

Dual Coding and Effects of Global Feedback in Multilayered Neural Networks

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Abstract

Two dynamical regimes characterized by the dominance of the synchronous firing code and the population rate code 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.

1 Introduction

The information coding by firing rates requires longer time than biologically acceptable if time averaging is involved. As opposed to the rate coding, the temporal codes with high temporal resolutions based on precisely timed spiking or synchronous firing have been argued [1, 4, 5]. Accurate timing of individual spikes and temporal patterns of interspike intervals may have nontrivial meanings. For example, neurons with common preferred stimuli synchronize probably to bind the corresponding objects. Nonetheless, the 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 the firing patterns of less than 100 neurons as population firing rates [8, 9, 10, 11].

Although the rate coding and the 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 [8, 11] or other model parameters [9]. Weak dynamical noise, strongly correlated inputs, strong intralayer feedback, large membrane leak rates, and homogeneity in neural networks drive the neurons toward synchronization, where the network encodes the signal crudely but robustly in its inter-synchronization intervals [8]. This synchronous coding also has the merit of less power consumption since downstream neurons fire more easily with synchronous inputs [1]. On the other hand, the coding accuracy is limited by the duration of the typical interspike interval. At the other extreme, asynchronously firing neurons collect versatile information on external signals. As a result, the temporal waveform of the signal is well approximated by the population firing rates [10].

These theoretical results accompanied by the experimental results on switching between synchronous and asynchronous modes [3] suggest that two coding schemes may dually work in real neural networks 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 they have adapted to the situation, the modulation of internal parameters or background activities may occur in the brain to shift to the less accurate but more robust synchronous coding. In this paper, we extend the dual coding to multi-layered networks to discuss how

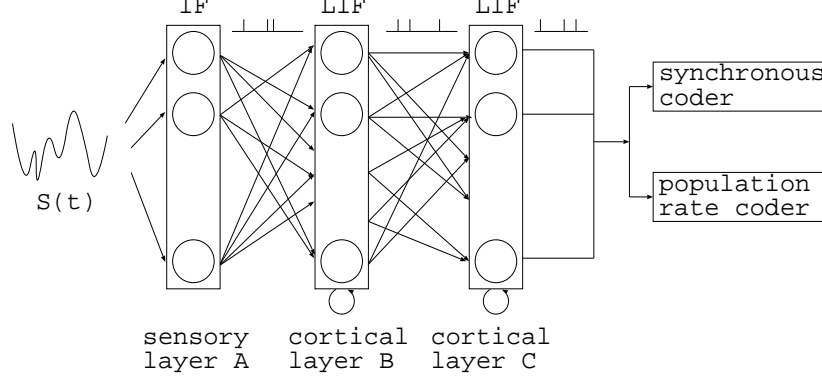


Figure 1: Architecture of the feedforward neural network model.

the coding mode shifts from layer to layer and how inter-layer feedback influences the information coding.

In Sec. 2, we describe the model neural network and the performance measures for two coding schemes. In Sec. 3, we examine in terms of various model parameter values how the coding modes change as spatio-temporal spike trains pass through layers. The effects of global feedback are examined in Sec. 4.

2 Model

The neural network model used in this work is depicted in Fig. 1. The network consists of three layers: a sensory layer A with $n_1 = 480$ neurons, an upstream cortical layer B with $n_2 = 30$ neurons, and a downstream cortical layer C with $n_3 = 30$ neurons. Sensory neurons are nonleaky integrate-and-fire (IF) neurons driven by common continuous external input $S(t)$. The i th sensory neuron fires when the membrane potential reaches 1, and it is instantaneously reset to the resting potential 0, and at the same time, it sends a spike with amplitude $\bar{\epsilon}$ to cortical neurons in 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 [7, 11]. The results in the following can be extended to more realistic sensory neurons with a leak [7].

Every cortical neuron in layer B receives instantaneous incident spike trains from $n'_1 = 240$ sensory neurons and the global feedback input \hat{I}_i from layer C . The neurons in layer B are 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 $v_i(t) = 0$. With constant synaptic delay τ , this cortical neuron sends an instantaneous feedback spike with amplitude ϵ to the other neurons within layer B . The dynamics of the i th cortical neuron in layer B is described by

$$\frac{dv_i}{dt} = \sum_{i' \in S_i} \sum_j \bar{\epsilon} \delta(t - T_{i',j}) + \sum_{i' \neq i, i'=1}^{n_2} \sum_j \epsilon \delta(t - T'_{i',j} - \tau) - \gamma v_i(t) + \hat{I}_i, \quad (1 \leq i \leq n_2) \quad (1)$$

where $\gamma > 0$ 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 sensory neuron at $t = T_{i',j}$. The delay between the sensory and cortical layers is not assumed for simplicity. The i th cortical neuron receives incident spikes only from the i' th sensory neuron with $i' \in S_i$ where $|S_i| = n'_1$. The j th firing of the i' th ($1 \leq i' \leq n_2$) cortical neuron occurs at $t = T'_{i',j}$. Layer C consists of completely connected n_3 LIF neurons with the

same properties as those in layer B . The neurons receive feedforward incident spikes with amplitude $\tilde{\epsilon}$ and local feedback spikes with amplitude ϵ and delay τ . We set $\gamma = 0.025 \text{ ms}^{-1}$, $\tau = 2.6 \text{ ms}$, $\epsilon = 0.002$, $\bar{\epsilon} = 0.007$, $\tilde{\epsilon} = 0.05$ so that the firing rate in each layer is maintained around 20 Hz [3]. Finally, the global feedback from layer C to layer B is given by

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

where $\hat{\tau} = 3.0 \text{ ms}$, and $T_{i',j}''$ 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 $[1 - \Delta_\Theta, 1 + \Delta_\Theta]$. The strength of heterogeneity is determined by Δ_Θ . Layer B prefers the synchronous coding when Δ_Θ is small whereas the population rate coding with asynchronous firing is more efficient with increased Δ_Θ [9].

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 continuous signal $S(t)$ models non-random dynamical rules with complexity contained in complex external stimuli such as visual scenes and sounds, but similar results are obtained with stochastic $S(t)$ [9, 11]. The change rate $a = 0.03$ so that the characteristic time scale of $S(t)$ is smaller than interspike intervals. Accordingly, synchronous firing cannot capture the high-frequency components of the signal, and it can encode $S(t)$ only with low temporal resolutions.

The spike trains emitted from layer C are observed by the synchronous coder and the population rate coder. To evaluate the degree of synchrony, we calculate the order parameter [6] defined by

$$r = \frac{1}{n_3} \left\langle \left| \sum_{j=1}^{n_3} e^{2\pi\sqrt{-1}\tilde{v}_j(t)} \right| \right\rangle, \quad (3)$$

where $\langle \cdot \rangle$ is the temporal average. Complete synchrony and full asynchrony mark the maximum ($r = 1$) and minimum ($r = 0$) values of r , respectively. Performance of the population rate coding is evaluated by the correlation coefficient *corr* between the external signal and the short-time population firing rate derived by counting the number of spikes that fall in one of the regularly arranged bins each of which is 3.8 ms wide.

Each sensory neuron integrates the external stimulus to encode its different aspect. In principle, each cortical neuron in layer B or C gathers small contributions from many sensory neurons to reconstruct the signal information [7, 10]. However, the cortical neurons synchronize for certain configuration of neuronal and coupling properties to switch to the degenerated but robust coding [8, 9, 11].

3 Switching of Coding Modes through Layers

In our previous papers with two-layered networks, we showed that the cortical layer (layer B) works in the rate code mode or the synchronous code mode when the sensory layer (layer A) works as an efficient rate coder without synchronous firing [8, 9]. Repeating the same argument, we can generalize the results to multi-layered cases. In feedforward networks with three layers (Fig. 1), when layer B works as the population rate coder, layer C works in the rate code mode or the synchronous code mode dependent on situations. When layer C and the subsequent layers work as effective rate coders with, for example, sufficiently strong noise or heterogeneity in neurons, the accurate information on the input is transmitted through many layers [11].

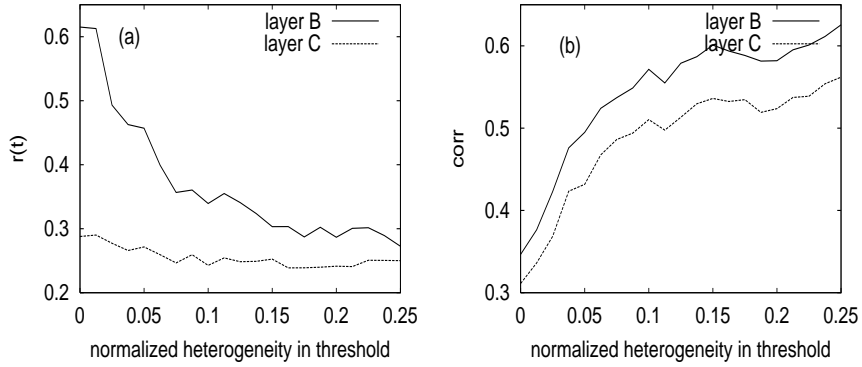


Figure 2: The coding performance measures (a) r and (b) $corr$ for layers B and C when Δ_{Θ} is varied in purely feedforward networks. The trial averages based on 100 runs are taken to calculate r and $corr$.

On the other hand, what happens in layer C when layer B is the synchronous coder? Once synchronous firing is realized in a layer, the network loses high-resolutional signal information necessary for accurate signal estimation 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 the downstream layers [1, 4, 11]. Though the neurons in layer C could desynchronize under strong noise or heterogeneity, layer C is no longer capable of efficient population rate coding of $S(t)$ because information on the stimulus is already degraded when spatio-temporal spike trains pass through layer B that is in synchrony. Layer C and the subsequent layers encode no more than the coarse information on the signal encoded by B .

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

In Fig. 2, we compare the coding performances of two different asynchronous states in layer C of the purely feedforward networks. Namely, we set $\hat{\epsilon} = 0$, and gradually increase Δ_{Θ} to continuously change the dynamical state of layer B from synchrony to asynchrony. Moreover, additive Gaussian white noise with amplitude 0.007 per $dt = 0.02$ ms and heterogeneous firing thresholds (25 %) are assumed for layer C so that layer C lies in the asynchronous states. Figure 2(a) actually guarantees the asynchrony of layer C accompanied by small values of r . Figure 2 shows that the high-resolutional population rate coding in layer C is realized only when layer B is in the rate code mode with large Δ_{Θ} .

4 Effects of Global Feedback

Global feedback exists among layers in real neural networks. It may contribute to reverberate the global information on stimuli into upstream layers where the information on the local and global stimulus features can be combined. Model analysis indicates that global feedback may induce and reinforce synchronization in upstream layers [2]. Generally speaking, correlated inputs compel

neurons to synchronize [9, 10].

We numerically examine the effect of global feedback in the network with three layers. Figure 3 shows r and $corr$ in layers B and C when the global feedback strength $\hat{\epsilon}$ is varied between -0.02 and 0 . We assume the inhibitory feedback to prevent the great variability in the firing rates due to positive feedback whose effects are not discussed in this paper. We set $\Delta_{\Theta} = 0.25$ so that layer B is engaged in the population rate coding in the absence of global feedback. To compare how two coding modes in layer C influence the behavior of layer B , we let layer C work as the synchronous coder without heterogeneity (lines with legend $C-S$) or the population rate coder with 20 % inhomogeneity in the threshold in layer C (line with legend $C-R$). To this end, layer C also receives small Gaussian white noise with amplitude 0.001 per $dt = 0.02$ ms. The difference between the two conditions is recognized 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 reminiscent of the all-to-all coupling (Eq. (2)). Stronger global feedback induces better synchrony in layer B (Fig. 3(a)) and deteriorates the estimation of external stimuli (Fig. 3(b)). The two coding modes in layer B are bridged by the strength of the global feedback. As the two lines in Fig. 3(a) demonstrate, for a fixed strength of the global feedback, the neurons in layer B are slightly more likely to synchronize when receiving synchronous volleys than asynchronous inputs. Another 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 coding modes not only in B but also C .

Synchrony may be also stabilized by global feedback. If layer B were synchronized from the beginning, global feedback from layer C to layer B , which is synchronous, may enhance the synchrony in layer B to shift the whole network toward the robust regime. Our results suggest possible roles of global feedback to induce and stabilize synchronous firing in feedforward networks [2].

5 Conclusions

We have shown that coding mode can unidirectionally switch from the rate coding to the synchronous coding in multi-layered feedforward networks and that global feedback can induce the synchronous coding in upstream layers and itself. The effect of more informative global feedback with more sophisticated coupling structure, as is the case for error-correcting signals back to the upstream layers, should be examined in the future. Feedforward networks with partial feedback reverberating activities of downstream neurons into upstream layers are general cortical architectures [1, 2], and our results suggest how feedforward and feedback connections cooperatively organize cortical dynamics. Experimental results regarding multi-layered networks with global feedback have been scarce, and we expect more of them to become accessible.

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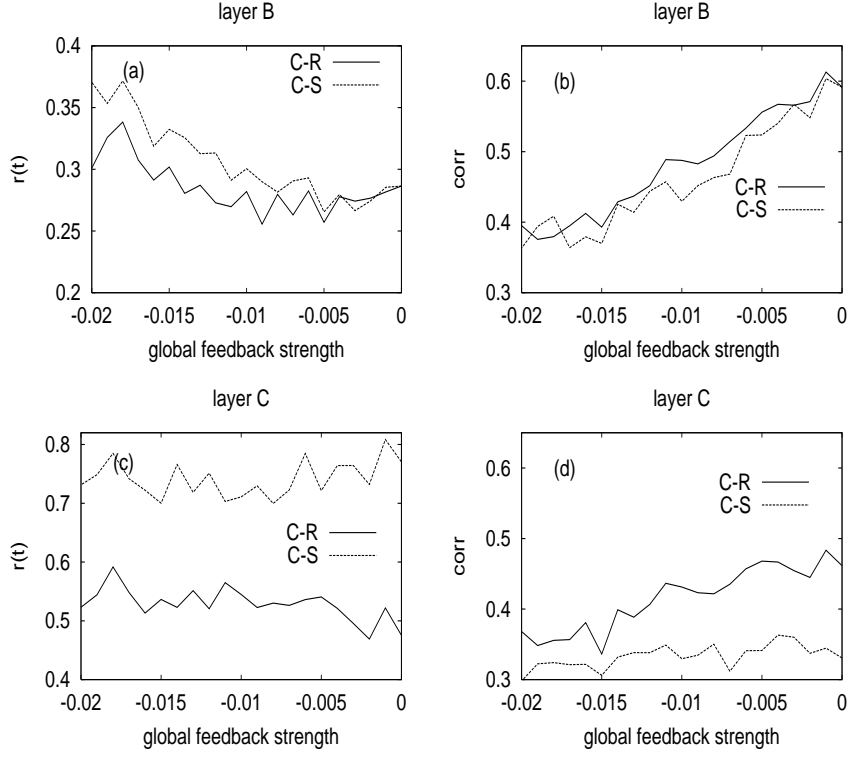


Figure 3: The coding performances r (a,c) and $corr$ (b,d) for layers B (a,b) and C (c,d) when the global feedback strength $\hat{\epsilon}$ is changed. Layer B is in the rate code mode when $\hat{\epsilon} = 0$ while layer C is either in the rate code mode ($C-R$) or the synchronous code mode ($C-S$). The trial averages based on 100 runs are taken to calculate r and $corr$.

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