

Dual Coding and Effects of Global Feedback in Multilayered Neural Networks

Naoki Masuda¹, Kazuyuki Aihara²

¹ Faculty of Engineering, Yokohama National University, Yokohama, Japan
masuda@lam.osu.sci.ynu.ac.jp

² Institute of Industrial Science, The University of Tokyo, Tokyo, Japan

Abstract

The synchronous firing code mode and the population rate code mode can alternatively appear in a single neural network to be dually used depending upon situations. In this paper, we examine by using multi-layered feedforward networks how the preferred coding mode switches as signals pass through layers. It is also shown that global feedback synchronizes neurons in the upstream layers.

Keywords: Integrate-and-fire neurons; Rate coding; Synchrony; Feedback

1 Introduction

As opposed to rate coding [7], temporal codes based on precisely timed spiking or synchronous firing have been studied [1, 4]. For example, neurons receiving common preferred stimuli tend to synchronize probably to bind the corresponding information. Nonetheless, functional meanings of precisely timed neural activities are still putative. Even without it, signal estimation with short-term firing rates can be improved by pooling just less than 100 neurons and resorting to population firing rates [5, 6, 7, 8].

Although rate coding and temporal coding have been often discussed as competitive hypotheses, they may work complementarily rather than exclusively. In a single feedforward network with leaky integrate-and-fire (LIF) neurons, they are bridged by changing the noise intensity [5, 8] or other model parameters [6]. Weak dynamical noise, strongly correlated inputs, strong intralayer feedback,

large membrane leak rates, and homogeneity drive the neurons toward synchronization, where the network encodes the signal crudely but robustly with inter-synchronization intervals [2, 5]. This synchronous coding also saves consumed power since downstream neurons fire more easily with synchronous inputs [1]. On the other hand, coding accuracy is limited by the duration of the typical interspike interval. At the other extreme, the temporal waveform of the signal is well approximated by population firing rates when neurons are asynchronously firing [7]. These theoretical results [6] suggest that two coding schemes may dually work dependent on physiological conditions and anatomical structure [1]. Animals may resort to the population rate code with higher accuracy when they are exposed to imminent circumstances. After adapting to the situation, internal parameters or background activities may be modulated in the brain to shift to the less accurate but more robust synchronous coding.

In this paper, we extend the framework to multi-layered networks to discuss how the coding mode changes from layer to layer and how interlayer or global feedback influences the dynamics. In Sec. 2, we describe the model neural network and the performance measures. In Sec. 3, we examine in terms of various model parameters how coding modes change as spike trains propagate through layers. Effects of global feedback are investigated in Sec. 4.

2 Model

The network model is depicted in Fig. 1. The network consists of three layers A , B , and C , each with $n_1 = 300$, $n_2 = 60$, and $n_3 = 30$ neurons, respectively. The neurons in layer A are nonleaky integrate-and-fire (IF) neurons driven by a common input $S(t)$. Each neuron fires when the membrane potential reaches 1, and it is instantaneously reset to the resting potential 0. At the same time, it sends instantaneous spikes with amplitude ϵ_{BA} to layer B . The initial membrane potentials are chosen randomly from the uniform distribution on $[0, 1]$ to ensure that layer A operates as an efficient population rate coder without synchronization [8]. The results in the following can be extended to more realistic cases with a leak.

Every neuron in layer B receives spike trains from $n'_1 = 150$ neurons in layer A and the global

feedback input $\hat{I}_i(t)$ from layer C . Layer B consists of LIF neurons without external bias. The i th neuron ($1 \leq i \leq n_2$) has a membrane potential $v_i(t)$, a threshold for firing $v_i(t) = \Theta_i$ ($E[\Theta_i] = 1$), and a resting potential $v_i(t) = 0$. Upon firing, it sends instantaneous spikes with delay $\tau = 2$ ms and amplitude ϵ_{BB} to the other neurons in layer B . The dynamics of the i th neuron in layer B is described by

$$\frac{dv_i}{dt} = \sum_{i' \in S_i} \sum_j \epsilon_{BA} \delta(t - T_{i',j}^A) + \sum_{i' \neq i, i'=1}^{n_2} \sum_j \epsilon_{BB} \delta(t - T_{i',j}^B - \tau) - \gamma v_i(t) + \hat{I}_i(t), \quad (1 \leq i \leq n_2) \quad (1)$$

where $\gamma = 0.025 \text{ ms}^{-1}$ is the membrane leak rate, and δ is the delta function. The i th neuron in layer B receives the j th spike of the i' th neuron in layer A at $t = T_{i',j}^A$ only if $i' \in S_i$ where $|S_i| = n'_1$. The j th firing of the i' th ($1 \leq i' \leq n_2$) neuron in layer B occurs at $t = T_{i',j}^B$. Layer C consists of completely connected n_3 LIF neurons with the same properties as those in layer B . The neurons receive feedforward spikes with amplitude ϵ_{CB} from randomly chosen $n'_2 = 60$ neurons in layer B , and intralayer feedback spikes with amplitude ϵ_{CC} and delay τ . We set $\epsilon_{BB} = \epsilon_{CC} = 0.002$, $\epsilon_{BA} = 0.007$, $\epsilon_{CB} = 0.05$ so that the firing rate in each layer is maintained around 20 Hz [6]. Finally, the global feedback from layer C to layer B is given by

$$\hat{I}_i(t) = \sum_{i'=1}^{n_3} \sum_j \epsilon_{BC} \delta(t - T_{i',j}^C - \hat{\tau}), \quad (1 \leq i \leq n_2) \quad (2)$$

where $\hat{\tau} = 3$ ms, and $T_{i',j}^C$ is the j th firing time of the i' th neuron in layer C . To layer B and layer C , we introduce heterogeneity in the firing threshold that is inherent in real neurons. The threshold Θ_i of the i th neuron in layer B is drawn randomly according to the uniform distribution $[1 - \Delta_\Theta, 1 + \Delta_\Theta]$. Layer B tends to synchronize for small Δ_Θ , whereas accurate population rate coding with asynchronous firing is realized with increased Δ_Θ [6].

The external input $S(t)$ is generated from the Lorenz equations: $\dot{x} = a(10y - 10x)$, $\dot{y} = a(28x - y - xz)$, $\dot{z} = a(-\frac{8}{3}z + xy)$, and $S(t) = 2.25 \times 10^{-2} + 7.00 \times 10^{-4}x$. The chaotic signal $S(t)$ models non-random dynamical rules with complexity contained in complex external stimuli, but similar results are also obtained with stochastic $S(t)$ [6, 8]. The change rate $a = 0.03$ so that the characteristic time scale of $S(t)$ is smaller than interspike intervals. Accordingly, synchronous firing can encode $S(t)$ only with low temporal resolutions.

To evaluate the degree of synchrony in layer B , we calculate the order parameter [5, 6] defined by $r = \left\langle \left| \sum_{j=1}^{n_2} e^{2\pi\sqrt{-1}v_j(t)} \right| \right\rangle / n_2$ where $\langle \cdot \rangle$ is the temporal average, and similarly for layer C . Full synchrony and full asynchrony mark the maximum ($r = 1$) and the minimum ($r = 0$) of r , respectively. Performance of rate coding is evaluated by the correlation coefficient *corr* between $S(t)$ and short-time population firing rates calculated with a bin width of 4 ms.

In principle, each neuron in layer B or C gathers small contributions from layer A , which is assumed to be asynchronous, to restore the signal information [7]. However, the neurons in downstream layers synchronize for certain configurations to switch to the degenerated but robust synchronous regime [5, 6, 8].

3 Switching of Coding Modes through Layers

Previously, we showed with two-layered networks that layer B works in the rate code mode or the synchronous code mode when layer A is asynchronous and works as an efficient rate coder [5, 6]. Repeating the same argument, we can generalize the results to multilayered cases. In this section, let us suppose that the network is purely feedforward by setting $\epsilon_{BC} = 0$. When layer B works as the population rate coder, layer C is in synchrony or asynchrony dependent on situations [6]. When layer C and subsequent layers are asynchronous and serve as effective rate coders with, for example, strong noise or heterogeneity, accurate information on the input is transmitted through many layers [8].

What does layer C do when layer B is synchronous? Once a layer is synchronized, the network loses high-resolutional signal information in exchange for robustness. If layer C receives synchronous volleys from layer B , the neurons in layer C tend to synchronize, and synchronous volleys are passed on to subsequent layers [1, 4, 8]. Though the neurons in layer C could desynchronize under strong noise or heterogeneity, layer C is no longer capable of accurate rate coding because information on $S(t)$ is already degraded when the neural activity has passed through layer B that is in synchrony [6]. Layer C and subsequent layers encode no more than the coarse information on the input rates encoded by layer B .

In sum, it is easy to switch from population rate code to synchronous code while the reverse is difficult [1]. This unidirectional modal change can occur at a certain stage. Once synchrony is reached, it is used in all the downstream layers. However, we do not exclude the possibility that rate codes are again used in a layer posterior to the synchronous layer. In fact, actuators such as muscle are likely to be controlled by firing rates although the signal is relayed from the cortex, where temporal codes seem to be important [1]. In this situation, the rate codes in downstream circuits are different from those in the upstream circuits that may simply reproduce external stimuli.

In Fig. 2, we compare coding performances of two different asynchronous states in layer C of the purely feedforward networks. We gradually increase Δ_{Θ} to continuously change the dynamical state of layer B from synchrony to asynchrony. Moreover, additive Gaussian white noise with amplitude 0.006 per $dt = 0.02$ ms and firing thresholds with 25 % heterogeneity are assumed for layer C so that layer C is in asynchrony (see Fig. 2(a)). Figure 2(b) shows that accurate rate coding by layer C is realized only when layer B is asynchronous with large Δ_{Θ} .

4 Effects of Global Feedback

Global feedback exists among layers in real neural networks. It may contribute to reverberate global information on stimuli into upstream layers where the information on local and global stimulus features can be combined. Model analysis indicates that global feedback may induce and reinforce synchronization in upstream layers [3], which agrees with a general understanding that correlated inputs compel neurons to synchronize [6, 7].

Figure 3 shows r and $corr$ in layers B and C when the global feedback strength ϵ_{BC} is varied. We assume the inhibitory feedback to prevent explosion in firing rates, which is characteristic of positive feedback. We set $\Delta_{\Theta} = 0.25$ so that layer B is asynchronous in the absence of global feedback. To compare how two modes in layer C influence the dynamics of layer B , we let layer C synchronous by introducing Gaussian white noise with amplitude 0.001 per $dt = 0.02$ ms and no heterogeneity (dotted lines), or asynchronous by introducing Gaussian white noise with amplitude 0.001 per $dt = 0.02$ ms and 20 % inhomogeneity in the firing threshold (solid lines). The results

for the two cases are distinguished by the discrepancy in the values of r and $corr$ of layer C shown in Figs. 3(c) and (d).

Layer C sends correlated inputs back into layer B because of the high shared connectivity of the global feedback (Eq. (2)). Stronger global feedback induces more synchrony in layer B (Fig. 3(a)) and deteriorates the estimation of external stimuli (Fig. 3(b)). The two modes in layer B are bridged by modulating ϵ_{BC} . An observation is that the population rate coding also deteriorates in layer C (Fig. 3(d)) with the global feedback while the degree of synchrony remains almost constant (Fig. 3(c)). This is because layer C receives synchronous volleys that give arise in layer B . Such feedforward inputs are fairly irrelevant to the external stimuli and deteriorate the signal estimation in layer C . It is interesting that the global feedback can affect the dynamical states not only of layer B but also of layer C .

Synchrony may be also stabilized by global feedback. Introduction of global feedback can enhance synchrony in layer B to boost the whole network toward a robust regime. Our results suggest possible roles of global feedback to induce and stabilize synchronous firing in feedforward networks [3].

5 Conclusions

We have shown that coding modes can unidirectionally switch from rate coding to synchronous coding in multi-layered feedforward networks and that global feedback can induce synchronous coding in the relevant layers. Feedforward networks with partial reverberation of activities from downstream neurons into upstream neurons are general cortical architectures [1, 3]. Our results suggest how feedforward and feedback connections cooperatively organize cortical dynamics.

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Biosketch:

Naoki Masuda received the B.E. degree, the master degree, and Ph.D degree in mathematical engineering and information physics in 1998, in 2000, and in 2002, respectively, from the University of Tokyo, Japan. Currently, he is postdoctoral fellow at Yokohama National University, Japan. His research interests include theoretical neuroscience, social dynamics, network theory, chaotic cryptosystems, and time series analysis.

Kazuyuki Aihara received the B.E.degree in electrical engineering and the Ph.D. in electronic engineering, both from the University of Tokyo, Tokyo, Japan, in 1977 and 1982, respectively. He is now Professor at Institute of Industrial Science and at Department of Complexity Science and Engineering in the University of Tokyo. His research interests include mathematical modeling of biological systems, parallel distributed processing with chaotic neural networks, and time series analysis of chaotic data.

Figure captions:

Figure 1: Architecture of the multilayered feedforward network model.

Figure 2: Coding performance measures (a) r and (b) $corr$ for layers B (solid lines) and C (dotted lines) when Δ_{Θ} is varied in purely feedforward networks. Trial averages over 100 runs are taken to calculate r and $corr$.

Figure 3: Coding performances r (a, c) and $corr$ (b, d) for layers B (a, b) and C (c, d) when the global feedback strength ϵ_{BC} is changed. When $\epsilon_{BC} = 0$, layer B is asynchronous while layer C is either asynchronous (solid lines) or synchronous (dotted lines).

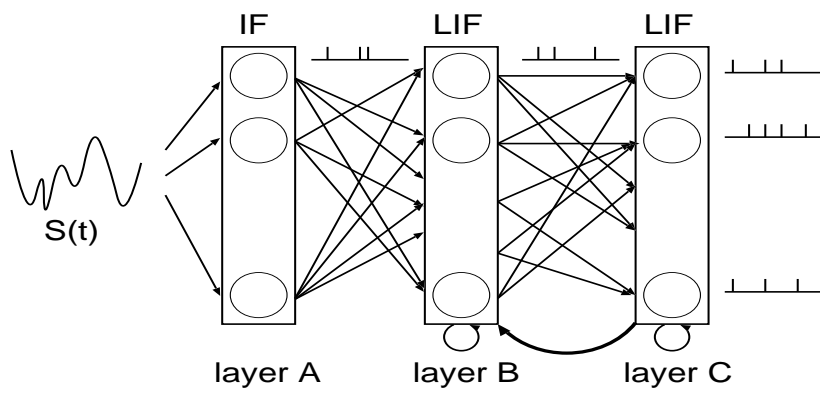


Figure 1:

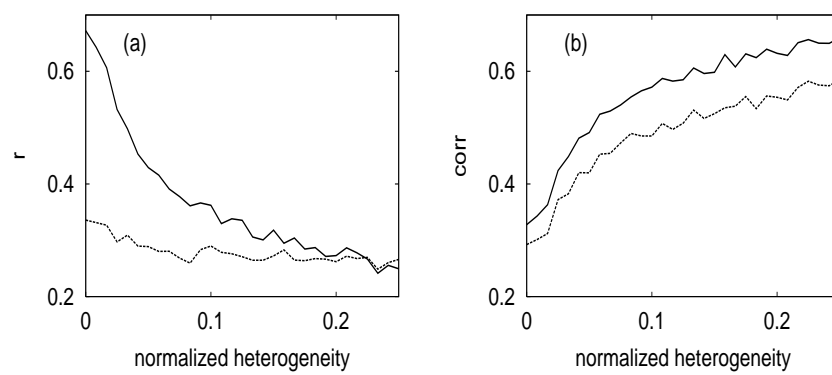


Figure 2:

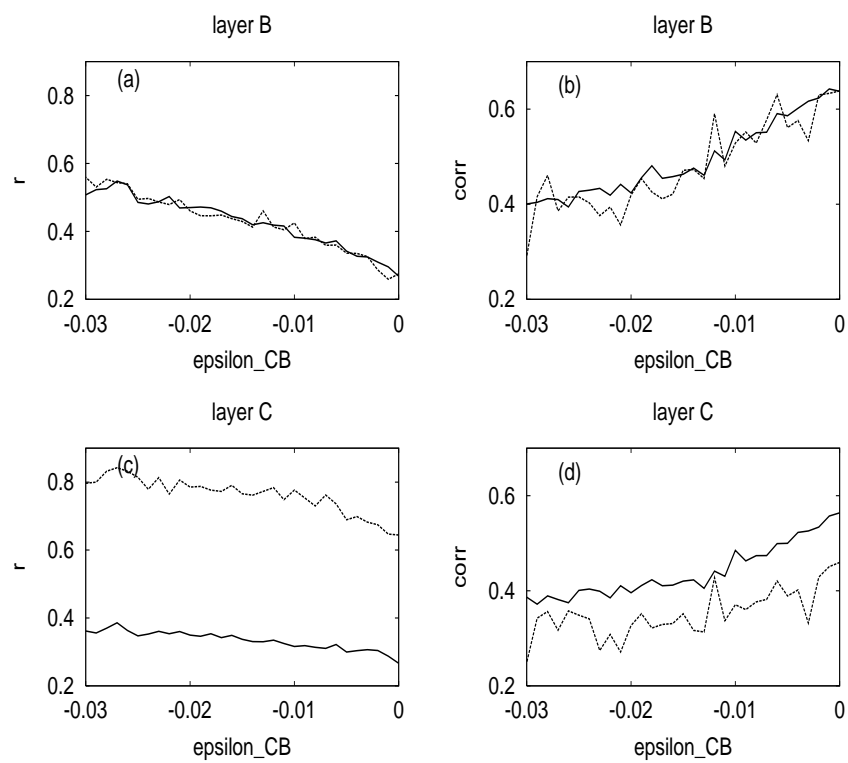


Figure 3: