Propagation of Firing Rate in a Feed-Forward Neuronal Network

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Propagation of the firing rate and synchronous firings in a 10-layer feed-forward neuronal network are studied. When neurons in layer 1 are subject to white noise, synchrony can be built up in deep layers and the firing rate can be propagated. A network with 6 layers is found to be enough for such behavior. A periodic signal with frequencies of 30–80 Hz can be selectively transmitted through the network. These abilities in information processing due to synchrony can be modulated by noise and the operating mode of neurons, and our results are relevant to experimental findings.

Neurons fire spikes when the total dendritic inputs reach a threshold, and information is encoded in the spike trains. There are two kinds of encoding mechanisms, namely, the firing rate and the spike timing. The firing rate encodes information by the numbers of spikes in time bins, which is an averaged effect [1]. Differently, the spike timing encodes information via precise locations of spikes, which is of a spatial-temporal scheme [2]. In nervous systems, every informational processing is related to many functional groups of neurons by which information is transferred from one group to its next groups [1]. Thus an interesting, but not well studied, model of network is multilayer feed-forward. It was found that synchronous firings can be propagated in a stable manner through such a network under appropriate conditions [3]. It was also shown that firing rates of deep layers seem to be independent of the input firing rate in an integrate-and-fire model [4]. Then propagation of the rate code in a feed-forward network was argued to be almost impossible [4]. However, this may be neuronal model dependent since experiments showed that synchronous firings can be formed and the firing rate can be propagated [5], implying that synchrony plays an important role in the rate coding scheme. Thus, it still needs to clarify what mechanism leads to the synchrony and how the firing rate is propagated in the multilayer network.

Here, we report a study on a 10-layer feed-forward network. The Hodgkin-Huxley (HH) neurons are used since they model firings more realistically. When background noise is delivered only to the neurons of layer 1, synchronous firings can be built up gradually layer by layer. The output rate strongly depends on the input rate, showing propagation of firing rate in the network. This can be modulated by the operating mode of the neurons depending on the synaptic time constant. It is found that a network with 6 layers is enough for such propagation. Thus we show that synchrony can be developed and the firing rate can be propagated in a multilayer feed-forward neuronal network. This is relevant to the propagation of the rate signal, consistent with experimental findings [5]. Our model is the first one to study the related behaviors, and

our work provides a theoretical interpretation of the synchrony-based code of the firing rate.

A 10-layer feed-forward network with $N = 200$ HH neurons in each layer is constructed. Each neuron randomly receives synaptic inputs from about 20, i.e., 10%, neurons in the previous layer. There are no couplings between the neurons within the same layer [Fig. 1(a)]. The dynamical equations for the network are [6]

$$C_m \frac{dV_{i,j}}{dt} = -g_{Na}m_{i,j}^3 h_{i,j}(V_{i,j} - V_{Na}) - g_K n_{i,j}^4(V_{i,j} - V_K)$$
$$- g_l(V_{i,j} - V_l) + I_0 + I_{i,j}^{\text{syn}}(t) + \eta_{i,j}(t), \quad (1)$$
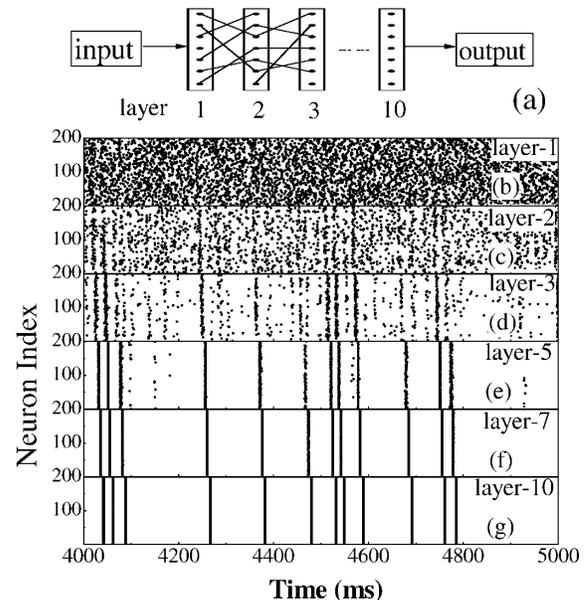
FIG. 1. (a) The model of a 10-layer feed-forward network with 200 neurons in each layer. Each neuron receives 20 inputs from the previous layer. (b)–(g) Dot-raster plots showing the firing patterns in different layers for $D_1 = 3$ and $D_s = 0$. Each row of dots represents a spike train for a single neuron with index $1 \leq j \leq 200$. A synchrony means that all (or almost all) 200 neurons fire spikes about simultaneously.

with $dm_{i,j}/dt = \alpha_m(V_{i,j})(1 - m_{i,j}) - \beta_m(V_{i,j})m_{i,j}$, $dh_{i,j}/dt = \alpha_h(V_{i,j})(1 - h_{i,j}) - \beta_h(V_{i,j})h_{i,j}$, and $dn_{i,j}/dt = \alpha_n(V_{i,j})(1 - n_{i,j}) - \beta_n(V_{i,j})n_{i,j}$. Here 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 related maximum conductance. C_m is the membrane capacity. Values of all these parameters and functions $\alpha_m(V)$, $\alpha_h(V)$, $\alpha_n(V)$, $\beta_m(V)$, $\beta_h(V)$, and $\beta_n(V)$ can be found in Ref. [6]. $I_0 = 1 \ \mu A/cm^2$ is a constant bias. The layer indices are $i = 1, \ldots, 10$, and the neuron indices are $j = 1, \ldots, 200$. The Gaussian white noise $\eta_{i,j}(t)$ satisfies $\langle \eta_{i,j}(t) \rangle = 0$ and $\langle \eta_{i,j}(t_1)\eta_{i,m}(t_2) \rangle = 2D_i\delta_{j,m}\delta(t_1 - t_2)$. Here D_i is referred to as the noise intensity of layer i with D_1 and $D_s = D_2 = \cdots = D_{10}$. The synaptic input from layer $(i - 1)$ to the neurons in layer i is $I_{i,j}^{syn}(t) = -N_{i,j}^{-1} \sum_{p=1}^{N_{i,j}} g_{syn}\alpha(t - t_{i-1,p})(V_{i,j} - V_{syn})$ 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 with synaptic weight $g_{syn} = 0.6$. The synaptic reversal potential $V_{syn} = 0$ implies that all the couplings are excitatory. $t_{i-1,p}$ is the firing time of the pth presynaptic neuron in layer $(i - 1)$ coupled with neuron (i, j). The rising time of the synaptic input τ is set to 2 ms unless specified elsewhere. Firings of each neuron are recorded and converted into a time series of standard pulses $U_j = U_A$ or U_B with $U_A = 1$ of width 2 ms and $U_B = 0$ corresponding to the firing and nonfiring states. The output of layer i is $I_i^{out}(t) = N^{-1} \sum_{j=1}^{N} U_j(t)$. Numerical integration of Eq. (1) is done by a second-order stochastic algorithm [7]. The firing rate of each layer is obtained by averaging over all the neurons in this layer within a long time window of 20 s.

Now, let us report the results for a case of noise input only to layer 1, i.e., $D_1 \neq 0$ and $D_s = 0$. Since the inputs are white noise, each neuron in layer 1 fires spikes irregularly [Fig. 1(b)]. In layer 2 and layer 3 [Fig. 1(c) and 1(d)], the numbers of spikes decrease, implying that the firing rate decreases. However, there is a tendency of synchrony, and several blurry columns of spikes appear in the firing pattern in layer 2. This becomes clear in layer 3 where there are several distinct columns of firings. From layer 5 [Figs. 1(e)–1(g)], the synchrony is well established and can be quantified by a coherence measure K_i [8]. Here K_i is obtained by averaging the pair coherence $K_{i,jm}(\gamma)$ between neurons j and m over all neuronal pairs in layer i, i.e., $K_i = [N(N-1)]^{-1} \sum_{j=1}^{N} \sum_{m=1,j\neq m}^{N} K_{i,jm}(\gamma)$. The pair coherence $K_{i,jm}(\gamma) = \sum_{l=1}^{k} X(l)Y(l)/[\sum_{l=1}^{k} X(l) \sum_{l=1}^{k} Y(l)]^{-1/2}$ is measured by the cross correlation of spike trains at zero time lag within a time bin γ. A long time interval $T = 5$ s is divided into k bins of $\gamma = 1$ ms, and two spike trains for neurons j and m are given by $X(l) = 0$ or 1 and $Y(l) = 0$ or 1 with $l = 1, 2, \ldots, k$ (here $T/k = \gamma$). Figure 2(a)
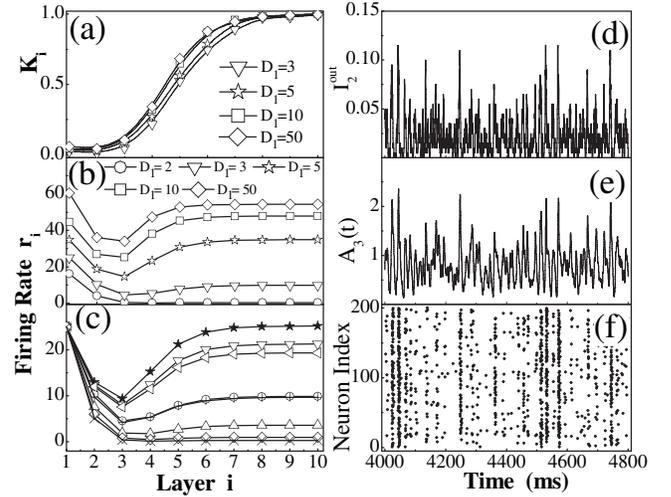
FIG. 2. (a) Coherence measure K_i versus layer i for $D_s = 0$ and different noise intensities D_1. (b) Firing rate r_i versus layer i for $D_s = 0$ and different noise intensities D_1. (c) Firing rate r_i versus layer i for $D_1 = 3$, $D_s = 0$, and different time constants of the synaptic input τ: 2 ms ($\bigcirc$), 2.5 ms ($\bigtriangledown$), 3 ms (*), 4 ms ($\triangleleft$), 5 ms (+), 6 ms ($\triangle$), 7 ms ($\diamond$), 8 ms ($\times$). (d) $I_2^{out}(t)$ as a function of time for $D_1 = 3$ and $D_s = 0$. (e) The synaptic input current $A_3(t)$ of layer 3 as a function of time. (f) The dot-raster plot of firings for the neurons in layer 3.

shows that the degree of synchrony increases and is saturated to $K = 1$ at layer 8. Note that such a development of synchrony is really related to the experimental observation in Ref. [5] where neuronal firings in iteratively constructed networks *in vitro* are asynchronous for the first 2–3 layers but become progressively more synchronous in successive layers [cf. Fig. 2(a) in Ref. [5]]. The saturation of the coherence measure K at layer 8 is the same as that of the area of the cross-correlation histogram peak since the area, which also quantifies the synchrony, increases sigmoidally with layer and is saturated at layer 8 too [5].

The underlying mechanism can be interpreted as follows. The membrane time constant of neurons, $C_m/g_l = 3.3$ ms, is larger than the rising time of synaptic inputs $\tau = 2$ ms. Each synaptic input results in a fast change of the membrane potential. Thus, all neurons in the network operate as coincidence detectors [9] and are sensitive to the exact timing of synaptic inputs. Since all neurons in the same layer have basically the same magnitude of synaptic inputs due to the correlation between the neurons of two neighboring layers, the fast changes of potentials make the neurons fire synchronously. It can be seen clearly from the output of layer-i $I_i^{out}(t)$ where the peaks generate large transient synaptic inputs $A_{i+1}(t) = N^{-1} \sum_{j=1}^{N} I_{i+1,j}^{syn}(t)$ to layer $(i + 1)$. These inputs may be larger than the threshold of the neurons and effectively trigger the firings. An example of such a synaptic effect is shown in Figs. 2(d)–2(f), and all the main peaks in layer 2 [Fig. 2(d)], the large synaptic current [Fig. 2(e)], and the firings in layer 3

[Fig. 2(f)] are clearly related. Note that small peaks generate only small responses in the synaptic currents at layer 3, which may not be enough to fire the neurons or may lead only to sparse firings. These cannot effectively trigger the postsynaptic neurons in the next layer to fire, and thus the sparse firings disappear gradually in the next layers. In contrast, the packets of synchronous firings survive and develop.

The firing rate decreases in the first three layers, and then increases to a saturated value except for cases of very small noise [Fig. 2(b)]. This is also similar to the experimental measurements [cf. Fig. 6(b) in Ref. [5]]. The saturated values are different for different noise intensities. From layer 1 to layer 3, the firing rate decreases because the numbers of filtered firings are quite large. Differently, from layer 5 to layer 10, the firing rate increases and is finally saturated to a value since the synchronous firings can be propagated stably and the sparse firings almost disappear. Because the firings of spikes are quite sparse in layer 1 for the case of small noise $D_1 = 2$, the synchrony in later layers hardly occurs and the firing rate cannot be propagated in the network. Thus the occurrence of synchronous firings in the first several layers depends on the firing rate of layer 1, termed the input rate r_{in}. As a result, the firing rate of layer 10, termed the output rate r_{out}, depends on the input rate. This means a propagation of the rate signal as long as the noise intensity is large enough. Such a propagation of the firing rate through the network occurs due to the synchronous firings that result from the correlation between the neurons. Note that the input rate r_{in} and the output rate r_{out} are the same only when the noise intensity is about $D_1 = 5$–10 although the synchrony is robust to various values of noise intensity.

Interestingly, the propagation of the firing rate can be controlled by modulating the operation mode of neurons, i.e., by changing the synaptic time constant τ, which enables the neurons sensitive to the change of synaptic inputs. Figure 2(c) shows results for various values of the time constant τ. It is found that the most optimal time constant for the propagation is about $\tau = 2.5$–4 ms, and the best one is $\tau = 3$ ms with which the input firing rate r_{in} can be exactly propagated. Beyond this region, the firing rate is hardly propagated. For a small time constant, such as $\tau < 2$ ms, the change of the synaptic input is so fast that the neurons cannot fire following every change of the synaptic current. As a result, the neurons working as coincidence detectors may miss some synaptic current, implying that the firing rate is low. When $\tau > 6$ ms, since the variation of the synaptic current is quite slow, the neurons, operating as temporal integrators [9], could not sum up enough synaptic current to reach their threshold for firing. Thus the neurons do not fire spikes effectively, and the firing rate is low or the temporal patterns are propagated with low reliability [10].

A plot of the firing rate r_i of layer i versus the input rate r_{in} clearly shows the variation of the firing rates (Fig. 3). It
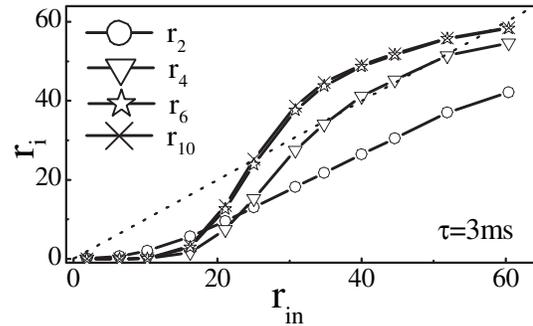
FIG. 3.   Firing rate r_i versus the input firing rate r_{in} for $\tau = 3$ ms and $D_s = 0$. The dashed line is for $r_i = r_{in}$.

is seen that the firing rates of these layers depend on the input rate r_{in}. The firing rate r_2 shows basically a linear increasing as the input rate r_{in} increases when $r_{in} > 10$, while the firing rates r_4, r_6, and r_{out} versus r_{in} have a sigmoid increasing. That is, after layer 4, the firing rate r_i increases rapidly when the input firing rate $r_{in} > 20$, and almost becomes saturated when $r_{in} > 55$. Especially the values of r_6 and r_{out} are almost the same, and even the rate gain r_i/r_{in} can be larger than 1 when $r_{in} > 25$ since the synchrony is well built up after layer 5. These really imply the propagation of the input firing rate. Importantly, such variation of the firing rate r_i versus r_{in} depends on the time constant τ (Fig. 4). For different values of τ, the values of r_2 are almost the same [Fig. 4(a)]. The firing rates of layer 4, layer 6, and layer 10 show a nonlinear dependence on r_{in}, and an optimized time constant $\tau = 3$ ms can be obtained. Moreover, a range of r_{in} values with the rate gain $r_i/r_{in} > 1$ is zero for layer 4 [Fig. 4(b)], and is from $r_{in} = 25$ to 60 for layer 6 and layer 10 [Figs. 4(c) and 4(d)] when $\tau = 3$ ms, respectively. For low values of τ, such a range is narrow or even disappears. In addition, because the synchrony develops very well about in layer 6, all the curves of the firing rate versus the input rate r_{in} for layer 6 are almost the same as those for layer 10 [Figs. 4(c) and 4(d)]. That is,
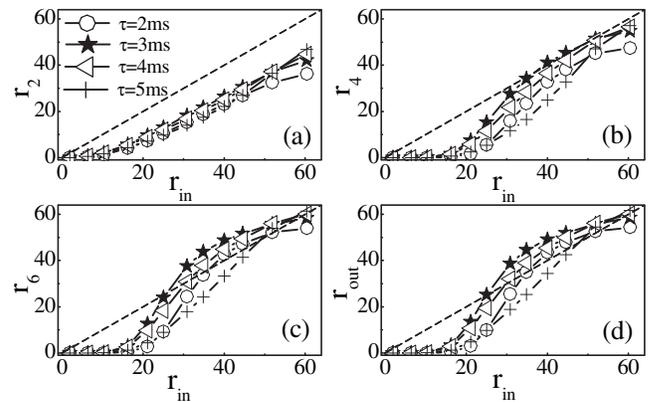
FIG. 4.   Firing rate r_2 of layer 2 (a), r_4 of layer 4 (b), r_6 of layer 6 (c), and r_{out}, i.e., the output rate of the network (d) versus the input rate r_{in}. The dashed line is for $r_i = r_{in}$.
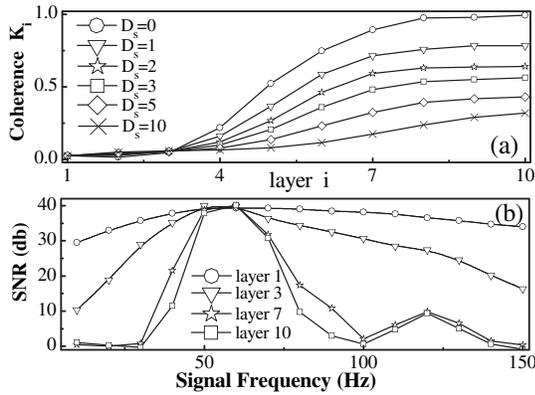
FIG. 5. (a) Coherence measure K_i versus layer index i for $D_1 = 3$ and different noise intensities D_s. (b) SNR as a function of the input signal frequency at different layers for $D_1 = D_s = 5$.

the firing rate r_i with $i > 5$ converges to the output of the network r_{out}. This indicates that a network with 6 layers is enough for the propagation of the firing rate if the neurons work in an optimized firing mode with time constant $\tau = 3$ ms.

As discussed above, synchrony is the default state in the feed-forward network. Let us consider a more realistic case with white noise injected to all the neurons of the network. As shown in Fig. 5(a), the degree of synchrony decreases as the noise intensity D_s increases. This is reasonable since stronger noise, of course, introduces more random input to the neurons. What role does the synchrony play in signal transmission, such as for a periodic subthreshold signal $A\cos(2\pi f_s t)$ with amplitude $A = 1$ and frequency f_s subjected to each neuron in layer 1? Figure 5(b) shows the signal-to-noise ratio (SNR) [11] for various layers versus the frequency of the signal. As the layer index increases, the values of SNR decrease. But at layer 7 the values of SNR become saturated, which is relevant to the saturation of the synchrony and the firing rate. There is a most sensitive range of 30–80 Hz in which the signal can be transmitted more efficiently and the firings are well synchronized. This phenomenon is a consequence of the na-

ture of the HH neurons themselves [12]. Obviously, synchrony encodes the signal with high precision, improving the signal transmission within the network. In addition, such a sensitive range is really relevant to the 40 Hz oscillations in nervous systems due to the multilayer feature [13,14].

In conclusion, synchronous firings can develop gradually within a feed-forward multilayer network, and help the propagation of firing rate and temporal signal in the network. The output rate depends on the input rate, resulting from the dependence of the occurrence of synchronous activities in the first several layers on the input rate. These can be modulated by the operating mode of neurons, which may be lacking for some simplified neuronal models. A most sensitive region of frequencies is found, showing a preference to the periodic signal.

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