# Effect of Sparse Random Connectivity on the Stochastic Spiking Coherence of Inhibitory Subthreshold Neurons

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(Received 12 May 2011, in final form 11 August 2011)

We study the effect of network structure on the stochastic spiking coherence (*i.e.*, collective coherence emerging via cooperation of noise-induced neural spikings) in an inhibitory population of subthreshold neurons (which cannot fire spontaneously without noise). Previously, stochastic spiking coherence was found to occur for the case of global coupling. However, "sparseness" of a real neural network is well known. Hence, we investigate the effect of sparse random connectivity on the stochastic spiking coherence by varying the average number of synaptic inputs per neuron  $M_{syn}$ . From our numerical results, stochastic spiking coherence seems to emerge if  $M_{syn}$  is larger than a threshold  $M^*_{syn}$  whose dependence on the network size N seems to be quite weak. This stochastic spiking coherence may be well visualized in a raster plot of neural spikes. For a coherent case, partially-occupied "stripes" (composed of spikes and indicating collective coherence) appear. As  $M_{syn}$  is decreased from N-1 (globally-coupled case), the average occupation degree of spikes increases very slowly. On the other hand, the average pacing degree between spikes (representing the precision of spike timing) decreases slowly, but near  $M^*_{syn}$  its decrease becomes very rapid. This decrease in the pacing degree can also be well seen through merging of multiple peaks in the interspike interval histograms. Due to the effect of the pacing degree, the degree of stochastic spiking coherence decreases abruptly near the threshold  $M_{syn}^*$ .

PACS numbers: 87.19.lm, 87.19.lc Keywords: Sparse random connectivity, Stochastic spiking coherence DOI: 10.3938/jkps.59.2840

## I. INTRODUCTION

Recently, much attention has been paid to coherent brain rhythms [1,2]. Coherent oscillations in neural systems may be used for efficient sensory processing (*e.g.*, visual binding) [3]. This kind of neural coherence is also correlated with pathological rhythms associated with neural diseases (*e.g.*, epileptic seizures and tremors in Parkinson's disease) [4]. Here, we are interested in these coherent neural oscillations.

Neural circuits in major parts of the brain are composed of a few types of excitatory principal cells and diverse types of inhibitory interneurons. Interneuron diversity increases the computational power of principal cells [1,5]. The mechanisms of coherent brain rhythms have been much investigated, and three types of coherence mechanisms for chemical synapses have been found [2,6]. Historically, the first coherence mechanism is just recurrent excitation between principal cells [7]. However, if the decay time of the synaptic interaction is sufficiently long, mutual inhibition between interneurons (rather than excitation) may synchronize individual neural firings [8,9]. By giving a coherent oscillatory output to the principal cells, interneuronal networks play the role of backbones (*i.e.*, pacemakers) for many brain rhythms such as the thalamocortical spindle rhythms [10, 11] and the fast gamma rhythms in the hippocampus and the neocortex [12–15]. If the feedback between the excitatory and the inhibitory populations is strong enough, neural coherence occurs via the "cross-talk" between the two populations [14–17].

Most previous works exploring the mechanisms of neural coherence by chemical synapses were done in neural systems consisting of spontaneously firing (*i.e.*, selfoscillating) suprathreshold neurons. For this case, neural coherence occurs through cooperation of regular firings of suprathreshold neurons. In contrast, neural systems consisting of subthreshold neurons have received little attention in the exploration of coherence mechanism. Unlike the suprathreshold case, a subthreshold neuron can-

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not fire spontaneously without noise. Recently, stochastic spiking coherence (*i.e.*, collective coherence emerging via cooperation of noise-induced spikings) was observed in a population of pulse-coupled excitatory subthreshold neurons [18,19]. This kind of work may be regarded as a "subthreshold version" of neural coherence through mutual excitation.

In this paper, we are concerned with the subthreshold version of neural coherence via mutual inhibition. For the case of global coupling where each neuron is coupled to all the other ones with equal strength, stochastic spiking coherence was found to occur in an inhibitory population of subthreshold neurons [20]. For this case, a fast collective small-amplitude oscillation emerges from sparsely synchronized neurons discharging at a lower frequency. These sparsely synchronized oscillations have been intensively investigated in other types of neural networks [21], and they are believed to be associated with fast cortical rhythms with irregular and sparse neural discharges [2]. However, in a real brain, each neuron is coupled to only a certain number of neurons, which is much smaller than the total number of neurons. Due to the "sparseness" of the network architecture, the stochastic spiking coherence (seen in the globally-coupled case) is expected to be reduced or destroyed. Models often assume that the coupling between neurons is random [17, 22–24]. In Sec. II, we investigate the effect of sparse random connectivity on the stochastic spiking coherence by varying the average number of synaptic inputs per neuron  $M_{syn}$  in an inhibitory ensemble of N randomly coupled subthreshold ML neurons. The emergence of the stochastic spiking coherence seems to persist only if  $M_{syn}$ is larger than a threshold  $M^*_{syn}$  whose dependence on the network size N seems to be quite weak. We characterize the stochastic spiking coherence (seen well in a raster plot of neural spikes) in terms of a statistical-mechanical spike-based coherence measure  $M_s$  (introduced by considering the occupation pattern and the pacing pattern of spikes in the stripes in the raster plot [20]). As  $M_{syn}$  is decreased from N-1 (corresponding to the case of global coupling), the average pacing degree between spikes (denoting the precision of spike timing) decreases slowly, but near  $M_{sun}^*$ , its value drops very rapidly while the average occupation degree of spikes increases very slowly over the whole coherent region. The decrease in the pacing degree can also be well seen through merging of multiple peaks in the interspike interval (ISI) histograms. Due to the effect of the pacing degree, the degree of stochastic spiking coherence decreases abruptly near the threshold  $M_{syn}^*$ . In Sec. III, a summary is given.

### II. EFFECT OF SPARSE RANDOM CONNECTIVITY ON STOCHASTIC SPIKING COHERENCE

We consider a large inhibitory population of N randomly coupled subthreshold neurons. As an element in our neural system, we choose the conductance-based Morris-Lecar (ML) neuron model, originally proposed to describe the time-evolution pattern of the membrane potential for the giant muscle fibers of barnacles [25–27]. The population dynamics in this neural network is governed by the following set of differential equations:

$$C\frac{dv_i}{dt} = -I_{ion,i} + I_{DC} + D\xi_i - I_{syn,i}, \qquad (1a)$$

$$\frac{dw_i}{dt} = \phi \frac{(w_{\infty}(v_i) - w_i)}{\tau_R(v_i)},$$
(1b)

$$\frac{ds_i}{dt} = \alpha s_{\infty}(v_i)(1-s_i) - \beta s_i, \quad i = 1, \cdots, N,$$
 (1c)

where

$$I_{ion,i} = I_{Ca,i} + I_{K,i} + I_{L,i}$$
(2a)  
=  $g_{Ca}m_{\infty}(v_i)(v_i - V_{Ca}) + g_K w_i(v_i - V_K)$   
+ $g_L(v_i - V_L),$ (2b)

$$L(v_i - V_L), \tag{2D}$$

$$I_{syn,i} = \frac{J}{M_{syn}} \sum_{j(\neq i)}^{N} w_{ij} s_j(t) (v_i - V_{syn}), \qquad (2c)$$

$$m_{\infty}(v) = 0.5 [1 + \tanh\{(v - V_1)/V_2\}],$$
 (2d)

$$w_{\infty}(v) = 0.5 [1 + \tanh\{(v - V_3)/V_4\}],$$
 (2e)

$$\tau_R(v) = 1/\cosh\left\{(v - V_3)/(2V_4)\right\},\tag{21}$$

$$s_{\infty}(v_i) = 1/[1 + e^{-(v_i - v_j)/\delta}].$$
 (2g)

Here, the state of the *i*th neuron at a time *t* (measured in units of ms) is characterized by three state variables: the membrane potential  $v_i$  (measured in units of mV), the slow recovery variable  $w_i$  representing the activation of the  $K^+$  current (*i.e.*, the fraction of open  $K^+$  channels), and the synaptic gate variable  $s_i$  denoting the fraction of open synaptic ion channels. In Eq. (1a), *C* represents the capacitance of the membrane of each neuron, and the time evolution of  $v_i$  is governed by four kinds of source currents.

The total ionic current  $I_{ion,i}$  of the *i*th neuron consists of the calcium current  $I_{Ca,i}$ , the potassium current  $I_{K,i}$ , and the leakage current  $I_{L,i}$ . Each ionic current obeys Ohm's law. The constants  $g_{Ca}$ ,  $g_K$ , and  $g_L$  are the maximum conductances for the ion and the leakage channels, and the constants  $V_{Ca}$ ,  $V_K$ , and  $V_L$  are the reversal potentials at which each current is balanced by the ionic concentration difference across the membrane. Since the calcium current  $I_{Ca,i}$  changes much faster than the potassium current  $I_{K,i}$ , the gate variable  $m_i$  for the  $Ca^{2+}$  channel is assumed to always take its saturation value  $m_{\infty}(v_i)$ . On the other hand, the activation variable  $w_i$  for the  $K^+$  channel approaches its saturation value  $w_{\infty}(v_i)$  with a relaxation time  $\tau_R(v_i)/\phi$ , where  $\tau_R$  has a dimension of ms and  $\phi$  is a (dimensionless) temperaturelike time scale factor.

Each ML neuron is also stimulated by using the common DC current  $I_{DC}$  and an independent Gaussian white noise  $\xi_i$  [see the 2nd and the 3rd terms in Eq. (1a)] satisfying  $\langle \xi_i(t) \rangle = 0$  and  $\langle \xi_i(t) \xi_j(t') \rangle = \delta_{ij} \delta(t-t')$ , where  $\langle \cdots \rangle$  denotes the ensemble average. The noise  $\xi$  is a parametric one that randomly perturbs the strength of the applied current  $I_{DC}$ , and its intensity is controlled by using the parameter D.

The last term in Eq. (1a) represents the synaptic coupling of the network. A (postsynaptic) neuron i receives a synaptic input from another (presynaptic) neuron jwith a connection probability  $P_{syn} (= M_{syn}/N)$ , where  $M_{syn}$  is the average number of synaptic inputs per neuron.  $I_{syn,i}$  of Eq. (2c) represents such a synaptic current injected into the *i*th neuron. Here,  $\{w_{ij}\}$  is the connectivity matrix.  $w_{ij} = 1$  if the neuron j is presynaptic to the neuron *i*; otherwise,  $w_{ij} = 0$ . Then, the number of synaptic inputs to the neuron *i* is given by  $M_i = \sum_{j(\neq i)}^{N} w_{ij}$ , with  $M_{syn} = \langle M_i \rangle$ . The coupling strength is controlled by the parameter *J*, and  $V_{syn}$  is the synaptic reversal potential. We use  $V_{syn} = -80 \text{ mV}$ for the inhibitory synapse. The synaptic gate variable s obeys the 1st-order kinetics of Eq. (1c) [11,12]. Here the normalized concentration of synaptic transmitters, activating the synapse, is assumed to be an instantaneous sigmoidal function of the membrane potential with a threshold  $v^*$  in Eq. (2g), where we set  $v^* = 0$  mV and  $\delta = 2$  mV. The transmitter release occurs only when the neuron emits a spike (i.e., its potential v is larger than $v^*$ ). For the inhibitory GABAergic synapse (involving the GABA<sub>A</sub> receptors), the synaptic channel opening rate, corresponding to the inverse of the synaptic rise time  $\tau_r$ , is  $\alpha = 10 \text{ ms}^{-1}$ , and the synaptic closing rate  $\beta$ , which is the inverse of the synaptic decay time  $\tau_d$ , is  $\beta = 0.1 \text{ ms}^{-1}$  [17]. Hence,  $I_{syn}$  rises fast and decays slowly.

The ML neuron may exhibit either type-I or type-II excitability, depending on the system parameters [26]. Throughout this paper, we consider the case of type-II excitability where  $g_{Ca} = 4.4 \text{ mS/cm}^2, g_K =$ 8 mS/cm<sup>2</sup>,  $g_L = 2$  mS/cm<sup>2</sup>,  $V_{Ca} = 120$  mV,  $V_K = -84$  mV,  $V_L = -60$  mV, C = 20  $\mu$ F/cm<sup>2</sup>,  $\phi = 0.04$ ,  $V_1 = -1.2 \text{ mV}, V_2 = 18 \text{ mV}, V_3 = 2 \text{ mV}, \text{ and } V_4 =$ 30 mV. As  $I_{DC}$  passes a threshold in the absence of noise, each single type-II ML neuron begins to fire with a nonzero frequency that is relatively insensitive to the change in  $I_{DC}$  [28,29]. Numerical integration of Eq. (1) is done using the Heun method [30] (with the time step  $\Delta t = 0.01$  ms), which is similar to the secondorder Runge-Kutta method, and data for  $(v_i, w_i, s_i)$  $(i = 1, \ldots, N)$  are obtained with the sampling time interval  $\Delta t = 1$  ms. For each realization of the stochastic process in Eq. (1), we choose a random initial point  $[v_i(0), w_i(0), s_i(0)]$  for the *i*th (i = 1, ..., N) neuron with uniform probability in the range of  $v_i(0) \in (-70, 50)$ ,  $w_i(0) \in (0.0, 0.6)$ , and  $s_i(0) \in (0.0, 1.0)$ .

We consider an inhibitory population of N randomly coupled subthreshold ML neurons for  $I_{DC} = 87 \ \mu \text{A/cm}^2$ and  $D = 20 \ \mu \text{A} \cdot \text{ms}^{1/2}/\text{cm}^2$  and set the coupling strength as  $J = 3 \text{ mS/cm}^2$ . (Hereafter, for convenience, we omit the dimensions of  $I_{DC}$ , D, and J.) In a real



Fig. 1. (a) Plots of the order parameter versus the connection probability  $P_{syn}$  (=  $M_{syn}/N$ ) and (b) plots of the order parameter versus the average number of synaptic inputs  $M_{syn}$  per neuron in an inhibitory population of N randomly coupled subthreshold ML neurons for  $I_{DC} = 87 \ \mu \text{A/cm}^2$ ,  $D = 20 \ \mu \text{A} \cdot \text{ms}^{1/2}/\text{cm}^2$ , and  $J = 3 \ \text{mS/cm}^2$ .

brain, each neuron is coupled to only a certain number of neurons, which is much smaller than the total number of neurons N. By varying the sparseness degree of the network architecture, we study the effect of the sparse random connectivity on the stochastic spiking coherence. Emergence of collective spiking coherence in the inhibitory population may be well described by using the (population-averaged) global potential

$$V_G(t) = \frac{1}{N} \sum_{i=1}^{N} v_i(t).$$
 (3)

In the thermodynamic limit  $(N \to \infty)$ , a collective state becomes coherent if  $\Delta V_G(t) = V_G(t) - \overline{V_G(t)}$  is nonstationary (*i.e.*, an oscillating global potential  $V_G$  appears for a coherent case), where the overbar represents the time average. Otherwise (*i.e.*, when  $\Delta V_G$  is stationary), it becomes incoherent. Thus, the mean square deviation of the global potential  $V_G$  (*i.e.*, time-averaged fluctuations of  $V_G$ ),

$$\mathcal{O} \equiv (V_G(t) - \overline{V_G(t)})^2, \tag{4}$$

plays the role of an order parameter used for describing the coherence-incoherence transition [31]. For the coherent (incoherent) state, the order parameter  $\mathcal{O}$  approaches a non-zero (zero) limit value as N goes to the infinity.

We first examine which one of the two parameters,  $P_{syn}$ (*i.e.*, the connection probability per neuron) and  $M_{syn}$ (*i.e.*, the average number of random synaptic inputs per neuron), plays an appropriate role as a "sparseness" parameter for describing the coherent transition. For this examination, we make plots of the order parameter versus both  $P_{syn}$  and  $M_{syn}$ . Figure 1(a) shows plots of the order parameter versus  $P_{syn}$  for  $N = 10^2$ ,  $10^3$ , and  $10^4$ . We note that as N is increased 10 times, the threshold value at which the order parameter begins to drop is decreased by a factor of about 1/10. In this way, the threshold value of  $P_{syn}$  for the transition depends strongly on N; hence,  $P_{syn}$  is not an appropriate sparseness parameter for the coherent transition. On the other hand, there seems to exist a threshold  $M^*_{syn}$  ( $\simeq 45$ ) for the coherent transition, whose dependence on N seems to be quite weak [see Fig. 1(b)]. For  $M_{syn} < M^*_{syn}$ , incoherent states exist because the order parameter  $\mathcal{O}$  tends to zero as  $N \to \infty$ . However, as  $M_{syn}$  passes the threshold  $M_{syn}^*$ , coherent states appear. Hence,  $M_{syn}$  seems to be an appropriate sparseness parameter. For this case, the total number of synaptic inputs grows linearly as N $(\sim N)$ . On the other hand, if a fixed critical value  $P_{sun}^*$ exists independently of N, the total number of synaptic inputs increases very quickly ( $\sim N^2$ ). If one compares the two cases based on the economy of synapse connectivity, it is easy to understand why the brain has evolved by choosing the case of  $M_{syn}^*$  rather than  $P_{syn}^*$  [5]. By decreasing  $M_{syn}$  from N-1 (corresponding to the

case of global coupling), we investigate the sparseness effect on the stochastic spiking coherence (seen well in a raster plot of neural spikes) in  $N (= 10^3)$  randomly coupled inhibitory subthreshold ML neurons. For the case of global coupling, partially-occupied "stripes" (indicating collective coherence) appear in the raster plot [see Fig. 2(a1)]; only a fraction (about 1/10) of the total neurons fire in each stripe. A fast regularly oscillating global potential  $V_G$  emerges via cooperation of irregular individual potentials. Local maxima of  $V_G$  appear at the centers of the stripes in the raster plot. When compared with the individual potentials, the amplitude of  $V_G$  is much decreased while its frequency  $f_G$  is much increased. For this coherent case, individual neurons exhibit intermittent spikings phase-locked to  $V_G$  at random multiples of the period of  $V_G$  [e.g., see the potential  $v_1$  of the first neuron in Fig. 2(b1)]. In addition to these coherent intermittent spiking phases, coherent hopping phases (showing coherent small subthreshold oscillations) appear in most of the global cycles. After the occurrence of each spiking, recovery from a hyperpolarized state to a resting state is made during the next global cycle. Hence, a "preparatory" phase without spiking and hopping (for preparation for generation of the next spike or hopping) follows each spiking phase (see the gray parts). Stochastic spike skipping (arising from stochastic phase locking) in the individual potential may be seen well in the ISI histogram. Multiple peaks appear at multiples of the period  $T_G$  of the global potential  $V_G$  [see Fig. 2(c1)]. However,



Fig. 2. Raster plots, the individual and the global potentials, and the interspike interval (ISI) histograms in an inhibitory population of  $N(=10^3)$  randomly coupled subthreshold ML neurons for  $I_{DC} = 87 \ \mu \text{A/cm}^2$ , D = 20 $\mu A \cdot ms^{1/2}/cm^2$ , and  $J = 3 mS/cm^2$ . Raster plots and the global potential  $V_G$  for  $M_{syn} = (a1)$  999 (global coupling), (a2) 100, (a3) 47, (a4) 10, and (a5) 5. Individual potential  $v_1$  of the first neuron for  $M_{syn} = (b1)$  999 (global coupling), (b2) 100, (b3) 47, (b4) 10, and (b5) 5. Vertical dashed lines in (b1) - (b3) represent the times at which local minima of  $V_G$  appear, and the preparatory cycles are shown in gray. ISI histograms for  $M_{syn} = (c1) 999$  (global coupling), (c2) 100, (c3) 47, (c4) 10, and (c5) 5; each ISI histogram is composed of  $5 \times 10^4$  ISIs, and the bin size for the histogram is 5 ms. Vertical dotted lines in (c1) - (c3) denote integer multiples of the global period  $T_G$  of  $V_G$ .

due to appearance of preparatory cycles, the 1st peak of the histogram appears at  $2T_G$  (not  $T_G$ ). Hence, individual neurons fire mostly in alternate global cycles. In this way, sparsely synchronized neurons exhibit mixedmode oscillations with two well-separated frequencies, a fast subthreshold hopping frequency imposed by the collective network frequency and a lower firing frequency of individual neurons.

As shown in Fig. 2(a2), the degree of stochastic spiking coherence seems to persist at least until  $M_{syn} = 100$  (corresponding to about 1/10 of the value of  $M_{syn}$  for the globally-coupled case). Hence, the individual potential  $v_1$  and the ISI histogram for  $M_{syn} = 100$  are similar to those for the global-coupling case. However, near the threshold  $M_{syn}^*$ , the stripes become more smeared, so the degree of stochastic spiking coherence (*i.e.*, the amplitude of  $V_G$ ) decreases rapidly [*e.g.*, see Fig. 2(a3)]. The smearing of stripes is associated with merging of peaks in the ISI histogram, as shown in Fig. 2(c3). For  $M_{syn} < M_{syn}^*$ , incoherent states appear [*e.g.*, see Figs. 2(a4) – 2(a5)]. As a result of complete merging,

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Fig. 3. Statistical-mechanical spike-based coherence measure in an inhibitory population of  $N(=10^3)$  randomly coupled subtreshold ML neurons for  $I_{DC} = 87 \ \mu\text{A/cm}^2$ ,  $D = 20 \ \mu\text{A} \cdot \text{ms}^{1/2}/\text{cm}^2$ , and  $J = 3 \ \text{mS/cm}^2$ . (a) Plot of the average occupation degree  $\langle O_i \rangle$  versus the average number of synaptic inputs  $M_{syn}$ , (b) plot of the average pacing degree  $\langle P_i \rangle$  versus  $M_{syn}$ , and (c) plot of the spike-based coherence measure  $M_s$ versus  $M_{syn}$ .

only a single peak appears in the ISI histogram, as shown in Figs. 2(c4) – 2(c5). Because the average value of the ISIs decreases, more intermittent spikings appear in  $v_1$ [*e.g.*, see Figs. 2(b4) – 2(b5)].

We also characterize the collective coherence in terms of a "statistical-mechanical" spike-based coherence measures. As shown in Figs. 2(a1) - 2(a5), collective coherence may be well visualized in a raster plot of spikes. For a coherent case, the raster plot is composed of partiallyoccupied stripes (indicating collective coherence). To measure the degree of the collective coherence seen in the raster plot, a new spike-based measure  $M_s$  was introduced by considering the occupation pattern and the pacing pattern of the spikes in the stripes [20]. Particularly, the pacing degree between spikes (representing the precision of spike timing) is determined in a statisticalmechanical way by quantifying the average contribution of microscopic individual spikes to the global potential  $V_G$ . The spiking coherence measure  $M_i$  of the *i*th stripe is defined by the product of the occupation degree  $O_i$  of spikes (representing the density of the *i*th stripe) and the pacing degree  $P_i$  of spikes (denoting the smearing of the *i*th stripe):

$$M_i = O_i \cdot P_i. \tag{5}$$

The occupation degree  $O_i$  in the *i*th stripe is given by the fraction of spiking neurons:

$$O_i = \frac{N_i^{(s)}}{N},\tag{6}$$

where  $N_i^{(s)}$  is the number of spiking neurons in the *i*th stripe. For full occupation,  $O_i = 1$  while for the partial occupation,  $O_i < 1$ . The pacing degree  $P_i$  of each microscopic spike in the *i*th stripe can be determined in a statistical-mechanical way by taking into consideration its contribution to the macroscopic global potential  $V_G$ . Each global cycle of  $V_G$  begins from its left minimum, passes the central maximum, and ends at the right minimum; the central maxima coincide with centers of stripes in the raster plot [see Figs. 2(a1) - 2(a3)]. An instantaneous global phase  $\Phi(t)$  of  $V_G$  is introduced via linear interpolation in the two successive subregions forming a global cycle. The global phase  $\Phi(t)$  between the left minimum (corresponding to the beginning point of the *i*th global cycle) and the central maximum is given by

$$\Phi(t) = 2\pi(i - 3/2) + \pi \left(\frac{t - t_i^{(min)}}{t_i^{(max)} - t_i^{(min)}}\right)$$
  
for  $t_i^{(min)} \le t < t_i^{(max)}$   $(i = 1, 2, 3, ...),$  (7)

and  $\Phi(t)$  between the central maximum and the right minimum (corresponding to the beginning point of the (i + 1)th cycle) is given by

$$\Phi(t) = 2\pi(i-1) + \pi \left(\frac{t - t_i^{(max)}}{t_{i+1}^{(min)} - t_i^{(max)}}\right)$$
  
$$\cdot \quad t_i^{(max)} \le t < t_{i+1}^{(min)} \quad (i = 1, 2, 3, ...),$$
(8)

for

where  $t_i^{(min)}$  is the beginning time of the *i*th global cycle  $(i.e., \text{ the time at which the left minimum of <math>V_G$  appears in the *i*th global cycle) and  $t_i^{(max)}$  is the time at which the maximum of  $V_G$  appears in the *i*th global cycle. Then, the contribution of the *k*th microscopic spike in the *i*th stripe occurring at the time  $t_k^{(s)}$  to  $V_G$  is given by  $\cos \Phi_k$ , where  $\Phi_k$  is the global phase at the *k*th spiking time  $[i.e., \Phi_k \equiv \Phi(t_k^{(s)})]$ . A microscopic spike makes the most constructive (in-phase) contribution to  $V_G$  when the corresponding global phase  $\Phi_k$  is  $2\pi n \ (n = 0, 1, 2, ...)$  while it makes the most destructive (anti-phase) contribution to  $V_G$  when  $\Phi_i$  is  $2\pi (n - 1/2)$ . By averaging the contributions of all microscopic spikes in the *i*th stripe to  $V_G$ , we obtain the pacing degree of spikes in the *i*th stripe:

$$P_i = \frac{1}{S_i} \sum_{k=1}^{S_i} \cos \Phi_k,\tag{9}$$

where  $S_i$  is the total number of microscopic spikes in the *i*th stripe. By averaging  $M_i$  of Eq. (5) over a sufficiently large number  $N_s$  of stripes, we obtain the spike-based

coherence measure  $M_s$ :

$$M_s = \frac{1}{N_s} \sum_{i=1}^{N_s} M_i.$$
 (10)

By varying  $M_{syn}$ , we follow  $3 \times 10^3$  stripes and measure the degree of collective spiking coherence in terms of  $\langle O_i \rangle$  (average occupation degree),  $\langle P_i \rangle$  (average pacing degree), and  $M_s$  for 17 values of  $M_{syn}$  in the coherent region, and the results are shown in Figs. 3(a) -3(c). As  $M_{syn}$  is decreased, the average occupation degree  $\langle O_i \rangle$  (denoting the average density of stripes in the raster plot) increases slowly, but its values are very small  $\langle O_i \rangle < 0.15 \rangle$ ; only a fraction (less than 3/20) of the total neurons fire in each stripe [see Figs. 2(a1) - 2(a3)]. This partial occupation results from stochastic spike skipping of individual neurons and is seen well in the multi-peaked ISI histograms [see Figs. 2(a1) - 2(a3)]. On the other hand, with decreasing  $M_{syn}$ , the average pacing degree  $\langle P_i \rangle$  decreases slowly, but near  $M^*_{syn}$ , its decrease becomes very rapid. This tendency may be understood from the change in the structure of the ISI histograms. As  $M_{syn}$  is decreased, merging of multiple peaks occurs; hence, the average pacing degree of the stripes becomes worse with decreasing  $M_{syn}$ . Consequently, the degree of stochastic spiking coherence decreases abruptly near the threshold  $M^*_{syn}$ .

Finally, we examine the dependence of  $M_{syn}^*$  on D and  $I_{DC}$ . For the globally-coupled case, coherent states appear in the range of  $D_l^*(\simeq 9.4) < D < D_h^*(\simeq 33.4)$  for  $I_{DC} = 87$  (refer to Fig. 2(a) in Ref. 20). As D is increased from  $D_I^*$ , the order parameter  $\mathcal{O}$  increases abruptly at first, showing onset of coherence, because noise stimulates collective coherence between neural spikings. Then, the values of the order parameter become nearly the same over a large range of intermediate D, but for large D, the order parameter decreases because noise spoils spiking coherence. In the above, we consider a coherent case of D = 20. We examine the effect of random sparse connectivity on stochastic spiking coherence for other values of D in the coherent region. Near  $D_l^*$ , the occupation degree of spikes in the raster plot is low for the case of global coupling, as shown in Fig. 4(a1) for D = 10. As  $M_{sun}$  is decreased, the inhibition for each neuron is decreased; hence, the occupation degree increases (see the cases of  $M_{syn} = 200$  and 30), leading to an increase in the coherence degree (*i.e.*, the amplitude of  $V_G$  increases). However, with further decrease in  $M_{sun}$ , the coherence degree begins to decrease because the pacing degree becomes worse, as shown in the case of  $M_{syn} = 15$ . For this case of  $D = 10, M_{syn}^* \simeq 11$ . As D is increased, the value of  $M^*_{syn}$  tends to increase;  $M^*_{syn} \simeq 20$  and 92 for D = 15 and 27, respectively [see Figs. 4(b1) - 4(b5) and Figs. 4(c1) - 4(c5)]. We also examine the dependence of  $M^*_{syn}$  on  $I_{DC}$ . As the value of  $I_{DC}$  is decreased, not only the coherent range of D, but also the degree of coherence is found to be decreased. For comparison with the above case of  $I_{DC} = 87$ , we con-

=200 (a3) M = 30 (a5) M...=5 М (a4) M\_=15 800 200 V<sub>G</sub> (mV) -25 -35 1800 1200 1800 1200 1800 1200 1800 1200 1800 t (ms) Globa =30 (b2) M\_=200 (b3) Μ (b4) M\_=15 (b5) M\_=5 800 200 V<sub>G</sub> (mV) -25 -35 1800 1200 1800 1200 1800 1200 1800 t (ms)(c2) M...=200 (c3) M =30 (c4) M =15 (c5) M\_=5 800 200 V<sub>6</sub> (mV) -25 -35 1800 1200 1800 1200 1800 1800 1200 1800 t (ms) Globa =30 =200 (d3) M (d4) M =15 (d2) M (d5) M =5 800 200 V<sub>G</sub> (mV) -25 -35 1800 1200 1800 1200 1800 1200 1800 1800 1200 t (ms)

Fig. 4. Raster plots of spikes and global potentials  $V_G$ in a population of  $N(=10^3)$  randomly coupled subthreshold ML neurons for  $J = 3 \text{ mS/cm}^2$ : (a1) – (a5) D = 10 $\mu \text{A} \cdot \text{ms}^{1/2}/\text{cm}^2$ , (b1) – (b5)  $D = 15 \ \mu \text{A} \cdot \text{ms}^{1/2}/\text{cm}^2$ , (c1) – (c5)  $D = 27 \ \mu \text{A} \cdot \text{ms}^{1/2}/\text{cm}^2$  for  $I_{DC} = 87 \ \mu \text{A/cm}^2$ , and (d1) – (d5)  $D = 20 \ \mu \text{A} \cdot \text{ms}^{1/2}/\text{cm}^2$   $I_{DC} = 84 \ \mu \text{A/cm}^2$ .

sider the case of  $I_{DC} = 84$  where coherent states exist in a range of  $D_l^* (\simeq 12.7) < D < D_h^* (\simeq 29.6)$ . For D = 20, the raster plots of spikes and the global potentials  $V_G$  are shown in Figs. 4(d1) – 4(d5). For this case, the value of  $M_{syn}^* (\simeq 97)$  is larger than that ( $\simeq 45$ ) for the above case of  $I_{DC} = 87$  and D = 20. Like the case of  $I_{DC} = 87$ , the value of  $M_{syn}^*$  also tends to increase with increasing D in the coherent region. In this way, the value of  $M_{syn}^*$  depends on both D and  $I_{DC}$ . However, we emphasize that just the existence of a threshold  $M_{syn}^*$  rather than its specific value is important for the emergence of stochastic spiking coherence in sparsely coupled random networks.

#### **III. SUMMARY**

We have investigated the effect of sparse connectivity on the stochastic spiking coherence by varying  $M_{syn}$ (*i.e.*, the average number of synaptic inputs per neuron) in an inhibitory ensemble of N randomly coupled sub-2846-

threshold ML neurons. Emergence of stochastic spiking coherence seems to persist only if  $M_{syn}$  is larger than a threshold value  $M^*_{syn}$  whose dependence on N seems to be quite weak. This stochastic spiking coherence has been characterized in terms of a statistical-mechanical spike-based measure. With decreasing  $M_{sun}$ , the average pacing degree between spikes decreases slowly, but near  $M^*_{syn}$  its value drops very rapidly while the average occupation degree of spikes increases very slowly over the whole coherent region. The decrease in the pacing degree results in merging between multiple peaks in the ISI histograms. Due to the decrease in the pacing degree, the degree of stochastic spiking coherence (seen well in a raster plot of spikes) decreases abruptly near the threshold  $M^*_{sun}$ . This kind of weak inhibitory coherence, which emerges from sparsely synchronized oscillations of subthreshold neurons, might be associated with fast cortical rhythms with irregular and sparse neural discharges.

#### ACKNOWLEDGMENTS

This research was supported by the Basic Science Research Program through the National Research Foundation of Korea funded by the Ministry of Education, Science and Technology (2010-0015730).

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