

## Bridging Rate Coding and Temporal Spike Coding by Effect of Noise

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It is controversial whether temporal spike coding or rate coding is dominant in the information processing of the brain. We show by a two-layered neural network model with noise that, when noise is small, cortical neurons fire synchronously and intervals of synchronous firing robustly encode the signal information, but that the neurons desynchronize with moderately strong noise to encode waveforms of the signal more accurately. Further increase of noise just deteriorates the encoding. A positive role of noise in the brain is suggested in a meaning different from stochastic resonance, coherence resonance, and deterministic chaos.

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Firing rates of spikes in the brain are thought to represent information in external stimuli. However, calculation in the brain often seems to complete in a shorter time scale than the time required for temporal averaging of spike signals necessary for obtaining firing rates. Actually, precisely timed reproducible spiking has been experimentally observed with a precision of milliseconds [1], suggesting the importance of precise spike timing in information processing. The precisely timed synchronous firing has also been found in different neural systems, and may represent coherent information with synchronous neurons forming a dynamical assembly [2]. Furthermore, a downstream neuron can also fire more easily when incident spikes arrive synchronously than when their arrival timing is not correlated [3]. Temporal spike coding schemes assume that neurons exchange information encoded by precisely timed spikes at an increased speed with decreased energy to realize brain functions. Shadlen and Newsome, on the other hand, showed that a short-term firing rate can be reliably estimated by ensemble averaging of about 100 neurons, or population rate coding, without resorting to classical temporal averaging [4]. It is still controversial which coding scheme is used in which parts of the brain. Appropriate coding strategies may be selected according to anatomical locations and functions in the brain [2,3].

In this Letter, we show by model analysis that the population rate coding and the temporal spike coding can be bridged with a noise intensity parameter.

We examine a two-layered neural network composed of sensory neurons and cortical neurons with noise described in Fig. 1. We use the integrate-and-fire neurons [5] for  $n_1$  sensory neurons. The membrane potential  $x_i(t)$  of the  $i$ th sensory neuron is obtained by perfect integration of the continuous external signal  $S(t)$ . The neuron fires when  $x_i(t)$  reaches 1. Then  $x_i(t)$  is reset to the resting potential  $x_i(t) = 0$  to restart integration. The initial condition on the membrane potential of each neuron is determined randomly and independently according to the uniform dis-

tribution on  $[0, 1]$ . Our results hold even if the sensory neurons have voltage leak [6]. The  $n_2$  cortical neurons are the leaky integrate-and-fire neurons [6]. Each cortical neuron receives delta-shaped spike trains from  $n_1^i \leq n_1$  randomly chosen sensory neurons, and each pair of cortical neurons share a part of the sensory neurons. The ratio of the shared connections to all the connections from sensory neurons to a cortical neuron is fixed to 0.5. The state of the  $i$ th cortical neuron is represented by the membrane potential  $v_i(t)$  with the threshold  $v_i(t) = 1$  and the resting potential  $v_i(t) = 0$ . When it fires, an instantaneous feedback spike with the amplitude  $\epsilon$  and the synaptic delay  $\tau$  is sent to the other cortical neurons. The dynamics of the cortical neurons is described by

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

where  $\gamma > 0$  is the membrane leak rate, and  $\delta$  is the delta function.  $T_{i',j}$  is the time when the  $j$ th spike generated by the  $i'$ th sensory neuron arrives at the  $i$ th cortical neuron. The delay between the sensory layer and the cortical layer is uniformly zero or, equivalently, uniformly constant.  $\bar{\epsilon}$  is the amplitude of a spike from a sensory neuron.  $T_{i',j}$  is the  $j$ th firing time of the  $i'$ th cortical neuron.  $\xi_i(t)$  is the

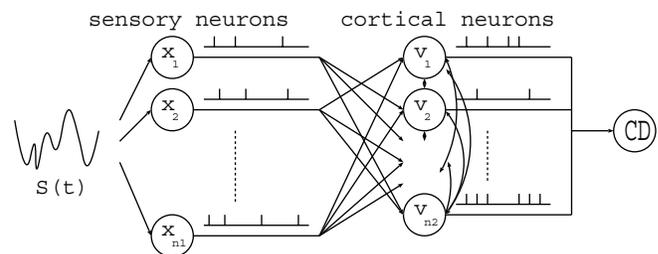


FIG. 1. Architecture of the model neural network.

Gaussian white noise with the standard deviation  $\sigma$ , which is applied at every integration time step of 0.02 ms. The  $i$ th cortical neuron receives incident spikes only from the  $i'$ th sensory neurons, where  $i' \in S_i$ ,  $|S_i| = n'_i$  with  $n'_i \leq n_1$ . A cortical neuron receives 100–200 spikes to emit one spike, and the firing rate is equal to 20 Hz. We set  $n_1 = 480$ ,  $n'_1 = 240$ ,  $n_2 = 30$ , and the delay  $\tau = 2.5$  ms [3]. Finally, a virtual coincidence detector (CD) observes synchronous firing [7]; the CD neuron fires when, and only when, incident spikes arrive from more than  $n_2/2$  cortical neurons within  $t_w = 1.5$  ms [8]. In addition to synchronization, we analyze the population firing rate calculated as the ensemble average of spike trains generated from all the cortical neurons [4].

We choose  $S(t)$  to be the chaotic time series generated from the Rössler and Lorenz systems modeling nonrandom dynamical rules contained in complex external stimuli such as visual scenes and sounds. The Rössler equations are represented by  $\dot{x} = a(-y - z)$ ,  $\dot{y} = a(x + 0.36y)$ ,  $\dot{z} = a[0.4 + z(x - 4.5)]$ , and we define  $S(t) = 0.02 + 0.001x$ . While the change rate  $a = 35$  in Fig. 2, we set  $a = 100$  in Fig. 3 to investigate the possibility of the population rate coding with asynchronous firing [4]. Similarly, for the Lorenz equations represented by  $\dot{x} = a(10.0y - 10.0x)$ ,  $\dot{y} = a(28.0x - y - xz)$ , and  $\dot{z} = a(-8.0/3.0z + xy)$ , we define  $S(t) = 0.019 + 0.0014x$ . We set  $a = 7$  in Fig. 2, and  $a = 30$  in Fig. 3.

It is known that interspike intervals produced by a neuron with a continuous external stimulus  $S(t)$  can preserve its deterministic information [5,9]. The determinism of  $S(t)$  makes interspike intervals predictable in a short term

and useful for reconstructing the original strange attractor generating  $S(t)$ . Furthermore, we have shown that a single cortical neuron receiving spatiotemporal spike trains from sensory neurons can also encode stimulus information in interspike intervals [6]. Here we explore robust information coding schemes by multiple cortical neurons since the interspike interval coding by a single cortical neuron is possible but not robust.

Reconstruction of the deterministic information in  $S(t)$  with the intersynchronization intervals [7] of the cortical layer is shown in Fig. 2. Figure 2(a) demonstrates that the cortical neurons nearly synchronize in spite of the inhomogeneity in the spike inputs and the synaptic delay when  $\sigma = 0$ . We next examine the determinism of the intersynchronization intervals using the surrogate data methods [10]. The strange attractor generating  $S(t)$  can be reconstructed by delay coordinates with the intersynchronization interval time series  $\{t'_k : t'_k = T'_k - T'_{k-1}\}$ , where  $T'_k$  is the time of the  $k$ th synchronous firing [7]. To evaluate the determinism of  $\{t'_k\}$ , we examine the deterministic predictability of  $\{t'_k\}$  by a local prediction algorithm [5,9]; we transform  $\{t'_k\}$  into a  $d$ -dimensional reconstruction space with delay coordinates to obtain the state points  $(t'_k, t'_{k-1}, \dots, t'_{k-d+1})$ . To perform the  $h$ -step prediction of  $t'_{k_0}$ , we search  $l_0$  nearest neighborhoods  $(t'_{k_l}, t'_{k_l-1}, \dots, t'_{k_l-d+1})$ ,  $1 \leq l \leq l_0$  to  $(t'_{k_0}, t'_{k_0-1}, \dots, t'_{k_0-d+1})$ . Then the prediction  $\hat{t}'_{k_0+h}$  is defined by  $\hat{t}'_{k_0+h} = 1/l_0 \sum_{l=1}^{l_0} t'_{k_l+h}$ . The effectiveness of this algorithm is evaluated by the normalized prediction error defined by  $\text{NPE}(h) = \langle (t'_{k_0+h} - \hat{t}'_{k_0+h})^2 \rangle^{1/2} / \langle (m - t'_{k_0+h})^2 \rangle^{1/2}$ , where  $\langle \dots \rangle$  denotes the average over sample points, and  $m$  is the mean of  $\{t'_k\}$ . To

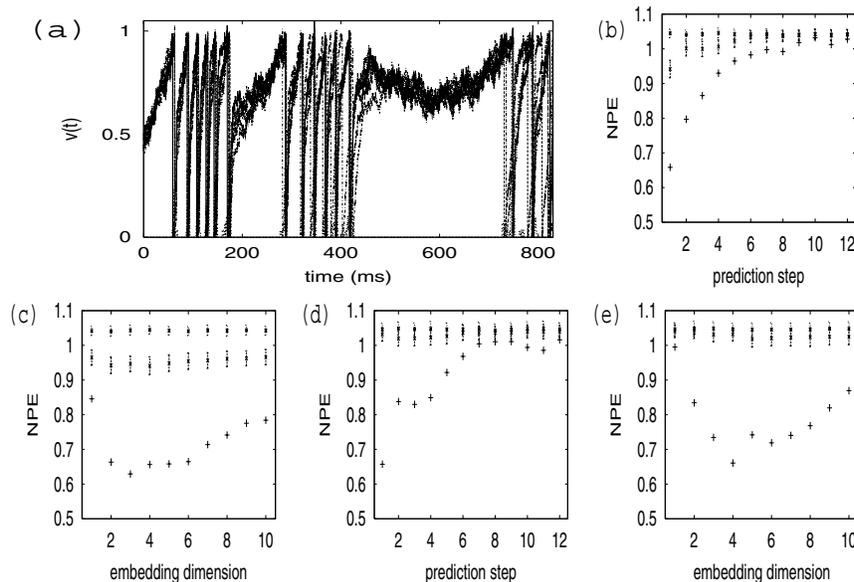


FIG. 2. Behavior of the neural network and estimation of the external stimuli using intersynchronization intervals with  $\epsilon = 0.02$ ,  $\gamma = 0.060 \text{ ms}^{-1}$ , and  $\sigma = 0$ . (a) Activities of 30 cortical neurons. (b),(d)  $\text{NPE}(h)$ s for the intersynchronization interval time series of the cortical neurons (+), the FS (x), and the AAFT (\*) surrogate data, accompanied by the error bars showing the standard deviations for 100 surrogate data for not only (b),(d) but also for (c),(e). The embedding dimension  $d = 4$ . (c),(e)  $\text{NPE}(1)$ s for the intersynchronization intervals, the FS, and the AAFT surrogate data with various embedding dimensions. (a)–(c) The results for the Rössler input with  $\bar{\epsilon} = 0.0105$ . (d),(e) The results for the Lorenz input with  $\bar{\epsilon} = 0.0095$ .

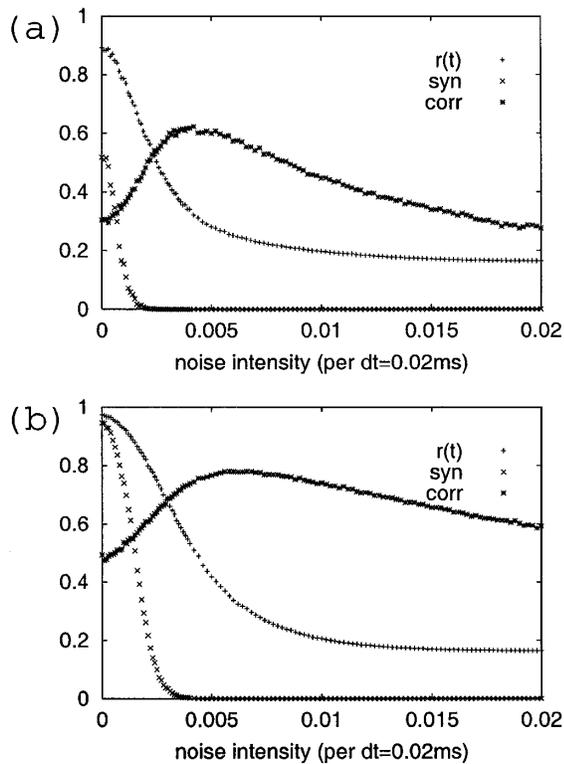


FIG. 3. Performance measurements of the synchronization-based coder and the population rate coder for various noise levels with  $\epsilon = 0.003$ ,  $\bar{\epsilon} = 0.007$ , and  $\gamma = 0.025 \text{ ms}^{-1}$ . Order parameters  $\text{syn}$  ( $\times$ ),  $r(t)$  ( $+$ ), and the correlation coefficient between  $S(t)$  and the short-term population firing rate of the cortical neurons ( $*$ ) calculated by using time bins with the width 4.5 ms are shown. The inputs are generated from the Rössler system (a) and the Lorenz system (b).

examine determinism of the time series, we also calculate the NPE( $h$ ) of the two surrogate data: the Fourier shuffled (FS) surrogate and the amplitude adjusted Fourier transform (AAFT) surrogate [10]. The length of  $\{t'_k\}$  used for the analysis is equal to 4096, and the last 10% of the intervals are predicted by the first 90% with  $l_0 = 12$ . The intersynchronization intervals have significant determinism compared with surrogate data; Figs. 2(b)–2(e) indicate that the deterministic information about  $S(t)$  is encoded in the intersynchronization intervals of the leaky integrate-and-fire cortical neurons.

The mechanism of the interspike interval reconstruction by single neurons driven by superimposed spike trains [6], or by continuous inputs such as  $S(t)$  [5,9], underlies the intersynchronization interval reconstruction [7]. Consequently, intersynchronization intervals encode  $S(t)$  with an instantaneous rate of synchronous firing, and this coding should be more robust than coding by a single neuron. The information transmission rate is limited by the duration of typical intersynchronization intervals. The stimulus information temporally finer than that length is discarded through the integration process.

Real neurons are subject to various types of noise that may cause neurons to desynchronize. The incorporation

of noise may lead to different consequences. Actually, we can consider the other extreme in which each cortical neuron encodes a different feature of  $S(t)$  with asynchronous firing. In this scheme, displacement in the firing time of each single spike may directly affect the signal estimation, in contrast to the synchronization-based coding. However, the coding is robust enough against the perturbation since single spike displacement influences the coding performance just slightly. The whole spatiotemporally asynchronous spikes from the cortical layer may preserve more precise information on the temporal waveform of  $S(t)$  than synchronous spikes. We apply additive noise to the cortical neurons as a possible means to drive the neural network out of synchrony. In Fig. 3, the degree of synchronous firing is shown for various noise levels. The order parameter “syn” defined by the ratio of the number of synchronous firing to the number of single-neuron firing measures the synchrony with precision  $t_w$ . The synchrony of membrane potentials of the cortical neurons is also evaluated by the order parameter [11] defined by  $r(t) = |\sum_{j=1}^{n_2} e^{2\pi i v_j(t)}|/n_2$ . The full synchrony gives  $\text{syn} = 1$  and  $r(t) = 1$ , while the full asynchrony results in  $\text{syn} = 0$  and  $r(t) = 0$ .

For both the Rössler and Lorenz inputs, very weak noise ( $\sigma \in [0, 0.002]$ ) does not prohibit synchronous firing of cortical neurons. In this situation, the information transmission rate is low since synchronous neurons redundantly encode the same aspect of a stimulus. Actually, Fig. 3 demonstrates small values of the correlation coefficient between  $S(t)$  and the short-term ensemble firing rate [4] of the cortical neurons at this noise level, indicating that the precise stimulus estimation based on the rate of synchronous firing is impossible since time averaging over intersynchronization intervals smooths out high-frequency information on  $S(t)$ .

On the other hand, the cortical neurons fire less synchronously as the noise increases ( $\sigma \geq 0.003$ ). When the noise level is intermediate ( $\sigma \in [0.003, 0.008]$ ), the cortical neurons desynchronize and each neuron encodes a different aspect of  $S(t)$ . For demonstration, let us suppose that  $S(t)$  has two peaks during an interspike interval. Then networks with asynchronously firing neurons can capture both peaks; some neurons encode the first peak of  $S(t)$  by firing nearby while others fire near the second peak to encode it. However, the synchronously firing cortical neurons encode only one peak at best since the cortical layer has only one chance to place its synchronous firing within a duration of the interspike interval. Indeed, when  $\sigma \in [0.003, 0.008]$ , the collective spike trains can restore more accurate information on waveforms of  $S(t)$  by the population rate coding than a single neuron or synchronous neurons can. When the cortical neurons fire entirely asynchronously, they can encode  $S(t)$  with the precision proportional to  $1/n_2$ . Still stronger noise ( $\sigma \geq 0.012$ ) seriously affects firing events. Consequently, signal integration by the cortical neurons is too deteriorated for reliable population rate coding although the neurons are well

desynchronized. Figure 3 suggests that there are optimal noise levels that realize the most accurate population rate coding for both the Rössler and Lorenz inputs.

Noise in sensory neurons is important for the interspike interval reconstruction of a single cortical neuron [6]. Here asynchronous firing of cortical neurons induced by noise may also play a positive role in the brain in a meaning different from stochastic resonance, coherence resonance, and deterministic chaos. The role of noise examined here is to help the cortical neurons collect versatile pieces of stimulus information by making them desynchronize. The coding by synchronous firing may be effectively used when animals are engaged in already learned tasks. Once unknown stimuli or new tasks are given, they have to adapt to the new circumstances. Until they complete the adaptation, the neurons may desynchronize to benefit from the population rate coding that encodes more signal information than the synchronization-based coding. It may enable them to reach an optimal solution as fast as possible. The transition from synchronization to desynchronization and vice versa also occurs when the stimulus or the task is switched [2]. The change in noise as background activities in cooperation with the stimulus/task-dependent inputs may contribute to such brain dynamics.

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*Note added.*—After submission of this Letter, we found an interesting related paper by van Rossum, Turrigiano, and Nelson [12].

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