

Synchronization and Complex Dynamics of Oscillators with Delayed Pulse Coupling**

Markus Bär,* Eckehard Schöll, and Alessandro Torcini

Belousov–Zhabotinsky reaction ·
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Networks of coupled nonlinear oscillators often exhibit synchronization and complex dynamic patterns that range from oscillator clusters and partially synchronized states to wave patterns and spatiotemporal chaos. The emerging behavior depends crucially on the type and strength of the coupling, the network topology, as well as on the frequency distributions of the oscillators in the network. The relevance of synchronization phenomena has been recognized for many important biological functions, and the pioneering studies of Winfree and Kuramoto has opened up a challenging field of mathematical and theoretical study.^[1]

Chemical systems such as the Belousov–Zhabotinsky (BZ) reaction or coupled electrochemical oscillators have previously been used to study synchronization and related phenomena, such as the formation of oscillatory clusters, experimentally. In the BZ system, the oscillators in the form of catalyst particles in a catalyst-free background^[2a] or microfluidic water droplets embedded in a nonreactive oil phase^[2b] are coupled diffusively, whereas electrochemical systems^[2c–e] constitute a realization of global all-to-all coupling of the involved oscillators. These systems proved to be flexible test beds for synchronization studies, because the number of oscillators (10–100 000) as well as the geometrical arrangement of the oscillators can be easily varied.

A further step in this success story was recently provided by Horvath et al.,^[3] who investigated a pair of pulse-coupled oscillators, with delay realized by continuously fed stirred tank reactors (CSTRs) filled with an oscillatory BZ mixture and coupled to a controlled sudden release of a chemical activator (AgNO₃) or inhibitor (Br[−]) of the BZ reaction. The reactors are operated in a regime of spiking oscillations, and

coupling occurs through the release of a chemical agent into one of the CSTRs only if a spike is recorded in the other CSTR. By changing the amount of the released substance Horvath et al. could vary the coupling strength, and by controlling the time of release (= time of the pulse coupling) they were able to introduce an arbitrary time delay. A detailed chemical kinetics model provides, in addition to the experiments, a convincing mechanistic explanation of the observed behavior.^[3]

Their study is highly relevant not only for nonlinear chemical dynamics but also for important fields of biological research, since most biological oscillators—from cardiac pacemakers to flashing fireflies—are, in fact, pulse coupled. This fact motivated a large number of mathematical studies and predictions of their behavior, such as the proof by Mirollo and Strogatz that an arbitrary number of oscillators with excitatory all-to-all pulse coupling synchronize.^[4] The importance of a time delay in the coupling has been recognized recently in a number of high-profile experimental studies in biology ranging from synthetic genetic oscillators^[5a] to the segmentation clock in the embryonic development of vertebrates.^[5] An important field where pulse-coupled oscillators with delay are widely discussed is neuroscience. In this context, experiments have been devoted to the investigation of two coupled neurons,^[6a] of the synchronous activity of different regions of the brain,^[6b] as well as of the emergence of β or γ oscillations in large neuronal populations, which are often detected by electroencephalography.^[6c] The importance of such experiments has resulted in numerous computational studies on delayed pulse-coupled oscillators in neuroscience. For pairs of oscillators, it was discovered that the presence of delayed inhibitory coupling leads to synchronization more reliably than does excitatory coupling.^[7a] Other researchers realized that optimal synchronization can be realized for inhibitory coupling with delay, whereas excitatory coupling at best provides synchronization with a finite phase lag.^[7b] Furthermore, it was shown that synchronization may be replaced by oscillator suppression or complex bursting activity.^[7c] Scenarios with in-phase and antiphase synchronization, bursting, and oscillator suppression have also been found in models of two neurons with delayed diffusive coupling and delayed feedback.^[7d] Experiments on the synchronous behavior of different areas of the brain often show zero phase lag, even though considerable propagation

[*] Prof. M. Bär
Physikalisch-Technische Bundesanstalt
Abbestrasse 2–12, 10587 Berlin (Germany)
E-mail: markus.baer@ptb.de

Prof. E. Schöll
Institut für Theoretische Physik, TU Berlin
Hardenbergstrasse 36, 10623 Berlin (Germany)

Prof. A. Torcini
CNR, Consiglio Nazionale delle Ricerche
Istituto dei Sistemi Complessi
Via Madonna del Piano 10, 50019 Sesto Fiorentino (Italy)

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delays are involved. Related investigations of delay-coupled units have revealed that a third oscillator which acts as a dynamic relay is necessary for the observation of zero lag synchronization of two excitatory coupled oscillators.^[8] Very recent studies have focused on the interplay of topology, delay, and synchronization in oscillator networks with complex topologies.^[9] Here, some universal results on the stability of the synchronization of periodic and chaotic oscillators have been obtained.

Horvath et al.^[3] found inhibitory coupling for antiphase oscillations with short delays and weak coupling strength, whereas perfectly synchronized in-phase oscillations were observed for intermediate coupling strength and a long delay. Complex behavior and eventually suppression of one of the

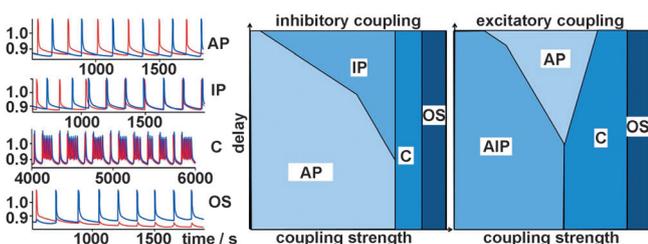


Figure 1. Left: Examples of dynamics for a pair of pulse-coupled oscillators showing antiphase (AP) and in-phase (IP) or almost in-phase (AIP) oscillations, complex bursting dynamics (C), and oscillator suppression (OS). Middle and right: Schematic experimental phase diagram for oscillators with different coupling.

oscillators was discovered when the coupling strength was large (Figure 1). For excitatory coupling, almost in-phase oscillations, namely almost synchronous oscillations with a small phase lag between the two oscillators, were found for short delays and weak coupling. Antiphase oscillations and synchronized bursting oscillations occur at larger coupling strength and delays (Figure 1). Interestingly, the experimental observation summarized in Figure 1 confirms many of the predictions from computational neuroscience described above^[7] and adds a rich variety of complex behaviors. With respect to future studies, it would be interesting to extend the study^[3] to more complex topologies. While studies on large numbers of coupled chemically reactors seem unfeasible from a practical viewpoint, small network motifs such as the three coupled oscillators investigated theoretically^[8] could be explored experimentally to advance the understanding of the complex dynamics of delay-coupled oscillators to a new level. Altogether, the study of Horvath et al. has demonstrated that simple nonlinear chemical systems provide surprisingly rich behavior and can be used for systematic studies by changing

crucial parameters such as coupling strength and delay that are not accessible in comparable biological systems.

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