# ORIGINAL PAPER

# Anticipating spike synchronization in nonidentical chaotic neurons

T. Pyragienė · K. Pyragas

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Abstract Anticipating synchronization is investigated in nonidentical chaotic systems unidirectionally coupled in a master-slave configuration without a timedelay feedback. We show that if the parameters of chaotic master and slave systems are mismatched in such a way that the mean frequency of a free slave system is greater than the mean frequency of a master system, then the phase synchronization regime can be achieved with the advanced phase of the slave system. In chaotic neural systems, this leads to the anticipating spike synchronization: unidirectionally coupled neurons synchronize in such a way that the slave neuron anticipates the chaotic spikes of the master neuron. We demonstrate our findings with coupled Rössler systems as well as with two different models of coupled neurons, namely, the Hindmarsh-Rose neurons and the adaptive exponential integrate-and-fire neurons.

**Keywords** Anticipating chaotic synchronization · Rössler system · Hindmarsh–Rose neuron · Adaptive exponential integrate-and-fire neuron

# **1** Introduction

Synchronization of chaotic systems is a fascinating subject that has been extensively studied since the pio-

T. Pyragienė (⊠) · K. Pyragas Center for Physical Sciences and Technology, 01108 Vilnius, Lithuania e-mail: pyragiene@pfi.lt neering works of Fujisaka and Yamada [1] and of Pecora and Carroll [2]. The synchronization phenomenon has attracted the attention of many researchers due to its potential applications in a variety of fields [3]. Many different synchronization regimes have been detected in coupled chaotic systems. The simplest form of synchronization in chaotic systems is identical (or compleat) synchronization [1, 2, 4], when two coupled identical systems demonstrate identical behavior. A more complex form of chaos synchronization is generalized synchronization [5, 6]. Here, a functional relationship between the state variables of coupled systems is established as they evolve in time. Another form of chaos synchronization, known as phase synchronization (PS), has been discovered in weakly coupled chaotic oscillators with different natural frequencies [7]. The PS manifests itself as the coincidence of the mean frequencies of the oscillators with the amplitudes remaining uncorrelated. Recently, the research on robust synchronization of chaotic systems with external disturbances and mismatched parameters (which always exist in real systems) has gained much attention [8-11].

The most intriguing form of chaotic synchronization is anticipating synchronization (AS), which has been discovered by Voss [12]. He showed that two identical chaotic systems coupled unidirectionally in a master-slave configuration can synchronize their motion in such a way that the trajectory of a slave system is advanced in time with respect to the trajectory of a master system. The AS was observed in two different schemes, with and without memory element in a master system. The latter scheme is more important for various applications, but it requires the presence of a time-delay self-feedback in a slave system. The scheme with a time-delay term in a slave system has received a great attention in the last decade. Different modifications have been proposed to increase the anticipation time of the scheme [13–15]. This scheme has been successfully implemented in a variety of models, e.g., in chaotic semiconductor lasers [16], in coupled inertial ratchets [17], in excitable systems driven by noise [18, 19], etc. Recently, the AS has been used as a mechanism to control dynamical systems [20-22] and to estimate the parameters of chaotic systems [23]. The existence of the anticipating chaotic synchronization has been justified experimentally in electronic circuits [18, 24-29] and lasers [30].

Though the AS is a very interesting phenomenon, it seems that it can appear only in man-made systems, since the classical scheme proposed by Voss has two artificial requirements: (i) the master and slave systems have to be identical and (ii) a time-delay selffeedback has to be introduced into the slave system. A reasonable question arises whether the AS can appear in natural (not man-made) systems, say in neural systems? Formally, the second requirement has been overcame in the modified scheme proposed in [25]. This scheme does not contain the time-delay selffeedback in the slave system, but still it remains rather artificial, since the coupling law in this scheme has a specific form; it is derived from the classical Voss scheme as a first-order approximation to true timedelay coupling. Recently, another way to overcome the second requirement has been proposed in [31]. Here, a biologically plausible neural model has been considered, in which the time-delay self-feedback in the slave neuron was provided by coupling it with an interneuron via a chemical synapse. However, the AS in this model was considered only for a periodically spiking regime.

In this paper, we show that the AS may appear in unidirectionally coupled nonidentical chaotic systems with rather arbitrarily mismatched parameters and without the time-delay self-feedback in the slave system. The main requirement is that the mean frequency of the free slave system has to be greater than the mean frequency of the master system. Since our research is focused on nonidentical systems, we cannot achieve an exact AS, i.e., the exact coincidence of the time-shifted signals of the master and slave systems as it is observed in the classical Voss scheme. Fortunately, the lack of an exact anticipation seems to be not crucial for neuroscience, since it is usually assumed that the information in neural systems is carried only in the spike arrival times and is independent of the specific shape of the action potential [32].

The rest of the paper is organized as follows. In Sect. 2, we investigate the PS in unidirectionally coupled chaotic systems with mismatched parameters and formulate a simple necessary condition to achieve synchronization regime with the advanced phase of the slave system. Investigations are performed with the Rössler [33] systems and the Hindmarsh–Rose [34] neurons. Section 3 is devoted to the anticipating spike synchronization (ASS) phenomenon in which a slave neuron anticipates the chaotic spikes of a master neuron. We demonstrate the ASS with the Hindmarsh– Rose neurons as well as with the adaptive integrate and fire neurons [35], and perform a statistical analysis of the ASS based spike prediction of the master neuron. The conclusions are presented in Sect. 4.

# 2 Chaotic PS with the advanced phase of a slave system

It is well known that the phase of a periodic selfsustained oscillator entrained by an external periodic force can be ahead of the phase of the external force if the frequency of the free oscillator is greater than the frequency of the external force [3]. The question about a phase relation becomes more complicated if the periodic oscillator is driven by a chaotic force or if a chaotic oscillator is driven by another chaotic oscillator. Here, we analyze the phase difference in unidirectionally coupled chaotic oscillators with slightly mismatched parameters. We show by examples that the above statement about a periodic oscillator can be naturally generalized for the chaotic case. Specifically, we show that if the parameters of chaotic master and slave systems are mismatched in such a way that the mean frequency of the free slave system is grater than the mean frequency of the master system then in synchronized state the phase of the slave system is ahead of the phase of the master system. We demonstrate this with unidirectionally coupled chaotic Rössler systems as well as with the Hindmarsh-Rose neurons in the regime of chaotic bursting.

#### 2.1 Rössler systems

First, we analyze the dynamics of phase difference in two unidirectionally coupled chaotic Rössler [33] systems with slightly mismatched parameters:

$$\dot{x}_1 = -\omega_1 y_1 - z_1,$$
 (1a)

$$\dot{y}_1 = \omega_1 x_1 + a y_1, \tag{1b}$$

$$\dot{z}_1 = b + z_1(x_1 - c),$$
 (1c)

$$\dot{x}_2 = -\omega_2 y_2 - z_2 + k(x_1 - x_2), \tag{1d}$$

$$\dot{y}_2 = \omega_2 x_2 + a y_2,\tag{1e}$$

$$\dot{z}_2 = b + z_2(x_2 - c).$$
 (1f)

Here,  $(x_1, y_1, z_1)$  and  $(x_2, y_2, z_2)$  are dynamic variables of master and slave systems, respectively. The parameters a = 0.165, b = 0.2, c = 10,  $\omega_1 = 0.95$ , and  $\omega_2 = 0.99$  are chosen in such a way that for the zero coupling strength, k = 0, both systems are in chaotic regime. The parameters  $\omega_1$  and  $\omega_2$  define the characteristic frequencies of the master and slave systems. We take  $\omega_2 > \omega_1$  to make the slave system faster than the master system. Note that the equations similar to Eqs. (1a)–(1f), but with the bidirectional coupling, have been considered in [7] to demonstrate the phenomenon of PS of chaotic oscillations.

We define the phases  $\varphi_{1,2}(t)$  of chaotic signals  $x_{1,2}(t)$  of the system (1a)–(1f) using the Hilbert transform [7, 36]:

$$x_{1,2}(t) + i\tilde{x}_{1,2}(t) = A_{1,2}(t)e^{i\varphi_{1,2}(t)}.$$
(2)

Here, functions  $\tilde{x}_{1,2}(t)$  are the Hilbert transforms of  $x_{1,2}(t)$ , and  $A_{1,2}(t)$  are the amplitudes of chaotic signals. The mean frequencies of the oscillators can be defined as  $\Omega_{1,2} = \langle \dot{\varphi}_{1,2}(t) \rangle$ . The mean frequency  $\Omega_1$  of the master system is independent of the coupling strength k, while the mean frequency  $\Omega_2$  of the slave system does depend on k:  $\Omega_2 = \Omega_2(k)$ . In what follows, we denote the natural mean frequency of the free slave system as  $\Omega_2^0 \equiv \Omega_2(0)$ . For the Rössler systems, we obtain  $\Omega_1 \approx 0.969$  and  $\Omega_2^0 \approx 1.019$ , i.e.,  $\Omega_2^0 > \Omega_1$ .

As stated above, the inequality

$$\Omega_2^0 > \Omega_1 \tag{3}$$

represents the main necessary condition in our conjecture about the existence of the PS regime with the advanced phase of a slave system.



Fig. 1 PS of chaotic oscillations for unidirectionally coupled nonidentical Rössler systems with an advanced phase of the slave system: (a) Dynamics of the phase difference for different coupling strength values; (b) Histogram of the phase difference for k = 0.14; (c) The difference between mean frequencies  $\Omega_2 - \Omega_1$  as a function of coupling strength k. The solid curve represents a polynomial fitting of the numerical results shown by *dots* (Color figure online)

The dynamics of the phase difference  $\varphi_2(t) - \varphi_1(t)$ for different values of the coupling strength k is shown in Fig. 1(a). As the coupling is increased, we observe a transition from the regime, where the phases rotate with different velocities  $\varphi_2 - \varphi_1 \sim \Delta \Omega t$ ,  $\Delta \Omega = \Omega_2 - \Omega_1 > 0$ , to the synchronous state, where the phase difference does not grow with time,  $\Delta \Omega = 0$ . In this synchronous state, the phase difference oscillates around some mean positive value  $\theta_0 = \langle \varphi_2(t) - \varphi_1(t) \rangle > 0$ . This is evident from the histogram of the phase difference presented in Fig. 1(b). Thus, the phase of the slave system is ahead of the phase of the master system when inequality (3) holds, i.e., the above conjuncture is indeed true for the Rössler systems.

Figure 1(c) shows the dependence of the difference between mean frequencies  $\Delta \Omega = \Omega_2 - \Omega_1$  on the coupling strength k. The characteristic value of the coupling strength at which this difference turns to zero defines the threshold of the PS. The threshold value of the PS can be estimated analytically in a similar way as in [7]. For the Rössler attractor, a phase  $\varphi$  and an amplitude A can be alternatively introduced through a polar coordinate system  $x = A \cos \varphi$  and  $y = A \sin \varphi$ and the approximate equation for the phase difference  $\theta = \varphi_2 - \varphi_1$  can be derived:

$$\dot{\theta} = \omega_2 - \omega_1 - \frac{kA_1}{2A_2}\sin\theta.$$
(4)



Fig. 2 The dynamics of the phase difference (*left-hand col-umn*) and the probability density function of the phase difference (*right-hand column*) for coupled chaotic Rössler systems in the presence of noise with different amplitudes: (**a**)–(**b**) D = 0; (**c**)–(**d**) D = 0.001; (**e**)–(**f**) D = 0.01; (**g**)–(**h**) D = 0.05. The value of the coupling strength is k = 0.2 (Color figure online)

If we neglect the variation of amplitudes and suppose that  $A_1 \approx A_2$ , we obtain the threshold of the PS  $k_p = 2(\omega_2 - \omega_1) = 0.08$ , which is in reasonable agreement with the numerical results presented in Fig. 1(c). The value of the stationary phase difference  $\theta_0 = \arcsin[2(\omega_2 - \omega_1)/k] \approx 0.61$  derived from Eq. (4) is also in rough agreement with the mean phase difference  $\langle \varphi_2 - \varphi_1 \rangle \approx 0.84$  numerically obtained from the histogram shown in Fig. 1(b).

To analyze the sensitivity of the above effects to small external perturbations, we added to the RHS of Eqs. (1a)–(1f) the white Gaussian noise terms  $D\xi_n(t)$ with  $\langle \xi_n(t) \rangle = 0$  and  $\langle \xi_n(t) \xi_{n'}(t') \rangle = \delta_{n,n'} \delta(t - t')$ . Here, the parameter D governs the amplitude of noise,  $\delta_{n,n'}$  is the Kroneker delta,  $\delta(t)$  is the Dirac delta function, and  $n = 1 \dots 6$  denotes the number of equation in system (1a)-(1f). The results of simulations are presented in Fig. 2. We see that the dynamics of the phase difference as well as the probability density function remains insensitive to noise when the noise amplitude is increased up to the value D = 0.01. Sufficiently large noise D = 0.05 causes the phase drift effect, however, the probability density function of the phase difference still has the pronounced maximum. These results show that the effect of the chaotic phase synchronization with the advanced phase in the slave system is robust against noise.

#### 2.2 Hindmarsh–Rose neurons

Now we support our conjuncture with the example of chaotic neural systems. We consider two unidirectionally coupled Hindmarsh–Rose [34] neurons with slightly mismatched parameters:

$$C_1 \dot{x}_1 = y_1 + x_1^2 (b - ax_1) - z_1 + J_0,$$
(5a)

$$\dot{y}_1 = c - dx_1^2 - y_1,$$
 (5b)

$$\dot{z}_1 = r[s(x_1 - xst) - z_1],$$
 (5c)

$$C_2 \dot{x}_2 = y_2 + x_2^2 (b - ax_2) - z_2 + J_0$$

$$+\kappa(x_1-x_2),$$
 (5d)

$$\dot{y}_2 = c - dx_2^2 - y_2,$$
 (5e)

$$\dot{z}_2 = r[s(x_2 - x_{st}) - z_2].$$
 (5f)

Here,  $(x_1, y_1, z_1)$  and  $(x_2, y_2, z_2)$  are the dynamic variables of master and slave neurons, respectively. We suppose that all the parameters of neurons are identical except for the membrane capacities  $C_{1,2}$ . We take  $C_2 < C_1$  to make the slave neuron faster than the master. We fix the values of parameters in such a way: a = 1, b = 3, c = 1, d = 5, s = 4, r = 0.005,  $x_{st} = -1.6$ ,  $J_0 = 3.25$ ,  $C_1 = 1$ .

For these values of parameters, the dynamics of the master neuron is shown in Fig. 3(a), while the dynamics of the slave neuron is presented in Figs. 3(b)–(e) for the different values of the coupling strength k. The master neuron demonstrates chaotic bursting. The free (k = 0) slave neuron is in the regime of periodic spiking; however, with the increase of the coupling strength its dynamics becomes chaotic and a transition to the PS is observed.

The Hindmarsh–Rose neuron has two characteristic time scales and the definition of a phase for this system is not trivial. A suitable definition, which we use in our analysis, has been introduced in [37]. The Hindmarsh–Rose attractor has a single rotation center in  $[\dot{x}(t), \dot{x}(t - \delta t)]$  plain and its phase can be defined as [37]

$$\varphi = \arctan\left[\frac{\dot{x}(t-\delta t) - \alpha_1}{\dot{x}(t) - \alpha_2}\right],\tag{6}$$

where  $(\alpha_1, \alpha_2)$  are the coordinates of the rotation center and  $\delta t$  is a suitable delay time. The trajectory of the master neuron in the plane  $[\dot{x}(t), \dot{x}(t-\delta t)]$  is shown in Fig. 4(a). In the phase definition (6), we take  $\delta t = 0.5$ ,

(5.1)



Fig. 3 (a) Dynamics of the master and (b)–(e) slave Hindmarsh–Rose neurons for  $C_2 = 0.7$  and for different coupling strength values: (b) k = 0; (c) k = 0.56; (d) k = 0.84; (e) k = 1.5 (Color figure online)

 $\alpha_1 = 0$  and  $\alpha_2 = -1$ . The phase of the slave system is difficult to define for transient regimes like those shown in Figs. 3(c) and (d), since the trajectory loses the rotation center. However, for the free slave system [Fig. 3(b)] as well as for the synchronized slave system [Fig. 3(e)] the phase definition (6) is applicable. The trajectory of the slave system in the plain  $[\dot{x}(t), \dot{x}(t-\delta t)]$  for the synchronized state at k = 1.5 is depicted in Fig. 4(b). Figure 4(c) shows the dynamics of phases  $\varphi_{1,2}(t)$  of the master and slave systems for k = 1.5 (in this plot they are indistinguishable). The phases of neurons change fast when the neurons spike; otherwise, the phases change slowly. When a spike occurs, the phase increases by a value of  $2\pi$ . The dynamics of phase difference  $\varphi_2(t) - \varphi_1(t)$  is shown in Fig. 4(d). The phase difference is approximately zero between the spikes and briefly increases when spikes occur. The positiveness of the phase difference means that the phase of the slave neuron is ahead of the phase of the master neuron, i.e., the slave fires before the master. The mean frequencies of the master and the free slave neuron estimated from phase definition (6) are  $\Omega_1 \approx 0.195$  and  $\Omega_2^0 \approx 0.227$ . Thus the inequality (3) holds and this model supports our main conjecture as well.

Note that the mean frequencies of the slave and master systems can be estimated in a simpler way, without a recourse to the Hilbert transform computations or phase definition (6). The mean frequency of a neuron can be evaluated as its mean firing rate



**Fig. 4** (a) and (b) The trajectories of the master and slave neuron (k = 1.5), respectively, in the plain  $[\dot{x}(t), \dot{x}(t - \delta t)]$ . (c) The phase dynamics of the master and slave (k = 1.5) neuron. (d) The dynamics of the phase difference between the master and slave neuron at (k = 1.5). The membrane capacity of the slave neuron is  $C_2 = 0.7$  (Color figure online)

(MFR). By the MFR of a neuron, we mean a ratio  $v = N_{\Delta t}/\Delta t$ , where  $N_{\Delta t}$  is the number of spikes on a given (sufficiently large) time interval  $\Delta t$ . The quantity v is simply related with the above mean angular frequency  $\Omega$ :  $\Omega = 2\pi v$ . Then the general necessary condition for the existence of the PS with the advanced phase of the slave system can be presented in the form  $v_2^0 > v_1$ , where  $v_1$  is the mean firing rate of the master neuron and  $v_2^0$  is the mean firing rate of the free slave neuron. For the Hinmarh–Rose neurons with the mismatched parameters  $C_1 = 1$  and  $C_2 = 0.7$ , we obtain  $v_1 \approx 0.0310$  and  $v_2^0 \approx 0.0362$ , so that the above condition indeed holds.

Here, we have presented the analysis of the Hinmarh–Rose neurons with mismatched membrane capacities, but the results would be similar if other parameters of the neurons were mismatched. Specifically, we simulated the Hinmarh-Rose neurons with mismatched parameters c, d, and  $x_{st}$  and in all cases we where able to achieve the PS with the positive phase difference between the slave and master neurons provided that the inequity  $v_2^0 > v_1$  holds.

### 3 Anticipating spike synchronization

The PS with the advanced phase of a slave system allows us to predict the appearance of chaotic spikes of a master neuron by observing the dynamics of the synchronized slave neuron. Indeed, if the phase of the slave system is ahead of the phase of the master system, one can expect that the slave neuron produces the spikes before the master neuron. We refer to such a phenomenon as the anticipating spike synchronization (ASS). Due to fluctuations of the phase difference of the synchronized systems, the exact forecasting of the spikes is impossible; the ASS provides the forecasting only with a finite accuracy. Here, we consider the ASS effect for the Hindmarsh–Rose neurons and for the adaptive exponential integrate-and-fire neurons.

## 3.1 Hindmarsh-Rose neurons

To demonstrate the ASS for the Hindmarsh–Rose neurons, in Fig. 5(a), we show the typical dynamics of the master and slave systems in a small time interval, which contains only two spikes. The parameter  $C_2 = 0.7$  is the same as in the previous consideration and the coupling strength k = 1.5 is taken beyond the threshold of the PS. As is expected, the slave neuron fires before the master neuron. Since the master and slave neurons are not identical, the profiles of their action potentials differ. Therefore, the ASS cannot be interpreted as an exact anticipating synchronization, which is observed in systems with time-delay coupling [12–15]. In the latter case, the slave system predicts exactly the whole profile of the master signal.

Though the details of action potentials of the master and slave neurons are different, there is one-toone correspondence between the number of spikes, i.e., the slave neuron generates a spike before each spike of the master neuron. We refer to this dynamical regime as the anticipating spike-to-spike synchronization (ASSS). Let us denote by  $t_n$  the moments when the membrane potential  $x_1(t)$  of the master system reaches the maxima. The moments corresponding to the nearest maxima of the membrane potential  $x_2(t)$  of the slave neuron we denote by  $\tilde{t}_n$  [see Fig. 5(a)]. The interspike intervals of the master neuron are  $T_n = t_n - t_{n-1}$ . In Fig. 6(a), we show the probability density function of  $T_n$ . This probability is located in two specific regions corresponding to large and small values of  $T_n$ . The small values of  $T_n$  are related to the interspike intervals inside the bursts, while the large values of  $T_n$  represent the intervals between the bursts. The intermediate values of  $T_n$  have a small probability.



**Fig. 5** Membrane potential dynamics of the master (*bold black*) and slave (*thin red*) Hindmarsh–Rose neurons in a small time interval for (**a**) the ASSS at k = 1.5 and  $C_2 = 0.7$  and for (**b**) the ASDSS at k = 1.7 and  $C_2 = 0.2$  (Color figure online)



Fig. 6 Statistical characteristics of coupled Hindmarsh–Rose neurons: (a) The probability density function of the interspike interval of the master neuron; (b) The intervals  $\tau_n = t_n - \tilde{t}_n$  between the spikes of the master and slave neurons as functions of interspike interval  $T_n$ . The *lower blue* and *upper red* points correspond to the ASSS regime at  $C_2 = 0.7$  and k = 1.5 and the ASDSS regime at  $C_2 = 0.2$  and k = 1.7, respectively; (c) and (d) The relative prediction error  $\varepsilon_n$  as a function of interspike interval  $T_n$  for (c) the ASSS at  $C_2 = 0.7$  and k = 1.5 and for (d) the ASDSS at  $C_2 = 0.2$  and k = 1.7 (Color figure online)

Now we discuss the statistics of spike prediction. In Fig. 6(b), we plot the intervals  $\tau_n = t_n - \tilde{t}_n$  between the nearest spikes of the master and slave neuron in dependence on the interspike interval  $T_n$  [the lower blue points in the diagram (b)]. We see that this difference is almost constant. The mean value of this difference can be interpreted as a spike prediction time  $\tau = \langle \tau_n \rangle$ . For the given values of the parameters, we have  $\tau \approx 0.256$  and the standard deviation  $\sigma = \sqrt{\langle (\tau_n - \tau)^2 \rangle} \approx 0.0648$ . Knowing  $\tau$  and the moment  $\tilde{t}_n$  of appearing the *n*th spike of the slave neuron, the moment of the *n*th spike of the master neuron can be predicted as  $t_n^{(\text{pred})} = \tilde{t}_n + \tau$ . The relative error of the prediction of the *n*th spike we define as follows:

$$\varepsilon_n = \frac{|t_n^{(\text{pred})} - t_n|}{T_n} = \frac{|\tilde{t}_n + \tau - t_n|}{T_n}.$$
(7)

The values of  $\varepsilon_n$  in the dependence on the interspike interval  $T_n$  are plotted in Fig. 6(c). The relative error increases with the decrease of  $T_n$ , but it remains below 1 % for any  $T_n$ .

The coupling scheme in this neural model satisfies the requirements of [25] and this allows us to evaluate the prediction time by the following analytical expression:  $\tau = (C_1 - C_2)/k$ . This result is obtained by rewriting the slave system in the form identical with the master system, but containing a time delay term in the coupling. Let us rewrite Eqs. (5a) and (5d)for the membrane potential of the master and slave neurons, respectively, as  $C_1 \dot{x}_1 = f(x_1, y_1, z_1)$  and  $C_2 \dot{x}_2 = f(x_2, y_2, z_2) + k(x_1 - x_2)$ , where f(x, y, z) = $y + x^2(b - ax) - z + J_0$ . Equation (5d) can be approximately presented in the form  $C_1 \dot{x}_2 = f(x_2, y_2, z_2) +$  $k[x_1(t) - x_2(t - \tau)]$  provided the delay time  $\tau$  defined above is a small parameter. Such a presentation admits an anticipating synchronization manifold on which the exact relationship  $x_2(t) = x_1(t + \tau)$  between the variables of the master and slave system exists [12]. Thus, the above analytical expression for  $\tau$  indeed evaluates the value of the prediction time. For the given values of the parameters  $C_1 = 1$ ,  $C_2 = 0.7$ , and k = 1.5, we obtain  $\tau = 0.2$ , which is in rough agreement with the above numerical result  $\tau = \langle \tau_n \rangle \approx 0.256$ .

Taking a look at the analytical expression  $\tau = (C_1 - C_2)/k$  it seems, that the prediction time can be enlarged by further decreasing the parameter  $C_2$ , i.e., by making the slave neuron even faster. However, the increase of the difference  $C_1 - C_2$  leads to the increase of the difference between the MFRs  $\nu_2^0 - \nu_1$  of the slave and master neurons. The larger mean frequency mismatch requires the larger coupling strength k to reach the spike-to-spike synchronization, so that  $\tau$  remains almost constant when decreasing  $C_2$ .

Nevertheless, the prediction time can be still enlarged by exploring a higher order phase synchronization, namely, a subharmonic frequency entrainment with the mean frequency relation  $\Omega_1 = \Omega_2/2$ . Numerical analysis shows that for a fixed k and decreasing  $C_2$  the ASSS regime undergoes a transition to a new anticipating spike-to-double-spike synchronization (ASDSS) regime in which each spike of the master neuron is preceded by the double-spike of the slave neuron. This happens when the MFR of the free slave neuron approaches the double value of the MFR of the master neuron,  $\nu_2^0\approx 2\nu_1.$  The ASDSS is demonstrated in Fig. 5(b) for k = 1.7 and  $C_2 = 0.2$  when  $v_2^0 \approx 0.0568$ . In the ASDSS regime, we can predict the spikes of the master neuron by fixing the moment of the first spike in the double-spike sequences of the slave neuron. Now we denote by  $\tilde{t}_n$  the moment of the first maximum in this double-spike sequence of the slave neuron [see Fig. 5(b)]. The dependence of  $\tau_n = t_n - \tilde{t}_n$  on  $T_n$  for the ASDSS is shown in Fig. 6(b) (the upper red points). The prediction time  $\tau = \langle \tau_n \rangle \approx 1.044$  for the ASDSS is four times larger than that for the ASSS regime. The standard deviation  $\sigma \approx 0.0238$  is almost three times smaller than for the ASSS. As is seen in Fig. 6(d), the relative prediction error has also considerably better characteristics than those of the ASSS.

#### 3.2 Adaptive exponential integrate-and-fire neurons

To demonstrate the universality of the ASSS and the ASDSS effects, we consider another neural model with chaotic dynamics: the adaptive exponential integrate-and-fire neuron introduced in [35]. The AEIF model is physiologically relevant in that its parameters can be easily related to physiological quantities. This model can reproduce correctly the spike trains of detailed physiological neuron models [35] as well as the firing patterns of real neurons [38].

Though the AEIF neuron is a simple two-equation model, it can generate (depending on the choice of parameter values) multiple firing patterns [38, 39]. The rich dynamics of the model is conditioned by interaction of the differential equations with the reset. Here, we consider two unidirectionally coupled AEIF neurons characterized by the membrane potential V and an adaptation current w, whose dynamics is governed by following differential equations [35]:

$$C\dot{V}_1 = -g_L(V_1 - E_L) + g_L\Delta_T \exp\left(\frac{V_1 - V_{T1}}{\Delta_T}\right) + I - w_1,$$
(8a)

$$\tau_w \dot{w}_1 = a(V_1 - E_L) - w_1, \tag{8b}$$

$$C\dot{V}_2 = -g_L(V_2 - E_L) + g_L\Delta_T \exp\left(\frac{V_2 - V_{T2}}{\Delta_T}\right)$$
$$+ L - w_2 + k(V_1 - V_2) \tag{8c}$$

$$\tau_{w}\dot{w}_{2} = a(V_{2} - E_{I}) - w_{2}.$$
(8d)

The subscripts "1" and "2" stand for the master and slave neuron, respectively. The last term in Eq. (8c) describes the coupling, where k is the coupling strength. When the membrane potential  $V_{1,2}$  of the master or slave neuron is high enough, the trajectory quickly diverges because of the exponential terms. This divergence to infinity models the spike. For displaying or simulation purposes, spikes are usually cut to some finite value (e.g., 0 mV). When a spike occurs, the membrane potential is instantaneously reset to some value  $V_r$  and the adaptation current is increased:

if 
$$V_1 > 0$$
, then 
$$\begin{cases} V_1 \to V_r, \\ w_1 \to w_r = w_1 + b, \end{cases}$$
 (9a)

if 
$$V_2 > 0$$
, then 
$$\begin{cases} V_2 \to V_r, \\ w_2 \to w_r = w_2 + b. \end{cases}$$
 (9b)

We take the parameters [35]  $C = 281 \text{ pF}, g_L = 30 \text{ nS},$  $E_L = -70 \text{ mV}, \Delta_T = 2 \text{ mV}, a = 4 \text{ nS}, \tau_w = 40 \text{ ms},$  $I = 800 \text{ pA}, b = 80 \text{ pA} \text{ and } V_r = -48 \text{ mV} \text{ of the mas-}$ ter and slave neuron identical, except of the threshold potential  $V_T$ , which is responsible for the reaction speed of the neuron. For the master neuron, we fix  $V_{T1} = -50.4$  mV. Then the above choice of the parameters leads to the chaotic spiking regime of the master neuron, which is shown in Fig. 7(a). The MFR of the master neuron is  $v_1 \approx 60.4$  Hz. To make the slave neuron faster than the master neuron, we take  $V_{T2} < V_{T1}$ . We emphasize that this parameter mismatch does not satisfy the requirements of the coupling law proposed in [25], i.e., this scheme cannot be considered as a first-order approximation of a true time-delay coupling of the classical Voss scheme.

In Figs. 7(b) and (d), the dynamics of the free (k = 0) slave neuron is presented for  $V_{T2} = -51$  mV and  $V_{T2} = -52$  mV, respectively. For these values of the parameters, the corresponding MFRs of the slave neuron are  $v_2^0 \approx 71.4$  Hz and  $v_2^0 \approx 105.1$  Hz. In both cases, the free slave neuron demonstrates



Fig. 7 (a) Dynamics of the master and (b)–(e) slave AEIF neurons. The diagrams (b) and (d) correspond to the free (k = 0) slave neuron with the parameters  $V_{T2} = -51$  mV and  $V_{T2} = -52$  mV, respectively. The diagrams (c) and (e) represent the ASSS ( $V_{T2} = -51$  mV, k = 450 nS) and ASDSS ( $V_{T2} = -52$  mV, k = 600 nS) regimes, respectively (Color figure online)



Fig. 8 The dynamics of (a) the master and the (b)-(c) slave neuron in the regime of (b) the ASSS, and (c) the ASDSS. The parts (a), (b), and (c) represent the enlargements of the diagrams (a), (c), and (e) of Fig. 7, respectively (Color figure online)

chaotic bursting. When the coupling with an appropriate strength is switched on, the first case leads to the ASSS [Fig. 7(c)], while the second case—to the ASDSS [Fig. 7(e)]. To demonstrate the ASSS and the ASDSS regimes more visibly, we enlarge the small time interval of the diagrams (a), (d) and (e) of Fig. 7. These enlargements are depicted in the parts (a), (b), and (c) of Fig. 8, respectively.



Fig. 9 The same graphs as in Fig. 6 but for the AEIF neurons. The parameters of the slave neuron for the ASSS and ASDSS regimes, respectively, are:  $V_{T2} = -51$  mV, k = 450 nS and  $V_{T2} = -52$  mV, k = 600 nS (Color figure online)

The statistical characteristics for the AEIF neurons are presented in Fig. 9. In the ASSS regime, the time of prediction is  $\tau = \langle \tau_n \rangle \approx 0.431$  ms and the standard deviation is  $\sigma \approx 0.0299$  ms. For the ASDSS regime, the corresponding parameters are:  $\tau \approx 1.131$  ms and  $\sigma \approx 0.0411$  ms. The relative prediction error in the both regimes is less than 1 %. Thus, this model demonstrates similar effects as have been observed in the Hindmarsh–Rose neurons.

Note that the MFR of the free slave neuron for the Hindmarsh–Rose systems and for the AEIF systems has been controlled by different strategies. In the Hindmarsh–Rose systems, the MFR of the slave neuron has been regulated by the membrane capacity  $C_2$ , while here we regulate it by the threshold potential  $V_{T2}$ . Despite this difference, the transition from the ASSS to the ASDSS regime was observed in both systems. The ASSS appears when the MFR of the free slave neuron is slightly larger than the MFR of the master neuron, and the ASDSS takes place when the MFR of the free slave neuron is close to the double MFR of the master neuron.

#### 4 Conclusions

In this paper, the anticipating synchronization in unidirectionally coupled chaotic systems with mismatched parameters has been analyzed. We have shown that if the mean frequency of the free slave system is greater than the mean frequency of the master system their phases may synchronize in such a way that the phase of the slave system is ahead of the phase of the master system. Applying to neural systems, this regime manifests itself as the anticipating spike synchronization, which means that in unidirectionally coupled neurons the slave neuron anticipates chaotic spikes of the master neuron.

The anticipating spike synchronization effect has been demonstrated with two different models of chaotic neurons, namely, the Hindmarsh-Rose neurons and the adaptive exponential integrate-and-fire neurons. Though a different parameter mismatch has been used in the neural models, the anticipating spike synchronization phenomenon has manifested itself in a similar way. For a small parameter mismatch, when the mean firing rate of the free slave neuron was slightly greater than the mean firing rate of the master neuron, the regime of the anticipating spike-to-spike synchronization was detected. For a larger parameter mismatch, when the mean firing rate of the free slave neuron was close to the double mean firing rate of the master neuron, the transition to the anticipating spike-to-double-spike synchronization regime was observed. The anticipating spike-to-double-spike synchronization provides larger anticipation time and has better statistical properties than those of the anticipating spike-to-spike synchronization.

We believe that our findings are relevant to real neural systems, since our analysis shows that the conditions for the existence of the anticipating spike synchronization are very weak; it may appear in nonidentical neurons with rather arbitrarily mismatched parameters and without time-delay feedback in the coupling. The considered phenomenon may provide a mechanism for compensating or even surpassing the communication delays between neurons, which appear due to the finite speed of propagation of information in axons.

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