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## Complete synchronization in coupled Type-I neurons

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For a system of type-I neurons bidirectionally coupled through a nonlinear feedback mechanism, we discuss the issue of noise-induced complete synchronization (CS). For the inputs to the neurons, we point out that the rate of change of instantaneous frequency with the instantaneous phase of the stochastic inputs to each neuron matches exactly with that for the other in the event of CS of their outputs. Our observation can be exploited in practical situations to produce completely synchronized outputs in artificial devices. For excitatory-excitatory synaptic coupling, a functional dependence for the synchronization error on coupling and noise strengths is obtained. Finally we report an observation of noise-induced CS between non-identical neurons coupled bidirectionally through random non-zero couplings in an all-to-all way in a large neuronal ensemble.

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## I. INTRODUCTION

Synchronous phenomena abound in nature and in our daily lives and have been studied from centuries past, right from Huygen's observations of synchronizing clocks. Various kinds of synchronous phenomena occur and have been identified (see for example [1–13]) (other references on the subject may also be found in [14]). Among these complete synchronization (CS) is one of the most interesting since the phase, frequency and amplitude of a subsystem all coincide with those of the other subsystem it is coupled to. It is seen therefore that in CS the trajectories of the coupled elements match exactly. CS is known to occur in identical systems, and was first demonstrated in chaotic systems in [1]. Neurons and neuronal networks have been a subject of frequent theoretical and experimental studies [15]. Synchronization of neural activity has elicited a great deal of interest since it is believed that such phenomena enable cognitive tasks such as feature extraction and recognition to be performed. Hodgkin and Huxley classified neuron excitability mechanisms broadly into two classes [16]: in type-II neurons the transition from a quiescent state to a periodically spiking state occurs through a Hopf bifurcation with a finite nonzero oscillation frequency. In type-I neurons, oscillations emerge through a saddle-node bifurcation on an invariant circle. As the bifurcation parameter changes, the stable and the unstable fixed points coalesce and then disappear, leaving a large amplitude stable periodic orbit. This is a global bifurcation and the frequency of the global loop can be arbitrarily small. Since axonal excitability patterns of mammalian neurons fall under the type-I class, it is but natural that this class has received special attention in the literature. Various observations have been made on type-I neurons, some prominent points of which are as follows. Equations for type-I neuronal dynamics can be reduced to the canonical normal form for a saddle-node bifurcation [17]. Repetitive firing occurs in the parameter regime when the system is in the close proximity of a saddle-node bifurcation on an invariant circle. Hansel *et al* [5] and Ermentrout have shown [6] that such neurons coupled via

a certain class of time-dependent synaptic conductances are difficult to synchronize. Börgers and Kopell made further investigations of such coupled systems. In particular they discussed the effects of random connectivity on synchronization and the PING mechanism in networks of excitatory (E) and inhibitory (I) neurons both in the presence and in the absence of external noise [7, 8].

In this work, we present some computer studies of generic type-I neurons coupled via synaptic conductances such as those considered in [7–9], which are governed by ordinary differential equations and which depend upon the outputs of the presynaptic neurons, and are subject to weak additive Gaussian white noise. We consider both excitatory-excitatory (EE) and inhibitory-excitatory (IE) bidirectional couplings and show that in certain regimes of the coupling constants and inputs, the system of coupled neurons shows complete synchronization (CS). The issue of CS in type-I neurons was not discussed in [7, 8]. As discussed in Section-2, largest Lyapunov exponents are shown to not adequately give information about CS in the system. We make an observation on the inputs to the neurons (and which are also modulated by the feedback in the system): we point out that the variation of the instantaneous frequency of the input received at each neuron with the instantaneous phase of the input it receives exactly coincides with that of the other neuron, in the event of complete synchronization of their outputs. It will be noted that in the presence of noise and feedback, this is not a trivial statement. We discuss the utility of this result in practical situations.

In general, for EE synapses, our results indicate that when a common, externally applied constant input is used to perturb two bidirectionally coupled type-I neurons having identical coupling strength magnitudes and synaptic rise & decay times, weak noise induces them to exhibit CS upto a critical value of the coupling strength  $g_c$ . For coupling strengths larger than  $g_c$ , we find the system de-synchronizes through a power-law before locking on to a partially synchronized state for larger coupling strengths. We obtain a functional dependence for the synchronization error for neuronal outputs on coupling and noise strengths, in the regimes leading to partial synchronization. Such

functional dependencies have not been reported in the literature yet, to the best of our knowledge. In the noiseless case for identical EE neurons separated by different initial conditions, we observe that the antiphase states are stable in agreement with [6] and become completely in-phase in the presence of noise. For just two neurons with IE coupling, noise does not induce complete synchrony. In an ensemble of 200 non-identical neurons however, we find unexpectedly that noise-induced CS is possible with all-to-all bidirectional IE random couplings.

## II. COUPLED TYPE-I NEURONS IN THE PRESENCE OF GAUSSIAN WHITE NOISE

In a system of  $n$  neurons, the activity of the  $i$ th neuron is described by a variable  $x_i$  which can be related to the membrane conductance. Its dynamics is represented by

$$\dot{x}_i = qx_i^2 + I_i, \quad I_i = \beta_i + \sum_{j=1}^n \alpha_j g_{ji} s_{ji}, \quad (1)$$

where  $q$  denotes an inverse time constant for the membrane potential,  $I_i$  denotes its total input comprising of a constant external input  $\beta_i$  and the contributions from the presynaptic neurons, with  $i = 1, \dots, n$ .  $s_{ij}$  is the synaptic gating variable and represents the fraction of ion channels open in the  $j$ th presynaptic neuron.  $g_{ij}$  is the measure of the strength of the synapse from neuron  $i$  to neuron  $j$ ; we have taken  $g_{ii} = 0$ . When  $I_j > 0$  this equation has no fixed points. Any initial condition tends to infinity in a finite time. To avoid this blow-up of solutions, a nonlinear transformation to new variables  $\theta_i$  may be made [6]:  $x_i = \tan \theta_i/2$  which maps the real line onto a circle. Eqn.(2) then becomes

$$\frac{d\theta_i}{dt} = q(1 - \cos \theta_i) + (\beta_i + \sum_{j=1}^n \alpha_j g_{ji} s_{ji}(\theta_j))(1 + \cos \theta_i) \quad (2)$$

The point  $x = \infty$  then gets mapped to the point  $\theta = \pi$  and is interpreted as firing of a spike. We set  $q^{-1} = 1$  and work in the parameter regime in which  $I/q \ll 1$  so that the width of the spikes turn out to be in milliseconds as in real neurons [7, 8] in these units. The  $s_{ij}(t)$  evolve in time

according to the differential equation which was considered in [7–9]

$$\frac{ds_{ij}}{dt} = -\frac{s_{ij}}{\tau_{ij}} + e^{-\eta(1+\cos\theta_i)} \frac{1-s_{ij}}{\tau_R} \quad (3)$$

where  $\tau_{ij}$  denotes the synaptic decay time and  $\tau_R$  the synaptic rise time. The values of  $s_{ij}$  always lie in the range 0 to 1, reaching the maximal value when the neuron spikes. The synapse is an excitatory one if  $\alpha_j = +1$ , and  $-1$  if it models an inhibitory synapse. Lest there be any confusion, we would like to clarify at the outset that when we refer to *identical* neurons, we mean neurons that have the same nature of synaptic coupling (EE) and have same coupling strengths  $g_{12} = g_{21}$ , have the same value of  $\tau_R$ ,  $\tau_{12} = \tau_{21}$ , and receive the same constant input  $\beta_1 = \beta_2$ , while their initial conditions differ by very little.

Transmembrane voltage and neuronal firing can be affected by various sources of neuronal noise, but predominantly by synaptic noise [18]. The synaptic noise itself occurs due to several factors, but chief among them is the synaptic bombardment at the inputs through the large number of neuronal connections, with each input spike adding a random contribution. We model this through an additive Gaussian white noise added to the neuronal input  $I_i$ . We study the dynamics of a system of two such neurons coupled bidirectionally as depicted in Fig.(1) and subject to Gaussian white noise  $\xi(t)$  with the following properties:  $\langle \xi(t) \rangle = 0$  ,  $\langle \xi(t)\xi(t') \rangle = 2\sigma\delta(t-t')$ , where the stochastic variables are taken to obey Stratonovich calculus. Addition of Gaussian white noise  $\xi$  to eqn.(1), manifests as multiplicative noise in eqn.(2) because of the change of variables to  $\theta$ , so that the equations now take the form

$$\frac{d\theta_i}{dt} = (1 - \cos\theta_i) + (\beta_i + \sum_{j=1}^n \alpha_j g_{ji} s_{ji}(\theta_j) + \xi(t))(1 + \cos\theta_i) \quad (4)$$

Eqns.(3) for the  $s_{ij}(\theta_i)$  define the feedback regulating the activity of the  $j$ th neuron since  $s_{ij}$  depends upon  $\theta_i$  which in turn depends upon  $\theta_j$  ( $i \neq j$ ) via  $s_{ji}(\theta_j)$ . The feedback increments or decrements the constant external input  $\beta_i$  received by neuron  $i$ . Thus the control parameter  $I_i$  acquires time dependence through the dynamical variables.

As in [19], we consider the neuronal output to be described by the variable  $u_i = (1 - \cos \theta_i)/2$  as its time evolution pattern resembles that of a membrane potential in real neurons. This transformation maps the resting point  $x_i = 0$  corresponding to  $\theta_i = 0$  to  $u_i = 0$ , and the spiking point  $\theta_i = \pi$  to  $u_i = 1$  via the relation  $u_i = x_i^2/(1 + x_i^2)$ . We choose to work with these variables as we get some new and interesting insights upon the dynamics underlying the phenomenon of complete synchronization. In terms of these variables, eqns.(4) and (3) become:

$$\begin{aligned} \dot{u}_i &= 2(u_i + (\beta_i + \sum_{j=1}^N \alpha_j g_{ji} s_{ji} + \xi)(1 - u_i))\sqrt{u_i(1 - u_i)} \\ \dot{s}_{ij} &= -\frac{s_{ij}}{\tau_{ij}} + \exp(-2\eta(1 - u_j))\frac{(1 - s_{ij})}{\tau_R} \end{aligned} \quad (5)$$

Numerous studies in the literature have reported the phenomenon of complete synchronization in various coupled systems [1–14, 20–25]. An adequately satisfying explanation of why and under what conditions CS can occur for systems with more complicated couplings, such as, for instance, that described by eqn.(5), is however, still lacking in our opinion.

In particular, in [21, 22] the authors study noise induced CS in systems subjected to a common additive white noise and show that a necessary condition for CS is the existence of a significant contraction region in phase space. The systems studied in [21, 22] were Lorenz and Rossler systems which are far more amenable to analytical treatment than the equations above in eqn.(5).

Since excitability in type-I neurons results from a saddle node on an invariant circle bifurcation, complete synchronization of two uncoupled neurons by common noise alone can be expected because of the existence of a contraction region close to the stable manifold of the saddle. On the other hand, when two such neurons are coupled together as in eqn.(5), the existence and nature of a contraction region would depend upon the eigenvalues of the Jacobian at the fixed points of the coupled system. However for eqns.(5), an analytical study becomes difficult since the Jacobian becomes singular at the fixed points. We therefore perform some computer studies on the system to learn more about the underlying dynamics. Moreover, since as we show below, Lyapunov exponents need not

adequately give information about CS, we seek other explanations for occurrence of CS.

As in [21, 22], we define CS between the activities of neurons 1 and 2 as a vanishing value for the quantity  $\langle |u_1 - u_2| \rangle$  which is the synchronization error averaged over all iterations.

Largest Lyapunov exponents for the system in eqn.(5) in the presence of noise for both EE and IE couplings were calculated following [26–28] and are shown in fig.(2). To incorporate noise in the numerical calculations, the stochastic Runge-Kutta-4 method [29–31] was used. We note that in both EE and IE cases, the largest Lyapunov exponent  $\lambda_1$  becomes more negative on the addition of noise. We observe also that for some intermediate values of the coupling constants (such as  $g_{12} = g_{21} = 0.5$ ), the  $\lambda_1$  values could be larger, i.e., less negative, than those for lower coupling strengths (e.g.,  $g_{12} = g_{21} = 0.3$ ). For EE coupling,  $\lambda_1$  is almost always less than or equal to zero. In the case of IE coupling however, we find that for smaller noise-strengths and smaller couplings, for small  $\beta$ ,  $\lambda_1$  fluctuates between positive and negative values in the presence of noise. This happens because of the oscillation of the bifurcation parameter (total input) between two regimes, depending upon the relative strengths of  $\beta_i$  and  $\alpha_j g_{ji} s_{ji}$ , since  $\alpha_j = -1$  for neuron  $j$ . Hence calculation of Lyapunov exponents may not adequately give information about CS or large windows of zero synchronization error, such as, for example, for the situation shown in Fig.(3), though they may certainly show the emergence of a definite order in the presence of noise and possible synchronization between the coupled units.

Indeed, CS is expected to occur between identical systems and finding CS between non-identical oscillators would be unusual. As we describe later, however, we do find noise-induced CS in a system of 200 non-identical oscillators with random all-to-all couplings. Equally intriguingly, we find that there are parameter regimes where identical oscillators do not show CS at all, though the Lyapunov exponents shown in Fig.(2a) remain negative. Negative transverse Lyapunov exponents are widely accepted as characterizing CS, but their calculation for the system of 200 neurons, with a nontrivial feedback mechanism for phase resetting, as in eqn.(5) is a difficult task and we have

not attempted it here. In our case, even for  $n = 2$ , if we were to define new variables:  $z = \frac{(u_1 - u_2)}{2}$  and  $w = \frac{(u_1 + u_2)}{2}$ , expressing the synchronization error dynamics through  $\dot{z}$  in terms of  $z$  and  $w$  alone is not at all straightforward for the equations in (5).

Moreover when each of the subsystems has a saddle-node-on-an-invariant circle bifurcation in the uncoupled limit, one could expect windows of intermittent firing patterns. In the coupled system, this is indeed observed in some parameter regimes, interspersed with large windows showing zero synchronization error, even in identical oscillators (EE case) for lower noise strengths (Fig.(3)). Hence we believe that negative largest Lyapunov exponents alone may not constitute conclusive proof for predicting noise-induced CS in coupled neurons.

We therefore looked for other indicators which could help in understanding the mechanism of CS better in systems with feedback, such as in eqns.(5). We found one such simple indicator for CS in the context of the model under study and which we will now describe. The same methods and analysis should also hold for getting information on CS in any other system. Since synchronous activity is brought about by a common input or through mutual interactions and since these include components which are highly random, we study the *instantaneous* values of the sum total of the *inputs* received by each unit of a coupled system. We first set up a framework for this purpose and then provide a physical motivation and explanation for understanding CS through this indicator.

### III. INSTANTANEOUS PHASE - INSTANTANEOUS FREQUENCY VARIATIONS OF THE NEURONAL INPUTS & CS

We construct the analytical signal [14, 20]:  $\Gamma_i(t) = I_i(t) + iH(I_i(t)) = B_i(t)e^{i\rho_i(t)}$  for the inputs  $I_i$  and similarly  $w(t) = u(t) + iH(u(t)) = R(t)e^{i\phi(t)}$  for  $u(t)$  using Hilbert transforms. The



instantaneous amplitudes and phases evolve according to:

$$\begin{aligned}\dot{R}_i(t) &= 2\sqrt{R_i(1 + R_i^2 - 2R_i \cos \phi_i)}\{R_i \cos(\zeta_i - \psi_i) - R_i B_i \cos(\zeta_i - \psi_i + \rho_i) + B_i \cos(\psi_i + \rho_i) + \xi_R\} \\ \dot{\phi}_i(t) &= 2\sqrt{\frac{(1 + R_i^2 - 2R_i \cos \phi_i)}{R_i}}\{R_i \sin(\zeta_i - \psi_i) - R_i B_i \sin(\zeta_i - \psi_i + \rho_i) + B_i \sin(\psi_i + \rho_i) + \xi_\phi\}\end{aligned}\quad (6)$$

where  $\zeta_i(t) = \arctan(\frac{R_i \sin \phi_i}{R_i \cos \phi_i - 1})$ , and  $\psi_i(t) = (\zeta_i(t) - \phi_i(t))/2$  denotes the instantaneous difference between the phase of the output of the  $i$ th neuron and that of the part it sends as feedback to the presynaptic conductance of the  $j$ th neuron — this feedback is a stochastic component of the input for neuron  $j$ . We have constructed the noise terms  $\xi_R(t)$  and  $\xi_\phi(t)$  from the analytical noise signal  $\xi(t) + i\nu(t) = \xi(t) + iH(\xi(t))$ :

$$\xi_{R_i} = (1 - R_i)(\xi \cos \psi_i + \nu \sin \psi_i), \quad \xi_{\phi_i} = (1 - R_i)(\xi \sin \psi_i + \nu \cos \psi_i) \quad (7)$$

$\xi_{R_i}(t)$  and  $\xi_{\phi_i}(t)$  are periodically modulated by  $\psi_i$  which evolves according to the differential equation:

$$\begin{aligned}\dot{\psi}_i &= \frac{1}{\sqrt{R_i(1 + R_i^2 - 2R_i \cos \phi_i)}}\{(R_i^2 - 1)[R_i \sin(\zeta_i - \psi_i) - B_i R_i \sin(\zeta_i - \psi_i + \rho_i) + B_i \sin(\psi_i + \rho_i) \\ &\quad + \xi_{\phi_i}] - R_i \sin \phi_i [R_i \cos(\zeta_i - \psi_i) - B_i R_i \cos(\zeta_i - \psi_i + \rho_i) + B_i \cos(\psi_i + \rho_i) + \xi_{R_i}]\} \\ &= \frac{1}{2\sqrt{(1 + R_i^2 - 2R_i \cos \phi_i)}}\{(R^2 - 1)\sqrt{R}\dot{\phi} - \sin \phi \dot{R}\}\end{aligned}\quad (8)$$

The instantaneous phase  $\phi_i$  therefore has no deterministic time scales and its drift and diffusion in time in the presence of noise is influenced by  $B_i$  and  $\rho_i$ , the instantaneous values of the amplitude and phase respectively of the input, and also by the instantaneous amplitude  $R_i$  of the neuronal output.  $B_i(t)$  and  $\rho_i(t)$  evolve as follows:

$$\begin{aligned}\dot{B}_i(t) &= -B_i\left(\frac{1}{\tau_{ji}} + \frac{e^{-2\eta(1-R_j \cos \phi_j)}}{\tau_R} \cos(2\eta R_j \sin \phi_j)\right) + \frac{\beta_i}{\tau_{ji}} \cos \rho_i \\ &\quad + \frac{1}{\tau_R}(\beta_i + \sum_j \frac{\alpha_j g_{ji}}{\tau_R}) \cos((2\eta R_j \sin \phi_j) - \rho_i) e^{-2\eta(1-R_j \cos \phi_j)} \\ \dot{\rho}_i(t) &= -\frac{e^{-2\eta(1-R_j \cos \phi_j)}}{\tau_R} \sin(2\eta R_j \sin \phi_j) - \frac{\beta_i}{B_i \tau_{ji}} \sin \rho_i \\ &\quad + \frac{1}{\tau_R B_i}(\beta_i + \sum_j \frac{\alpha_j g_{ji}}{\tau_R}) \sin((2\eta R_j \sin \phi_j) - \rho_i) e^{-2\eta(1-R_j \cos \phi_j)}\end{aligned}\quad (9)$$

These show the effect of feedback on neuronal response. It is seen that CS between the outputs of neurons 1 and 2 occurs when the changes in the instantaneous phases and amplitudes of the two neuronal *inputs* exactly match each other. In other words, CS in the inputs to the neurons is required for the outputs to synchronize in phase, amplitude and frequency. This observation is in general not quite obvious since the system is nonlinear, and has a feedback mechanism which depends upon the outputs of the other neurons.

In Fig.(4) we present the instantaneous-phase versus instantaneous-frequency plots of the inputs received by the two neurons. In all the numerous cases we studied for the coupled system for  $n = 2$ , we found that the signature of CS is the almost identical nature of these plots for the two systems that are in synchrony, be it with or without noise. On the other hand, the absence of CS gets reflected in the non-identical variation between instantaneous phase and instantaneous rates of phase-change of inputs to the two neurons, in the plots shown in Fig.(5). This is again true for both the noiseless as well as noisy cases.

The system of equations (eqn.(5)) is of the form

$$\dot{u}_i = f_D(u_i, s_i, u_j, t, \beta = 0, \alpha_j g_{ji} = 0) + (\beta_i + \alpha_j g_{ji}, s_i(u_j, t)) f_n(u_i) + \xi f_n(u_i), \quad (10)$$

where

$$f_D(u_i, s_i, \beta_i = 0, \alpha_j g_{ji} = 0) = 2u_i^{3/2}(1 - u_i)^{1/2}, \quad f_n(u_i) = 2u_i^{1/2}(1 - u_i)^{3/2}, \quad (11)$$

and since feedback to each neuron through the synaptic coupling is oscillatory, in a Fokker-Planck description of the stochastic process, the probability distribution  $P(u_1, u_2, t)$  of the neuronal ensemble will not be stationary in the  $t \rightarrow \infty$  limit [32]. In certain regimes of the noise strengths and coupling constants, where competing contributions from the drift and diffusion terms would make the noise-averaged difference in outputs  $\langle(u_1 - u_2)\rangle$  zero, CS occurs.

Physically, CS is brought about through the following sequence of events. Addition of a small amount of noise increases the decay time of the synaptic conductances  $s_{ij}$  gradually, and eventually,

lowers their minimum to zero. This delays the onset of the next  $s_{ij}$  peaks, and hence the input  $I_i$  to each neuron at any further instant of time. Increasing the noise strength further increases the decay time of  $s_{ij}$ . The periodically maximal values of the inputs thus take longer to arrive at the neurons and this becomes visible in the neuronal firing pattern as departures from the previous (noiseless) values of the phase differences between the neurons, and those of their output differences  $\langle u_1 - u_2 \rangle$ . The instantaneous values of the phases and the rate at which they change in time, i.e., the instantaneous frequencies of each neuron, is determined by the strengths  $\alpha_{ij}g_{ij}$  of the synaptic inputs it receives and the noise strength for any given set of  $\beta, \tau_R, \tau_{ij}, \eta$ . Hence for given initial conditions and different amplitudes for  $u_1$  &  $u_2$ , it would be reasonable to expect CS to occur when the following is satisfied for the inputs to the neurons: the variation of instantaneous values of the frequencies with instantaneous phases of the *input* for neuron 1 matches with that for neuron 2. This results in the instantaneous values  $\phi_1$  and  $\dot{\phi}_1$  of neuron 1 changing in step with  $\phi_2$  and  $\dot{\phi}_2$  respectively of neuron 2. This forces the amplitudes of neurons 1 & 2 to become identical with each other, since otherwise both conditions  $\phi_1 - \phi_2$  and  $\dot{\phi}_1 = \dot{\phi}_2$  cannot be simultaneously maintained. Thus CS results.

A striking feature of all these plots is their strange, flame-like structure. The flame shape is reminiscent of canards that are typically associated with systems exhibiting relaxation oscillations. Indeed, from the common factor occurring in the inverse square root on the right hand side of eqn.(8), it is apparent that  $\psi(t)$  does evolve on a time scale different from that for  $R(t), \phi(t), B(t)$  &  $\rho(t)$  in eqns.(6) & (9), though it is a dynamically varying time scale, determined also by the stochasticity of the system. The separation of time scales is in fact manifested in the time series for the neuronal inputs which show relaxation oscillations (Figs.(4) & (5)). This gives the input instantaneous phase-frequency curve its characteristic shape whenever noise is introduced. This is indicative of some order emerging in the phase. In fact, noise-induced phase synchronization can be demonstrated even in the IE system by interpreting the instantaneous phase differences

$\Phi = \phi_1 - \phi_2$  in a statistical sense as in [21]. The distribution  $P(\Phi)$ , of cyclic instantaneous phase differences,  $\Phi \in [-\pi, \pi]$  is shown in Fig.(6). Preferred phase differences between the 2 neurons manifest as peaks in  $\Phi$  which become sharper and taller with increasing noise-strengths – a clear indication of noise-induced phase coherence.

#### IV. NOISE-INDUCED CS & PARTIAL SYNCHRONIZATION IN EE & IE SYSTEMS

In Fig.(7a) we have plotted the synchronization error  $\langle |u_1 - u_2| \rangle$  for two coupled identical (EE) neurons and for coupled non-identical (IE) neurons, as a function of the coupling strength for different noise-strengths. We have considered here the special case of  $\beta_1 = \beta_2 = 0$ , and each neuron receives inputs only from the other neurons; *i.e.*, we look at the effect of feedback. Results and analysis for non-zero  $\beta_i$  are presented elsewhere [33]. We see that although CS is expected between identical oscillators, it does not happen for the noiseless (deterministic) case. Increasing noise-strength brings down  $\langle |u_1 - u_2| \rangle$  and indeed takes it down to zero for certain ranges of the coupling constant.

For the identical EE coupled neurons, when feedback constitutes the only input (there being no other explicit input), as in Figs.(7a,7b), then beyond a maximal critical coupling constant strength  $g_c$ , the system gets de-synchronized, with  $\langle |u_1 - u_2| \rangle \neq 0$ . For  $g > g_c$ , there then exists a regime in the de-synchronized system where noise strength  $\sigma$  still plays a role in determining the output. In this transition regime, for  $g > g_c$ , we find that the difference in outputs  $\langle |u_1 - u_2| \rangle_{trans}$  depends upon  $g$  through the expression

$$\langle |u_1 - u_2| \rangle_{trans} = (g - g_c)^{1/4} - \nu_\sigma, \quad (12)$$

where  $\nu_\sigma$  is a constant that depends upon the noise strength  $\sigma$ .

The critical coupling strength  $g_c$  depends upon the noise strength as well and we find that it varies

as

$$g_c \sim a\sqrt{\sigma}, \quad (13)$$

where  $a = 1.1$ . At very high  $g$  the system gets locked to a partially synchronized state, with  $\langle |u_1 - u_2| \rangle$  approaching a constant value, wherein noise strength no longer influences the difference in the outputs of the neurons. In Fig.(7a), this constant value approaches 0.5. For the curves in Fig.(7a,b), for the entire regime following the beginning of desynchronization, we find a functional dependence on the coupling constant  $g$  given by an equation of the form

$$\langle |u_1 - u_2| \rangle_\sigma \sim a(\sigma) - b(\sigma)g - \frac{g_c^4}{g^3}, \quad (\text{for } g > g_c), \quad (14)$$

where  $a(\sigma)$  and  $b(\sigma)$  depend on the noise-strength through

$$a(\sigma) = \frac{0.59}{\sigma^{0.13}}, \quad b(\sigma) = \frac{0.0181}{\sigma^{0.53}}, \quad (15)$$

so that

$$\langle |u_1 - u_2| \rangle_\sigma \sim \frac{0.59}{\sigma^{0.13}} - \frac{0.0181}{\sigma^{0.53}}g - \frac{1.4641}{g^3}\sigma^{2.01} \quad (\text{for } g > g_c). \quad (16)$$

This expression is plotted on the numerical data points in Fig.(7b). A rigorous theoretical treatment of the system needs to be done in future studies to establish these relations for the synchronization and desynchronization transitions through a Fokker-Planck approach.

In the IE case (Fig.(7c)), we see that noise-induced CS does not occur for two coupled neurons; however, there is partial synchronization (by this we mean that  $\langle |u_1 - u_2| \rangle = \text{constant} \neq 0$ ) since  $\langle |u_1 - u_2| \rangle$  gets locked to a finite, non-zero value ( $\sim 0.6$ ) for large  $g$ . Further, increasing noise-strength increases rather than decreases  $\langle |u_1 - u_2| \rangle$ , in the region before partial synchronization, in contrast to the observation for the EE case. We were unable to achieve CS in the IE case for two coupled neurons, even in the presence of noise.

However, for an ensemble of 200 coupled theta neurons of which 150 neurons are excitatory and 50 inhibitory, we obtain very different results. In this simulation shown in Fig.(8), each

neuron receives the same input  $\beta_i = 0.1$  and there is all to all random coupling with the coupling strengths varying between 0.05 and 0.1 and with different initial conditions. The excitatory neurons are shown in red while the inhibitory ones are in green. On introducing Gaussian white noise of strength  $\sigma = 5.0$  into the system we observe synchronous phenomena emerging between the excitatory and inhibitory neurons. The interesting thing to note here is that not only do most of the inhibitory neurons fire in synchrony with other inhibitory neurons, but that also most of them are synchronized with the excitatory neurons. This kind of noise-induced near-CS in coupled type-I neurons with random non-zero coupling strengths has not, to our knowledge, been reported previously in the literature. A detailed study of this situation is under way to explain the observed synchrony for  $n = 200$  and will be reported elsewhere: it is beyond the scope of the present work. Interestingly, in the literature, spatiotemporal synchronization has been shown to occur in networks of coupled chaotic maps with varying degrees of randomness in the coupling connections [12].

## V. CONCLUSION

We have studied the issue of noise-induced CS in coupled type-I neurons, a class of neurons that are especially important since mammalian neurons fall under this category. We find that complete synchronization between any two neurons is signalled whenever the variations of the instantaneous input phases  $\phi$  versus the instantaneous frequencies  $\dot{\phi}$  of the inputs of the neurons being studied are identical. We point out that such identical  $\phi$ - $\dot{\phi}$  plots of the neuronal inputs would be a signature of CS between the neurons. This suggests the possibility of producing completely synchronized outputs of coupled systems having feedback mechanisms in the presence of noise, by ensuring that the plots of the instantaneous frequency versus instantaneous phase of the *inputs* to the subsystems are identical. That this is a significant point will be appreciated when one recalls that this condition is required in the continued presence of noise and feedback. When monitoring

or control of neurons is required to be done in a living organism in the case where synchronized neuronal output is required at another, inaccessible spot through a given external input, this result becomes important.

Though CS is expected between coupled, identical neurons, we find that CS occurs only upto a critical value  $g_c$  of the coupling constant  $g$  for a given noise strength beyond which the system desynchronizes again, and then for large  $g$  gets locked to a partially-synchronized state. We find that the critical coupling strength  $g_c$  depends upon the noise-strength through a power law. For  $g$  greater than the critical value  $g_c$ , from the transition regime through upto the onset of partial synchronization, we find a functional dependence of the noise-averaged output difference on  $g$  and the noise strength  $\sigma$ , given by eqn.(14). For a larger ensemble of 200 neurons, we find unexpectedly that non-identical neurons can show near-complete synchronization.

Since type-I neurons model axonal excitability patterns in mammals, the results presented here would be useful in the study of synchronous mechanisms underlying the neural code. As an immediate application, we believe our results would be useful in explaining the experimental observations reported on cat & awake monkey visual cortex [34–38] which show synchronization of neuronal activity with a single stimulus, and which disappears when activated by different, independent stimuli. Since a single stimulus would correspond to neuronal inputs of identical amplitudes, instantaneous phase and frequency, this is actually the same scenario that we have found for CS to occur. It is also likewise clear why CS was experimentally observed to vanish on the activation of different stimuli, since the necessary conditions of identical input amplitude, phase and frequency are no longer met.

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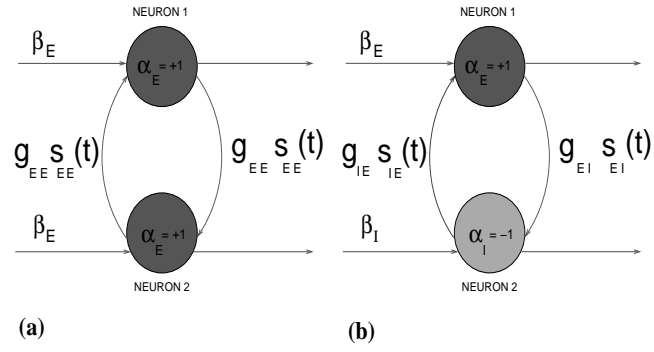
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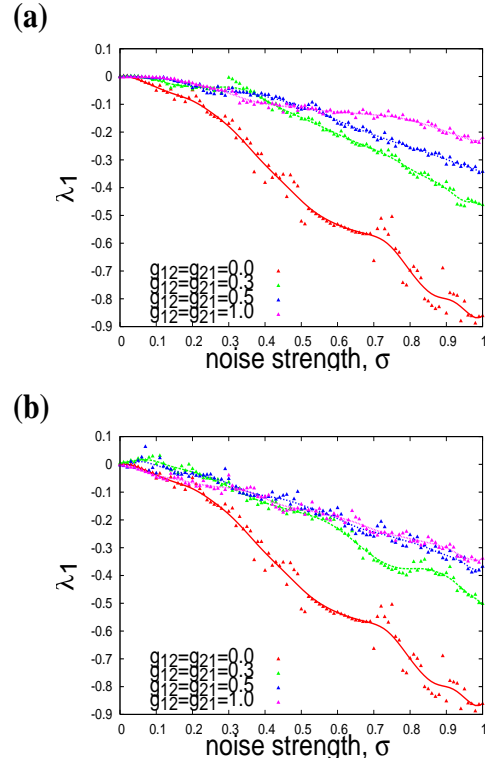
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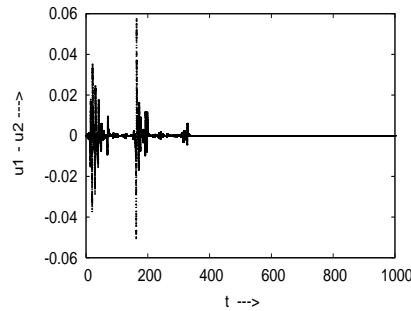
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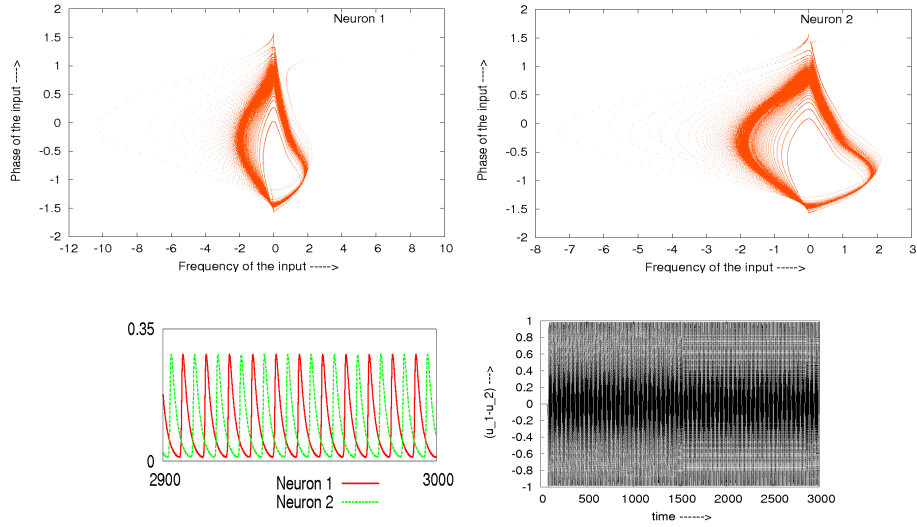
**Figure 1.** Bidirectional coupling between two theta neurons. Left: E-E coupling, Right: I-E coupling.



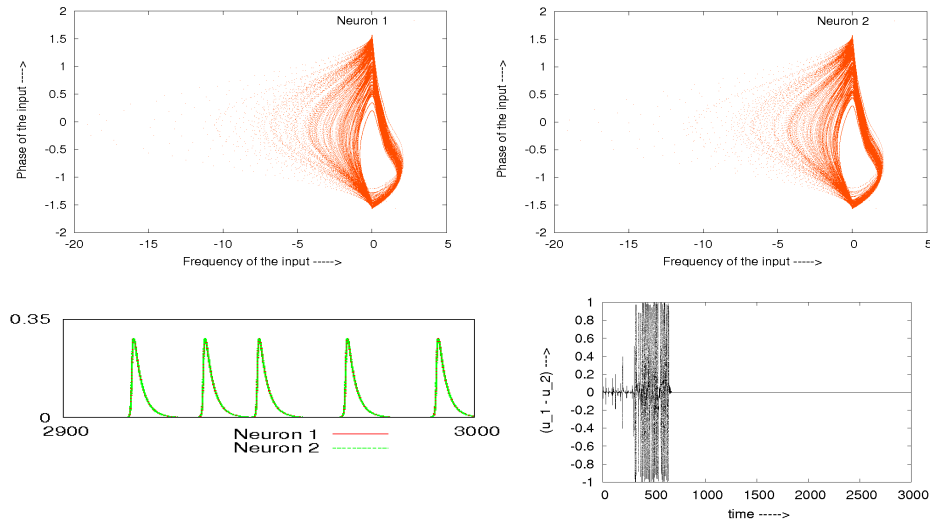
**Figure 2.** Lyapunov exponent in the presence of noise for: (at top) EE coupling and (at bottom) IE coupling. In both cases, the parameters which we used are  $\beta_1 = \beta_2 = 0.1$ ,  $\tau_{12} = \tau_{21} = 2.0$ ,  $\tau_R = 0.1$ ,  $\eta = 5.0$ .



**Figure 3.** Windows of zero synchronization error interspersed with intermittent bursts of firing in coupled identical EE neurons:  $g_{12} = g_{21} = 0.3$ ,  $\tau_{12} = \tau_{21} = 2.0$ ,  $\tau_R = 0.1$ ,  $\beta_1 = \beta_2 = 0.1$ ,  $\sigma = 0.2655$ .

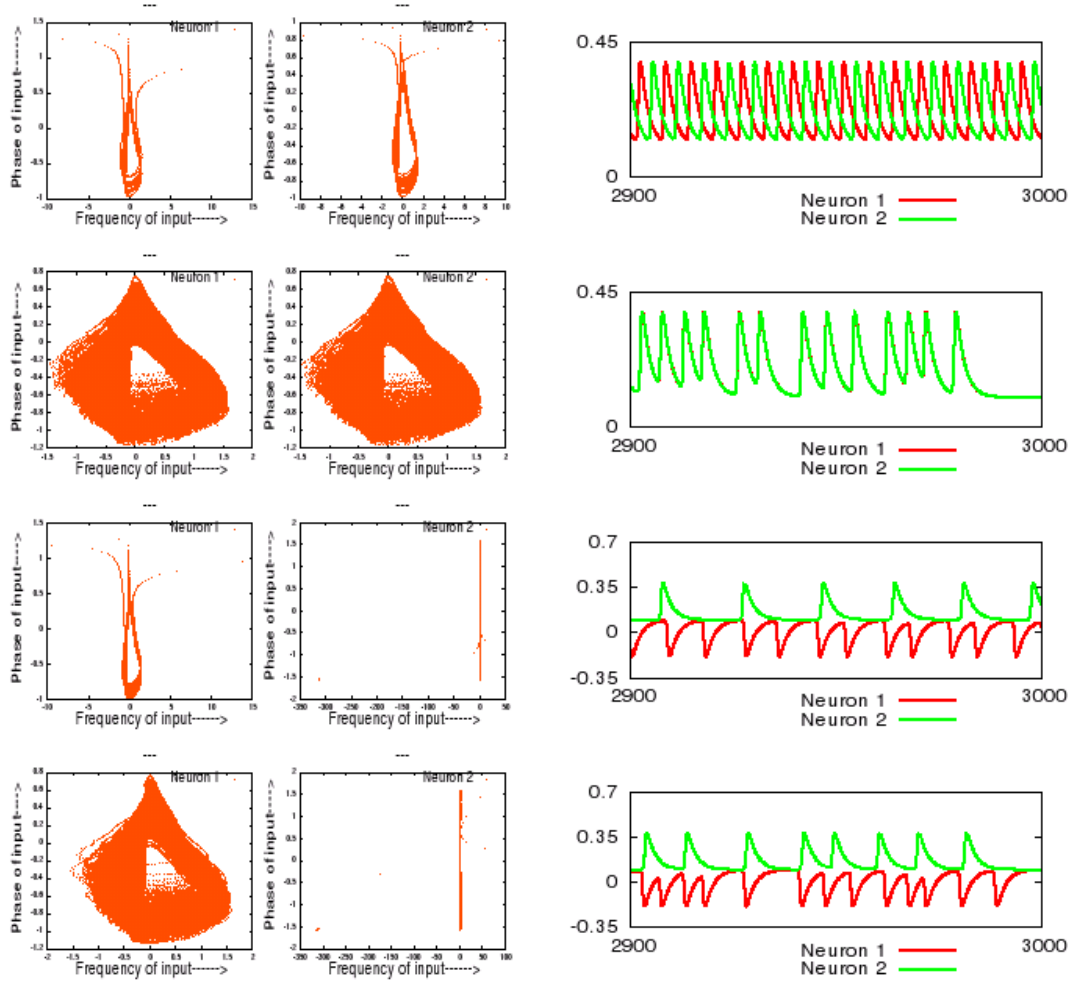


a

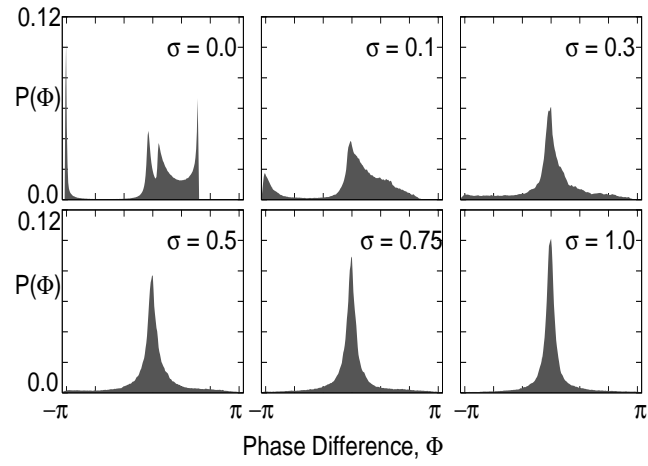


b

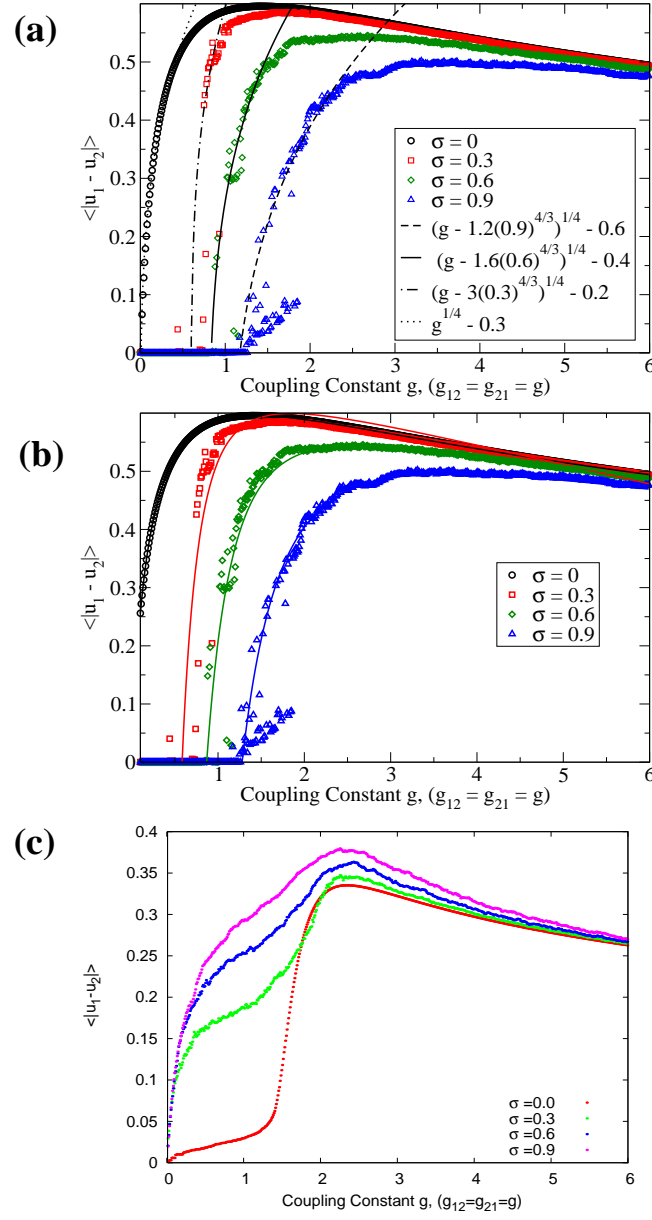
**Figure 4.** Instantaneous phase-frequency “flame” plots of stochastic **input**  $I_i = \beta_i + \sum_{j=1}^N \alpha_j g_{ji} s_{ji}$  to neuron  $i$ , for EE coupling, for **(a)**  $\sigma = 0$  (top) and **(b)**  $\sigma = 0.09$  (bottom). In these plots,  $\beta_1 = \beta_2 = 0.0$ , showing the effect of feedback. The extended panels below each set of flame plots show the corresponding time-series for neuronal input (at left) and the difference  $(u_1 - u_2)$  in neuronal outputs (at right). Parameter values are:  $g_{12} = g_{21} = 0.3$ ,  $\tau_{12} = \tau_{21} = 2.0$ ,  $\tau_R = 0.1$ .



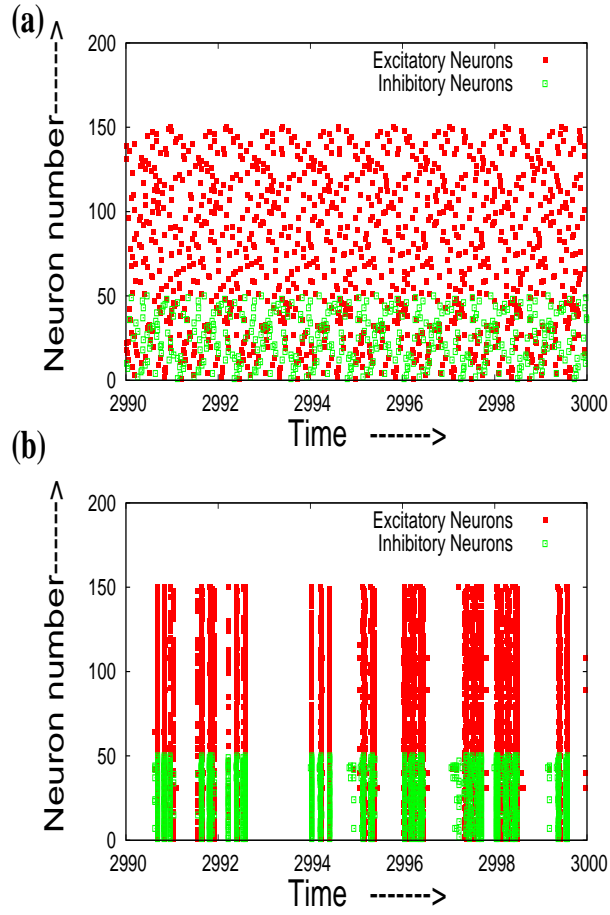
**Figure 5.** More instantaneous input phase-frequency “flame” plots with corresponding time-series of neuronal input. row 1: EE,  $\sigma = 0.0$ ; row 2: EE,  $\sigma = 0.301$ ; row 3: IE,  $\sigma = 0.0$ ; row 4: IE,  $\sigma = 0.301$ . Parameters used are:  $g_{12} = g_{21} = 0.3$ ,  $\tau_{12} = \tau_{21} = 2.0$ ,  $\beta_1 = \beta_2 = 0.1$ ,  $\tau_R = 0.1$ .



**Figure 6.** Distribution of instantaneous phase-differences for neuron pair with IE coupling, at different noise strengths. Here,  $g_{12} = g_{21} = 0.3$ ,  $\tau_{12} = \tau_{21} = 2.0$ ,  $\tau_R = 0.1$ ,  $\eta = 5.0$ ,  $\beta_1 = \beta_2 = 0.0$ ,  $\alpha_1 = +1$ ,  $\alpha_2 = -1$ .



**Figure 7.** Noise-induced synchronization in coupled Type-I neurons (a) EE case; transition from synchronized to partially synchronized state when  $g > g_c$  (b) EE case, as in (a); solid lines correspond to Eqn.(16). (c) IE case; noise-induced CS is absent but there is partial synchronization as the system gets locked to  $\langle |u_1 - u_2| \rangle \sim 0.6$  for large  $g$ . For both (a) & (b):  $\tau_{12} = \tau_{21} = 2.0$ ,  $\beta_1 = \beta_2 = 0.0$ ,  $\tau_R = 0.1$ , initial conditions  $\theta_1 = 0.0$ ,  $\theta_2 = 0.01$ ,  $s_{12} = s_{21} = 0.0$



**Figure 8.** Simulation of 200 bidirectionally-coupled theta neurons (150 EE (in red) and 50 IE (in green)) with random all-to-all couplings; top:  $\sigma = 0$ , bottom:  $\sigma = 5.0$ .