**Regular** Article

# From complete to modulated synchrony in networks of identical Hindmarsh-Rose neurons

Sebastian Ehrich, Arkady Pikovsky, and Michael Rosenblum<sup>a</sup>

Institute of Physics and Astronomy, University of Potsdam, Karl-Liebknecht-Str. 24/25, 14476 Potsdam-Golm, Germany

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**Abstract.** In most cases tendency to synchrony in networks of oscillatory units increases with the coupling strength. Using the popular Hindmarsh-Rose neuronal model, we demonstrate that even for identical neurons and simple coupling the dynamics can be more complicated. Our numerical analysis for globally coupled systems and oscillator lattices reveals a new scenario of synchrony breaking with the increase of coupling, resulting in a quasiperiodic, modulated synchronous state.

## **1** Introduction

Dynamics of coupled systems has been extensively studied within last decades. An important effect here is synchronization, when interacting oscillatory systems, and neuronal oscillators in particular, adjust their rhythms [1–6]. In large oscillator networks with high connectivity, the subject of our interest here, synchronization is reflected by an emergent collective mode, or a mean field; the amplitude of the mean field quantifies coherence of the network dynamics. In this context very popular are idealized models when the networks are considered to be fully and homogeneously connected. These models are often used in neuroscience [7,8], where investigation of cooperative neuronal dynamics plays a crucial role in understanding normal and pathological functioning of the brain [9]. Therefore, studies of different aspects of collective behaviour of neuronal networks, and in particular of neuronal synchrony, remain a challenge for nonlinear science. In this communication we consider all-toall coupled networks of identical model neurons as well as one-dimensional lattices of nearest-neighbour coupled units; we focus on the case, when increase of the *initially attractive coupling* does not facilitate synchrony in the network, as is frequently believed to be the general case, but destroys it.

Typically, the increase of the coupling strength between the units does not change the character of the interaction, i.e. for large coupling it remains of the same type, as it is for small coupling, i.e. either repulsive or attractive, and only the strength of the attraction or repulsion changes. However, there exist also interesting opposite cases when the increase of coupling turns, e.g. the synchronizing interaction, into desynchronizing one. Although it is known that increase of the coupling strength may destroy synchrony, see e.g. [10], the possible scenarios of the synchrony breaking

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<sup>&</sup>lt;sup>a</sup> e-mail: mros@uni-potsdam.de



Fig. 1. (a) For chosen parameters, isolated Hindmarsh-Rose neuron exhibits periodic spiking. (b) Projection of the limit cycle of the system onto x, y plane.

are not yet fully understood. Of particular interest are the cases when the breakup of synchrony does not result in a trivial asynchronous dynamics with zero mean field, but leads to a coherent, though only partially synchronous, state.

One possible scenario was analytically described in [11,12] within the phase approximation of a globally coupled network, by analysis of the extended Kuramoto-Sakaguchi model [13]:

$$\dot{\varphi}_k = \omega + \varepsilon A(R,\varepsilon) \sin[\Theta - \varphi_k + \beta(R,\varepsilon)], \tag{1}$$

where  $k = 1, \ldots, N$  is the oscillator index,  $\varepsilon > 0$  describes the coupling strength,  $Re^{i\Theta} = N^{-1} \sum_{j=1}^{N} e^{i\varphi_j}$  is the complex mean field, and  $A(R,\varepsilon)$  and  $\beta(R,\varepsilon)$  are some functions. It is easy to see that the complete synchrony  $\varphi_1 = \ldots = \varphi_k = \Theta$  becomes unstable if  $A(R,\varepsilon)$  attains zero or/and  $\beta(R,\varepsilon)$  attains  $\pm \pi/2$  (under assumption that  $A(1,\varepsilon) > 0$  and  $|\beta(1,\varepsilon)| < \pi/2$  for  $\varepsilon \to 0$ ). As a result, a self-organized quasiperiodic state with 0 < R < 1 appears. The model (1) was obtained by means of the phase reduction [1] of the system of nonlinearly coupled Stuart-Landau oscillators. Numerical study of the full model (which nicely corresponded to the theory) demonstrated that the breakup of the synchronous cluster occurred exactly when one real evaporation multiplier (see the discussion below) became larger than one. The same scenario was observed in a model of Josephson junctions, shunted via a common RLC load [11]. Here we demonstrate a new scenario of the synchrony breaking with increase of coupling which leads to a peculiar quasiperiodic state of modulated synchrony.

## 2 Coupled Hindmarsh-Rose neurons

We analyse a simple model of a neuronal network with N identical interacting units. Individual neurons are described by a popular Hindmarsh-Rose model [14]:

$$\dot{x}_{k} = y_{k} - x_{k}^{3} + 3x_{k}^{2} - z_{k} + 5 + \varepsilon C, 
\dot{y}_{k} = 1 - 5x_{k}^{2} - y_{k}, 
\dot{z}_{k} = 0.006[4(x_{k} + 1.56) - z_{k}],$$
(2)

where k = 1, ..., N. The standard parameter values chosen here correspond to the regime of periodic spiking of uncoupled neurons, i.e. to the limit-cycle solution of Eq. (2) for  $\varepsilon = 0$ , see Fig. 1. Here  $\varepsilon$  is the coupling strength, it is used below as a bifurcation parameter; C describes the form of the coupling between the units.



Fig. 2. (a) Absolute values of two largest multipliers for the infinitely large system (2,3). The inset shows the zoomed results for small coupling. At  $\varepsilon \approx 0.017$  two complex multipliers cross the unit circle and synchrony becomes unstable; for  $\varepsilon \gtrsim 0.85$  it becomes stable again. These results are confirmed by computation of the order parameter  $\rho$  (see text), shown in (b). Here the black bold lines shows the values obtained by increasing  $\varepsilon$  from zero to one; red solid lines corresponds to varying  $\varepsilon$  in the reverse order. Notice hysteresis at  $\varepsilon \approx 0.85$ .

#### 2.1 Large globally coupled network

We demonstrate the effect by considering very large systems,  $N \to \infty,$  with the all-to-all coupling of the form

$$\mathcal{C} = N^{-1} \sum_{j=1}^{N} x_j - x_k = X - x_k,$$
(3)

where  $X = N^{-1} \sum_{j=1}^{N} x_j$  is the mean field. The fully synchronous state  $x_k = x$ ,  $y_k = y$ , and  $z_k = z$  is obviously a solution, and its stability can be checked with the help of evaporation multipliers  $\mu$  [11,15,16]. The multipliers quantify whether the synchronous cluster is stable with respect to loss of one of its element. They correspond to Floquet multipliers, computed under the assumption of the unchanged X, i.e. with linearisation with respect to  $x_k$ ,  $y_k$ , and  $z_k$  only. The multipliers are related to the transversal Lyapunov exponents  $\lambda$  as  $|\mu| = e^{\lambda T}$ , where T is the oscillation period. Two largest multipliers of system (2,3) are shown in Fig. 2(a), they indicate that the synchronous solution is stable for  $\varepsilon \leq 0.017$  and for  $\varepsilon \geq 0.85$ . This result is confirmed by direct simulations of Eq. (2), see Fig. 2(b). Here we show the order parameter, defined as  $\rho = \operatorname{rms}(X)/\operatorname{rms}(x)$ . This quantity is  $\rho = 1$ , if all systems synchronize, and  $0 < \rho < 1$ , otherwise.

Figure 3 illustrates the dynamics of the system after synchrony breaking, for  $\varepsilon = 0.04$  and N = 5000. In the phase space representation we see, that the points corresponding to neurons move in a clump along the limit cycle. We emphasize that although this clump is very thin and visually can hardly be distinguished from a stripe, it is indeed a two-dimensional structure: the phase points slowly rotate around the center of the clump, while this center moves along the cycle.<sup>1</sup> Thus, the oscillators

<sup>&</sup>lt;sup>1</sup> Since the bifurcation occurs when two complex multipliers cross the unit circle, it is obvious that the phase approximation does not work here, even for a very small coupling.



Fig. 3. Snapshots of globally coupled Hindmarsh-Rose neurons after synchrony breaking, for  $\varepsilon = 0.04$ . (a) Black line shows the trajectory of one neuron, projected onto x, y plane; gray line shows the trajectory X, Y of the mean field. Position of all neurons in a snapshot are shown by circles, for the time instant when X = -3.2. These neurons form a clump, which elements slowly rotate around the center of the clump. The zoomed clump is shown in (b). Four neurons here are marked by large symbols. Panels (c,d,e,f) show snapshots after 20, 40, 60, and 80 rotations of the mean field, respectively. One can see that the marked neurons interchange their position within the clump in a complicated fashion.

perform a complicated, possibly weakly chaotic motion. In a different formulation, each oscillator has the same average frequency as the mean field, but its phase with respect to the mean field is slowly modulated. Another illustration is given by raster plots in Fig. 4.

Two remarks are in order. (i) Very long runs, of the order of  $10^7$  time units, demonstrated tendency to formation of two clusters which slowly rotated around a point, moving along the limit cycle, so that the modulation of oscillator phases was preserved. Since the reliability of such long runs is low and we are anyway interested in the modulated motion, in this computation we made the units slightly non-identical, to avoid clustering. For this purpose, we made parameter I different for all oscillators, with the discrepancy of the order from  $10^{-4}$  to  $10^{-6}$ . (ii) We have also considered large ensembles with non-diffusive coupling C = X; the results are similar. Additionally we have observed here multistability: for some initial conditions the neurons after the synchrony breaking form two clumps and the mean field has a doubled frequency. (Since the system is of very high dimension, we cannot exclude bi- or multistability in case of diffusive coupling, but we have never observed it for small  $\varepsilon$ .)

This counter-intuitive observation can be explained as follows. Consider the Floquet multipliers of an autonomous neuron (see the values of  $\mu_{1,2}$  for  $\varepsilon = 0$  in Fig. 2). The largest multiplier  $\mu = 1$  corresponds to the neutrally stable direction along the limit cycle. The second multiplier quantifies the stability in the direction, transversal to the limit cycle; here it is  $\mu_2 \approx 0.87$ , i.e. the cycle is only weakly stable (notice that  $\mu_3$  is very small) and the conditions for the validity of the phase approximation are not fulfilled.

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**Fig. 4.** Raster plots (showing spike events only) for system (2,3), for two values of the coupling strength,  $\varepsilon = 0.04$  (top) and  $\varepsilon = 0.13$  (bottom); dots denote the instant of time when a neuron fires, i.e. when the x variable attains a maximum (cf. Fig. 1(a)).



Fig. 5. Dynamics of two coupled neurons. Red dots show the projection of the phase trajectory, while triangles denote positions of two neurons for some instant of time. (a) For small coupling  $\varepsilon = 0.015$  the neurons synchronize. (b,c) For intermediate coupling,  $\varepsilon = 0.018$  and  $\varepsilon = 0.5$ , the motion is quasiperiodic. (d) Stronger coupling (here  $\varepsilon = 1$ ) yields again a synchronous state.

#### 2.2 Two neurons

For detailed analysis we take a low-dimensional system and consider the non-diffusive case  $\mathcal{C} = X$  for N = 2. In Fig. 5 we show projections of the phase space trajectory of one neuron onto the x, y plane, for different values of the coupling strength  $\varepsilon$ . Here we also show a snapshot, i.e. the position of two neurons on this trajectory for some instant of time. We see that for small coupling,  $\varepsilon \leq 0.016$ , the neurons synchronize. For larger coupling, they seem to move along the closed trajectory, but their positions do not coincide. In fact, the trajectory lays on a thin torus, and the motion of each point in the state space is quasiperiodic. With further increase of coupling the torus becomes visible (Fig. 5(c)). For coupling  $\varepsilon \gtrsim 0.62$  synchrony is re-established, and even stronger coupling suppresses the neuron firing. These results are consistent with computation of the Floquet multipliers for the six-dimensional system (not shown). Next, we have computed the Euclidian distance between the points i, j in the state space and took its maximum over all combinations of i, j and



Fig. 6. (a) Maximal Euclidian distance  $D_E$  between both oscillators. (b) Quasiperiodicity of the coupled system is revealed by the Poincaré plot, here for  $\varepsilon = 0.018$ . (c) Bifurcation diagram shows the stability of the synchronous, periodic solution. Green filled and blue open circles denote the maximal and minimal values of x for the cases of stable and unstable orbit, respectively. The black thin and red bold lines show unstable and stable fixed points. Notice the bistability between the synchronous periodic orbit and the fixed point at  $\varepsilon \approx 3.8$ .

over time. The plot of this maximal distance  $D_E$  (see Fig. 6(a)) reveals synchronous  $(D_E = 0)$  and asynchronous  $(D_E > 0)$  states. Besides the transition from synchrony to quasiperiodicity at  $\varepsilon \approx 0.016$ , we see that at  $\varepsilon \approx 0.62$  the synchronous state becomes stable again; however for  $0.62 \leq \varepsilon \leq 0.68$  it coexists with a stable quasiperiodic solution. For further illustration of the quasiperiodic motion, we plot for  $\varepsilon = 0.018$  the y and z coordinates of a neuron when it attains x = 0.34,  $\dot{x} > 0$ . These points fall on a closed curve, shown in Fig. 6(b), indicating quasiperiodicity. The revolution around this curve takes  $\approx 53T$ , where T is the average period of the revolution in the x, y plane. If we choose a larger coupling strength, the Poincaré plot becomes more complicated. The results are supported by the bifurcation diagram, computed with the XPPAUT package [17] and shown in Fig. 6(c).

#### 2.3 Lattice of neurons

After considering the simple model of two coupled neurons, we raise the complexity of the system by analysing a lattice of neurons with nearest neighbour diffusive coupling in Eq. (2)  $C = (x_{k-1} + x_k + x_{k+1})/3 - x_k$  and with periodic boundary conditions. Fixing all parameters as above, we study synchronization patterns in a lattice of 100 oscillators, in dependence on the coupling constant  $\varepsilon$ . For  $\varepsilon \leq 0.011$  the coupling is attractive and the regime of full synchrony in the lattice (Fig. 7(a)) is stable. Additionally, due to periodic boundary conditions, regimes with a constant phase shift between the oscillators (with the total phase shift  $2\pi m$ ,  $m = 1, 2, \ldots$ , over the lattice) are possible, see Fig. 7(b)); to observe such a state typically one has to prepare initial conditions properly.



Fig. 7. Panels (a,b) show two different types of synchrony for  $\varepsilon = 0.011$ . For  $\varepsilon = 0.03$  three types of asynchronous motion are possible: (c,d) are very similar to both synchronous cases, while (e) depicts a more complicated motion.



Fig. 8. (a) Splitting of the synchronous solution for  $\varepsilon = 0.012$  into two clusters (with odd and even indices). (b) The time interval T between the spikes changes periodically with an almost sinusoidal shape for both clusters.

As the synchronous state loses stability, a regular spatially modulated regime appears as shown in Fig. 8. Panel (a) illustrates the instantaneous spatial profile, which is the  $\pi$ -mode, so that one can say that the homogeneous lattice breaks into two clusters (with odd and with even indices). The time intervals between the spikes in these clusters are not constant, but vary periodically as depicted in Fig. 8(b).

For stronger coupling, the modulation becomes irregular, and one observes patterns like shown in Fig. 7(c),(d),(e) for  $\varepsilon = 0.03$ . Here patterns in panels (c,d) can be viewed as modulated versions of patterns (a,b), while in (e) we see additionally a "defect": at k = 77 a jump in the phase is observed. These regimes resemble very much the phase turbulence state near the border of instability of the spatially homogeneous solution in the complex Ginzburg-Landau equation [18]. However, in our case the transition to a weakly turbulent state occurs via different bifurcations, so that the state Fig. 7(c),(d) does not belong to the universality class of phase turbulence described by the Kuramoto-Sivashinsky equation. Remarkably, the defect in Fig. 7(e) is not pinned but moves slowly (and irregularly), so on the time scale of several billions of periods it travels through the whole lattice.



Fig. 9. Time evolution of interspike time interval T at different sites, for the regime depicted in Fig. 7e. (a) Irregular behaviour for k = 10, (b) sinusoidal shape with burstings for k = 60, (c) constancy with burstings for k = 80, and (d) periodic time evolution for k = 90.



Fig. 10. Plot of the differences of the interspike intervals for adjacent oscillators. The difference between oscillators with 65 < k < 85 is nearly constant, what indicates large spatial coherence, while for all other oscillators it is changing essentially. At k = 77 a very large difference corresponding to the defect in Fig. 7(e) is observed.

We characterize the statistical properties of the weakly turbulent state in Figs. 9, and 10, restricting ourselves to a relatively short time interval during which the defect does not move. In different panels of Fig. 9 we show the evolution of the time interval between the spikes T at different positions of the lattice. One can see that at some places the dynamics is irregular, while at other positions modulation of T is nearly periodic. Bursting events at some positions correspond presumably to moving irregular wave patches. Spatial coherence is illustrated in Fig. 10, where we show the difference between the interspike times at adjacent sites. Close to the defect (65 < k < 85) the spatial coherence is maximal, while in the other parts of the lattice the spatial variations of the interspike time T are large.

### **3** Discussion

Complex dynamical states emerging after synchrony breaking are not yet fully understood. One possible scenario of such a desynchronization transition in a network of identical Stuart-Landau oscillators with global nonlinear coupling was analytically described in [11,12] within the phase approximation framework, namely by analysis of the extended Kuramoto-Sakaguchi model. Numerical study of the full model demonstrated that breakup of the synchronous cluster occurred when one real multiplier became larger than one. The same scenario was observed in a model of Josephson junctions, shunted via a common RLC load [11]. For both models one observes emergence of a partially coherent state with nonzero mean field; noteworthy, the frequency of the mean field differs from frequency of individual units. (For an experimental demonstration of such dynamics see [19].) It is interesting, that the described scenario helps to interpret the well-known effect of dephasing and bursting in ensemble of Morris-Lecar neurons with global diffusive coupling [20]: computation of the evaporation multipliers for this model shows that the largest multiplier  $\mu$  is real and larger than one for positive coupling ( $\mu = 1$ for zero coupling), so that the state of complete synchrony is always unstable here.

In this communication we demonstrated the second, novel mechanism of synchrony breaking that occurs through another bifurcation and leads to a modulated synchrony. An important feature of this mechanism is that it occurs even in a system with simple *linear* coupling; crucial here is the strong nonlinearity of individual units. Further analysis of such a transition and of the state of modulated synchrony, especially for some solvable models, is an interesting topic for future studies.

We mention that understanding of the mechanisms of synchrony breaking is important, e.g., for neuroscience, where increase of the collective oscillatory mode of the neuronal population is typically associated with the increase of coupling. On the other hand, states of partial synchrony frequently appear in neuronal models [20,21].

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