18}$, $\alpha_n(V)=0.01(V+55)/(1-e^{-(V+55)/10})$, and $\beta_n(V)=0.125e^{-(V+65)/80}$. All the currents are in units of $\mu\text{A}/\text{cm}^2$. I_0 is constant bias and taken as $1 \mu\text{A}/\text{cm}^2$. The term $\eta_{i,j}(t)$ is a Gaussian white noise background satisfying $\langle \eta_{i,j}(t) \rangle = 0$, $\langle \eta_{i,j}(t_1)\eta_{i,m}(t_2) \rangle = 2D_i\delta_{i,m}\delta(t_1-t_2)$, where D_i is referred to as the noise intensity of the i th layer. Here, we set $D_2=D_3=\dots=D_{10}=D_s$. The synaptic inputs from the previous layer is $I_{i,j}^{\text{syn}} = -1/N \sum_{p=1}^{N_{i,j}} g_{\text{syn}} \alpha(t - t^{(i-1)p}) \times (V_{i,j} - V_{\text{syn}})$ with $\alpha(t) = t/\tau(e^{-t/\tau})$. $N_{i,j}$ is the number of neurons in layer $(i-1)$ coupled to the (i,j) th neuron. g_{syn} , the synaptic weight, is equal to 0.6. V_{syn} represents the synaptic reversal potential and is set to 0 mV, meaning that all the couplings in the network are excitatory. $t^{(i-1)p}$ is the firing time of the p th presynaptic neuron in the $(i-1)$ th layer coupled with the (i,j) th neuron. Note that a presynaptic spike alone cannot trigger the postsynaptic neuron to fire. $\tau=2 \text{ ms}$ is the rising time of the synaptic input.

The firings of each neuron are recorded and converted into a time series of standard pulses U_j with $U_A=1$ of width 2 ms and $U_B=0$ corresponding, respectively, to the firing and

nonfiring states. The output of each layer can be defined as $I_i^{\text{out}}(t) = 1/N \sum_{j=1}^N U_j(t)$. When a periodic signal input to layer 1 exists, the output signal-to-noise ratio (SNR) is defined as $10\log_{10}(S/B)$ with S and B representing the signal peak and the average amplitude of background noise at the input signal frequency in the power spectrum of $I_i^{\text{out}}(t)$, respectively. An average over 50 different realizations of noise seeds is taken to obtain the reported SNR values.

Numerical integration of these equations is performed by a second-order stochastic algorithm [10] and the integration step is taken as $1000/32768 \text{ ms}$. The average firing rate of each layer is obtained by averaging over all the neurons in this layer and over a long time, 20 s. All the error bars are computed as $\{\sum_i^n (x_i - \bar{x})^2/n\}^{1/2}$.

RESULTS AND DISCUSSION

To simulate a realistic situation, a white noise is injected to all the neurons in the network by setting $D_1=D_s$. The spatiotemporal firing pattern of layer 6 with $D_1=D_s=3$ is shown in Fig. 1a as an example. It is clearly seen that some

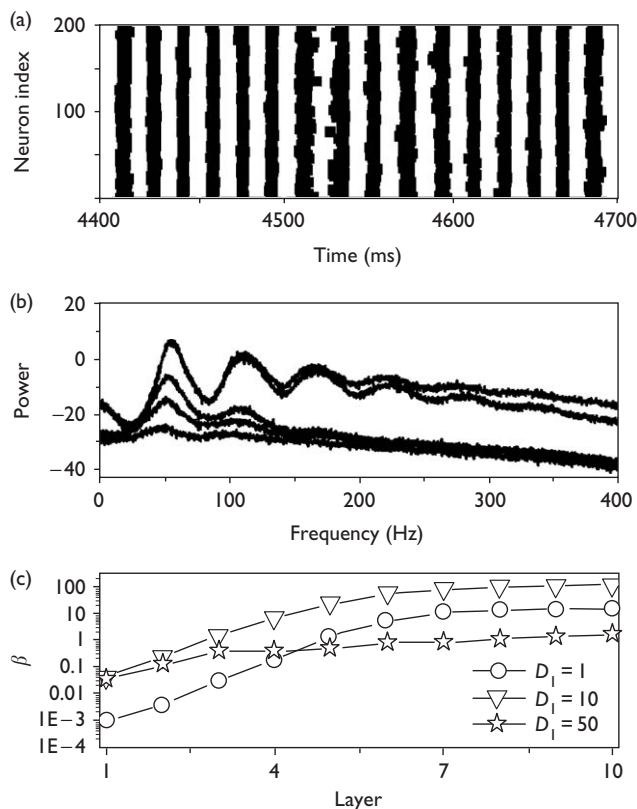


Fig. 1. (a) The spatiotemporal firing patterns of layer 6 with $D_1=D_s=3$. (b) Power spectrum of the spike trains of several layers with $D_1=D_s=3$ (in $10\log_{10}$ scale). The curves are layers 1, 2, 3, 6, and 10, respectively, from bottom to top. (c) β versus the layer index with $D_1=D_s=1, 10, 50$.

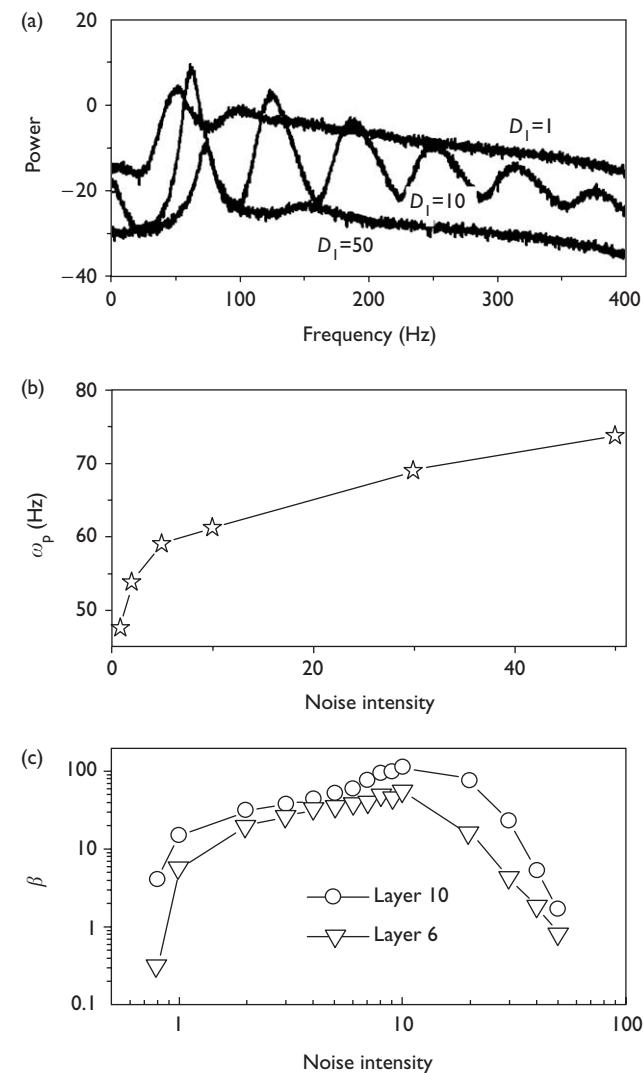


Fig. 2. (a) Power spectrum of the spike trains of layer 10 with $D_1=D_s=1, 10, 50$ (in $10\log_{10}$ scale). (b) ω_p in layer 10 versus noise intensity. (c) β versus noise intensity in the network in layers 6 and 10.

periodicity in spike trains exists. The power spectrum densities of spike trains of several layers with $D_1=D_s=3$ are plotted in Fig. 1b. In layer 1, a broad peak is observed. Such a broad peak is a manifestation of CR, resulting from the subthreshold intrinsic oscillation of HH neurons [9]. As the layer index increases, the peak becomes higher and sharper, meaning that the CR is enhanced. To characterize CR quantitatively, we compute a measure of coherence β , which is defined as $\beta=h\omega_p/\Delta\omega$. Here, h and ω_p are the height and the frequency at which the peak occurs and $\Delta\omega$ is the frequency width of the peak at half-maximum height [11]. β versus layer index is shown in Fig. 1c. It can be clearly seen that the enhancement of the CR is significant in the first five layers. Such a phenomenon also exists for different noise intensities. Figure 2a plots the power spectrum densities of spike trains of layer 10 with $D_1=D_s=1, 10, 50$. For $D_1=1$, the peak is broad. When D_1 increases to 10, the peak becomes higher and sharper. But as D_1 becomes equal to 50, the peak becomes lower. Note that when D_1 increases, the frequency at which the peak occurs increases, which is summarized in Fig. 2b. ω_p is mainly in a range of 40–80 Hz. β versus D_1 in layers 6 and 10 are shown in Fig. 2c. When D_1 increases, β increases first and then decreases, and there is an optimal noise intensity at which the value of β is maximal.

Next, we explore how a periodic signal is transmitted. Here we assume that each neuron in layer 1 is subject to a periodic subthreshold signal $A \cos(2\pi f_s t)$ with an amplitude $A=1$ and frequency f_s . The SNR versus layer index is plotted in Fig. 3a for $f_s=20, 60,$ and 120 Hz with $D_1=3$ and $D_s=0$, respectively. For $f_s=60$ Hz, the SNR decreases slowly as the layer index increases. But for $f_s=20$ and 120 Hz, the SNR drops fast. This phenomenon results from the fact that HH neurons are more sensitive to the signals whose frequencies

are located in the range of 30–80 Hz [9]. In such a sensitive range, the neurons in layer 1 fire spikes with more correlation. Synchronization can increase the safety factor of synaptic transmission and improve the precision with which temporal features of stimuli are transmitted [12]. Therefore, the signals in the sensitive range can be transmitted more efficiently [see Fig. 3b]. Such a sensitive range is really related to the so-called 40 Hz oscillations in nervous systems [13]. But for signals with frequencies beyond the sensitive range, there are many packets of synchronous activities in deep layers arising from the noise input, which result in signals being transmitted weakly. Note that the values of SNR become saturated in layer 7 because of the saturation of the synchronization. As shown in Fig. 3c, when there exists noise input in the whole network, the transmission of signal is almost impossible for $f_s=20$ and 120 Hz. However, the SNR can sustain nearly as a constant for $f_s=60$ Hz as the layer index increases, indicating that the signal with $f_s=60$ Hz can be transmitted better with $D_s=5$ than with $D_s=0$ (see Fig. 3a and c). For signals with frequencies outside the sensitive range, adding noise input to all layers can increase the number of packets of synchronous activities arising from the noise in deep layers. Clearly, these signals are transmitted more weakly. But for signals with frequencies in the sensitive range, synchronization arising from signal input can prevent synchronization arising from noise input developing in the network. This results in these signals being transmitted more efficiently (see Fig. 3d). That is, the noise input to all layers can make a periodic signal encoded more accurately in deep layers if the signal can evoke activities with more correlation in layer 1.

In order to examine more realistic situations, a random signal-like pulse, generated by poisson process, is injected to

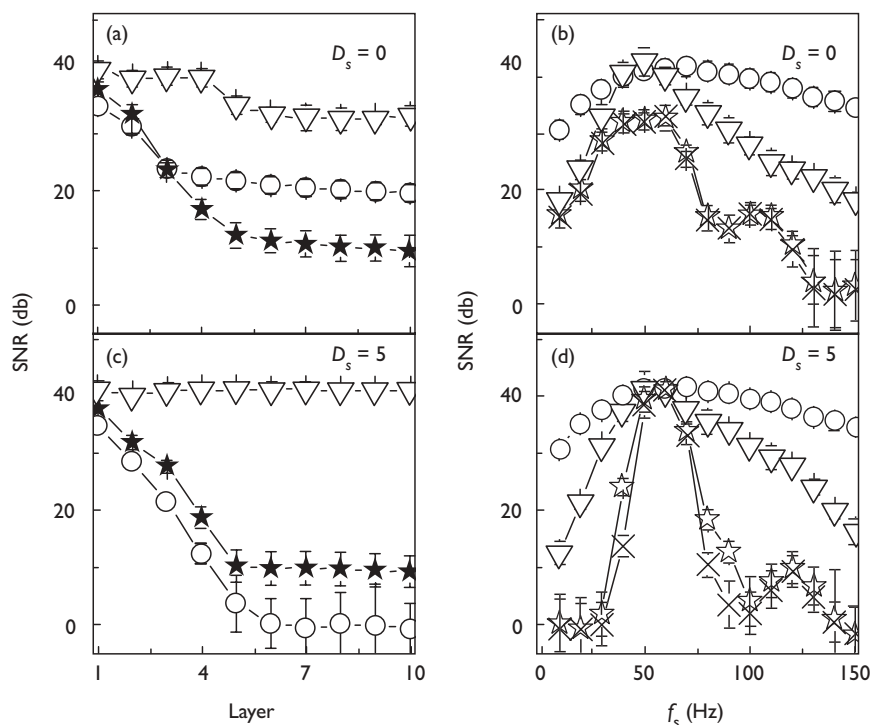


Fig. 3. (a,c) The signal-to-noise ratio (SNR) versus layer index with $D_1=3$ in the case of $D_s=0$ and 5 for different signal frequencies: 20 Hz (\circ), 60 Hz (∇), 120 Hz (\star). (b,d) The SNR versus signal frequency with $D_1=3$ in the case of $D_s=0$ and 5 of several layers: layer 1 (\circ), layer 3 (∇), layer 7 (\star), and layer 10 (\times).

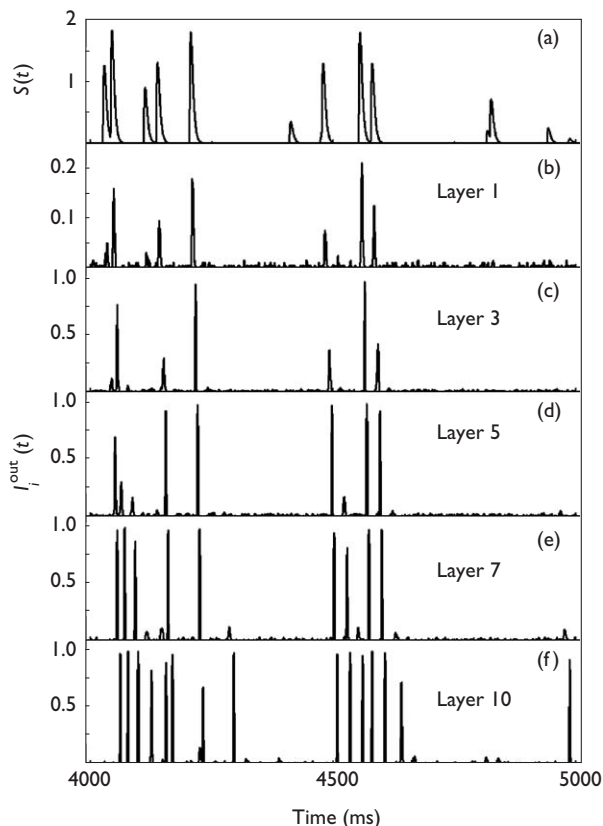


Fig. 4. (a) The input signal versus time with $D_1=D_s=0.7$. (b–f) Corresponding $I_i^{out}(t)$ of several layers.

the neurons of layer 1. The input takes the form $S(t) = \sum_{y=1} AP_y \alpha(t - t_y)$. Here, A is the amplitude and t_y is the time when the events take place. When an event happens, a random number P_y is generated, which lies between 0 and 1. Because $NI_i^{out}(t)$ can be regarded as the number of firings in a time bin in the i th layer, the performance of population rate coding in the i th layer can be evaluated by the maximum C_i of the coefficient $c_i(\tau)$, which is the correlation between $I_i^{out}(t)$ and the input signal. Here, $c_i(\tau)$ is defined as

$$c_i(\tau) = \frac{\sum (s(t) - \bar{s})(I_i^{out}(t + \tau) - \bar{I}_i^{out})}{\sqrt{\sum (s(t) - \bar{s})^2 \sum (I_i^{out}(t + \tau) - \bar{I}_i^{out})^2}} \quad (5)$$

The overbar represents an averaging over time. The input signal $I_i^{out}(t)$ and of several layers is plotted in Fig. 4(a–f). In the first three layers, the signal can be well read from $I_i^{out}(t)$, that is, these three layers work as efficient population rate coders. However, when neural activities propagate across the layers, only the packets of synchronous activities can survive and develop. This results in detailed information about the stimulus being gradually lost in the process of activity transmission. That is, the population rate code is gradually changed to the synchronous code through multiple layers, which makes the signal poorly encoded in deep layers. As shown in Fig. 5a, as the layer index increases, C_i decreases fast for different noise intensities. For each layer, there is a noise intensity with which the signal can be best

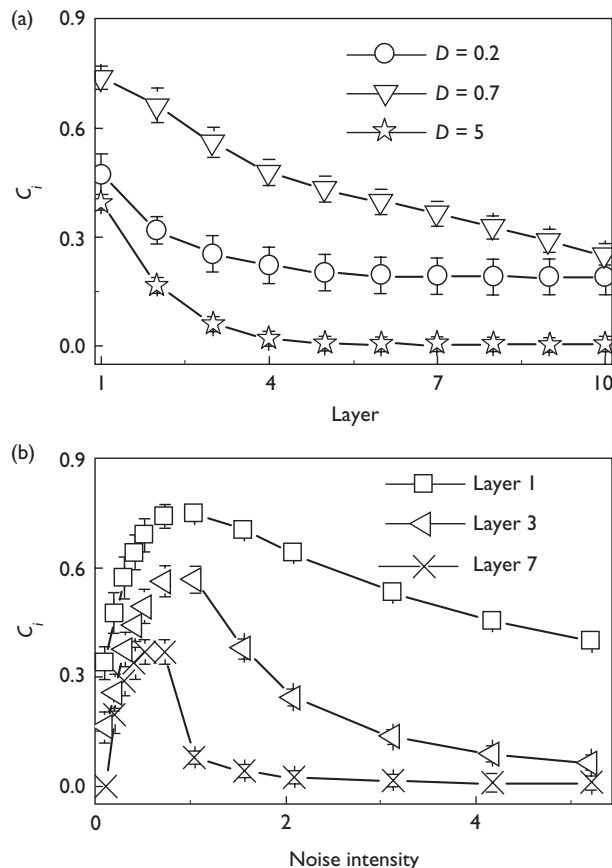


Fig. 5. (a) The maximum C_i versus the layer index with $D_1=D_s=0.2, 0.7, 5$. (b) The maximum C_i versus noise intensity in layers 1, 3, and 7.

read from the population rate (see Fig. 5b) because the signal used here is subthreshold. In addition, as can be seen from Fig. 4f, in deep layers, some synchronous packets result from only the noise input, which do not contribute to the encoding of the signal. When the noise intensity is large, much more synchronous packets arise from the noise input, which results in the signal being encoded more poorly. Therefore, in deep layers, the stimulus can hardly be read from the population rate with large noise intensity (see Fig. 5b). In our simulation with the HH neuron model, only the signals like pulse can be transmitted and the consecutive signals cannot be read from the population rate in deep layers. When there is a signal input like pulse in layer 1, the mode switch can take place in the process of activity transmission. By contrast, in [7], the mode is changed by altering the intensity of the noise current and the input signal is consecutive.

CONCLUSION

In this paper, it is found that CR is very significant in deep layers of a 10-layer feedforward network when noise current exists in all layers. On signal input to the network, the signal is encoded well by the population rate in the first three layers but the mode is switched to the synchronous mode in deep layers. In addition, a frequency sensitivity of signal transmission is also found for such a network.

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