Dynamical Systems and Chaos
Part II: Biology Applications

Lecture 10: Coupled Systems.

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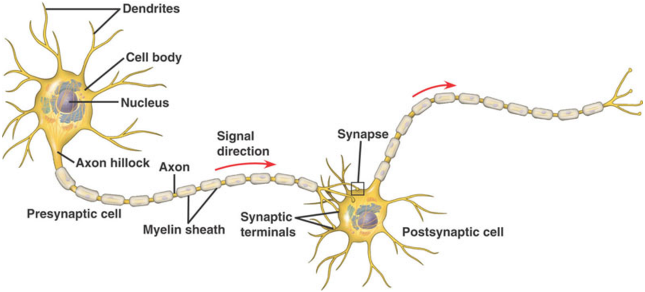
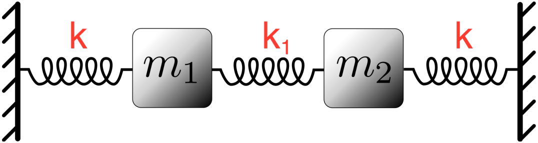
Foreword

- In order to model "populations" of physical/biological systems, represented as dynamical systems, one has to introduce **coupling** between sub-systems.
- Such a population will be the dynamical system itself, i.e. numerically and mathematically sub-systems are not distinguished.
- Structure of the coupling is crucial (one-to-one, all-to-all coupling etc.).
- In the coupled systems new dynamical regimes arise.
- Novelty is mainly due to breaking of symmetry (in **amplitudes** and/or **phase**).
- Amplitude: homogeneity/non-homogeneity.
- Phase: synchrony/asynchrony.

One-to-one coupling

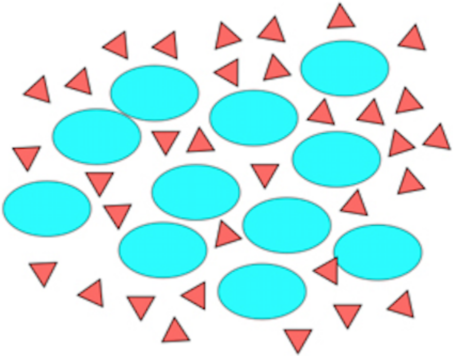
Neighboring elements get connected (e.g. neurons, harmonic oscillators, closely located pendulum clocks, neuro-mascular oscillators in the small intestine, coupling on a ring).





All-to-all coupling

All elements of the system connect to each other (bacterial population, biofilms, cells in a tissue, embryo etc.).



Homogeneity/inhomogeneity

- Symmetry break in variables' steady state levels, oscillatory levels or amplitude.
- This applies both to steady states and oscillations.
- Generally, through the pitchfork bifurcation (breaking of symmetry).

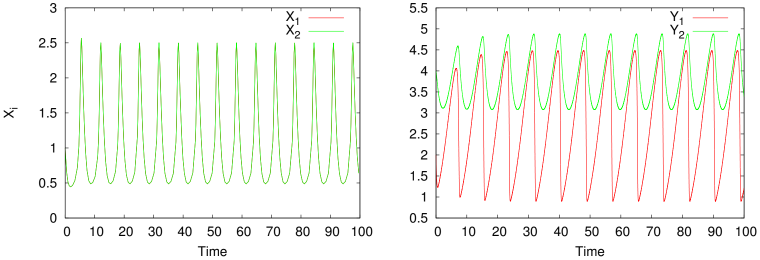


Figure: Left: homogeneous oscillatory regime — two subsystems have the same amplitude and levels of oscillations. Right: two subsystems have different amplitude and oscillatory levels — inhomogeneous solution.

(A)synchrony

- First observation: Huygens, pendulum clocks hanging on a wooden beam (17th century).

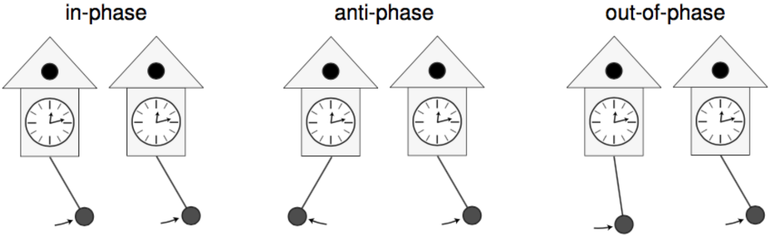


Figure 10.1: Different types of synchronization.

E. Izhikevich, *Dynamical Systems in Neuroscience*, MIT Press, 2007.

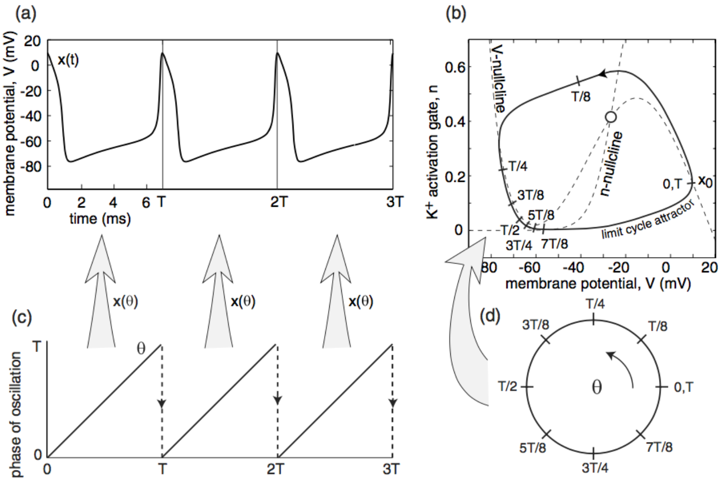
Phase of oscillation

- Let x_0 be an arbitrary point on a periodic orbit γ.
- Any other point on γ can be characterized by how much time ϑ has passed since the last visiting of x_0.
- ϑ is called *phase of oscillation*.
- The phase is always bounded by the period of oscillation T. Sometime ϑ is normalized by T.
- The phase is also defined outside of γ with *isochrons*, set of initial conditions having the same phase.
- Many oscillators can be rewritten in a simpler phase model form in vicinity of their γ sets:

$$\vartheta' = 1$$

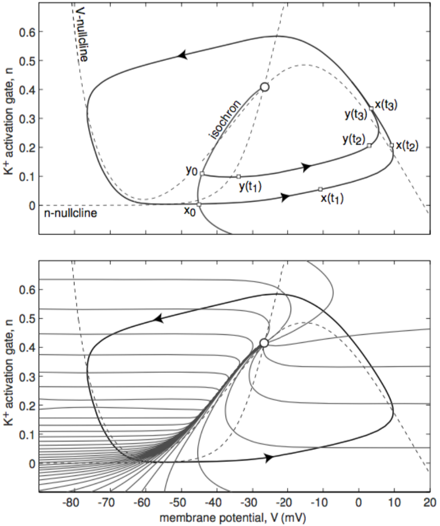
- It is useful to assume that the phase is defined on a unit circle (just as sine or cosine functions).

Phase of oscillation



E. Izhikevich, *Dynamical Systems in Neuroscience*, MIT Press, 2007.

Isochrons



E. Izhikevich, *Dynamical Systems in Neuroscience*, MIT Press, 2007.

Weak coupling

- Phase and amplitude has different relative stability to the external perturbation (external forcing or other oscillators).
- If timescale of relaxation to the limit cycle is τ_1 and timescale of the coupling/interaction between oscillators is τ_2, weak coupling implies $\tau_1 \ll \tau_2$.
- In this case, coupling does not affect amplitude of oscillation, but its phase $\Rightarrow$ essence of the synchronization phenomena.

Weak forcing: Arnold tongues

$$\frac{d\vartheta}{dt} = \omega_0 + \varepsilon Q(\vartheta, \omega t)$$

where ϑ and ω_0 are the oscillator's phase and frequency, respectively; Q is the coupling function, ω and ε are the external force frequency and amplitude, respectively.

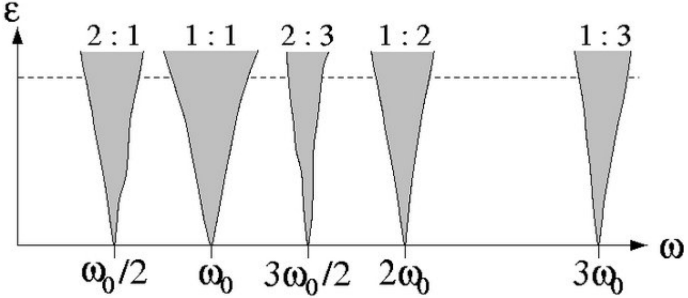


Figure: Arnold tongues.

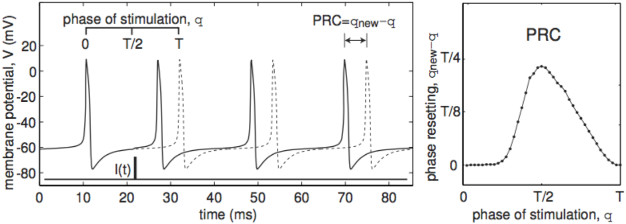
Pulsed Coupling

- Non-constant interaction.
- Single pulses at certain time moments (flashing fireflies, neurons).
- A dynamical system with a pulsed coupling can be represented:

$$\dot{x} = f(x) + A\delta(t - t_s)$$

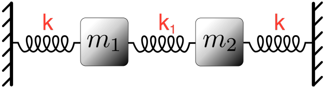
  where A is an amplitude of the signal given as a Dirac $\delta(t)$ function at time moment t_s.
- One just resets a state variable x by the constant A.

Phase response curve



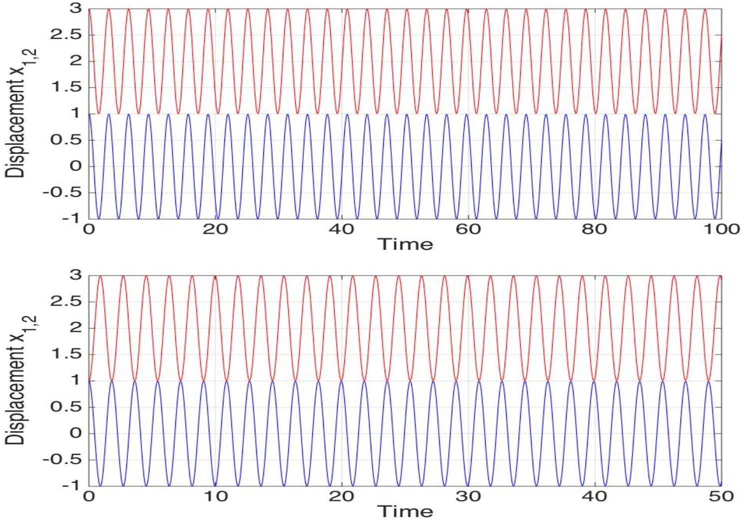
E. Izhikevich, *Dynamical Systems in Neuroscience*, MIT Press, 2007.

Two coupled harmonic oscillators



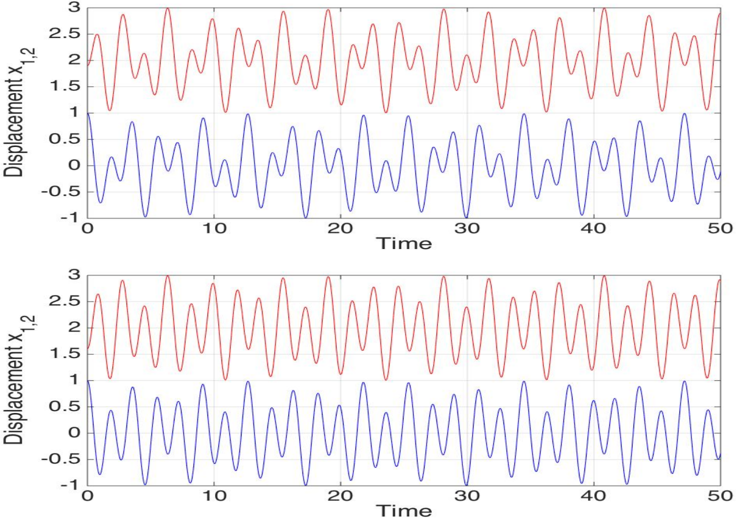
$$
\begin{cases}
I \begin{cases} \dfrac{dx_1}{dt} = y_1 \\[2ex] \dfrac{dy_1}{dt} = -\dfrac{k}{m}x_1 + \dfrac{k_1}{m}(x_2 - x_1) \end{cases} \\[6ex]
II \begin{cases} \dfrac{dx_2}{dt} = y_2 \\[2ex] \dfrac{dy_2}{dt} = -\dfrac{k}{m}x_1 - \dfrac{k_1}{m}(x_2 - x_1) \end{cases}
\end{cases}
$$

Two coupled harmonic oscillators: in- and anti-phase



Two harmonic oscillators: more complex oscillations

- One can vary both initial conditions and frequencies.

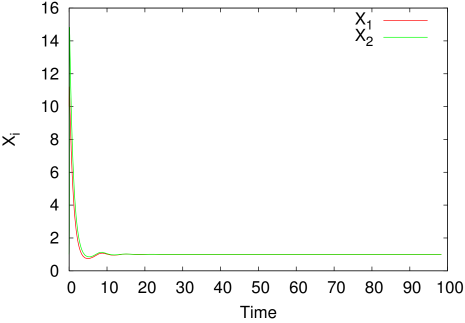


Two coupled Brusselators

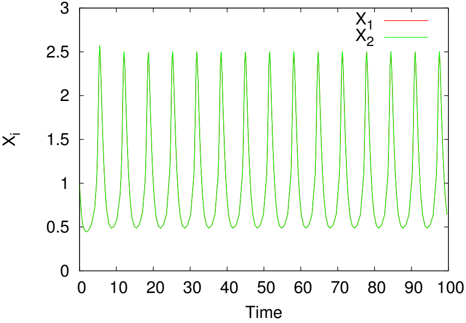
$$\begin{cases} I \begin{cases} \dfrac{dx_1}{dt} = A - (B+1)x_1 + x_1^2 y_1 \\ \dfrac{dy_1}{dt} = Bx_1 - x_1^2 y_1 + D(y_2 - y_1) \end{cases} \\ II \begin{cases} \dfrac{dx_2}{dt} = A - (B+1)x_2 + x_2^2 y_2 \\ \dfrac{dy_2}{dt} = Bx_2 - x_2^2 y_2 + D(y_1 - y_2) \end{cases} \end{cases}$$

Homogeneous dynamical regimes

$$A = 1,\ B = 1.5,\ D = 0.57$$

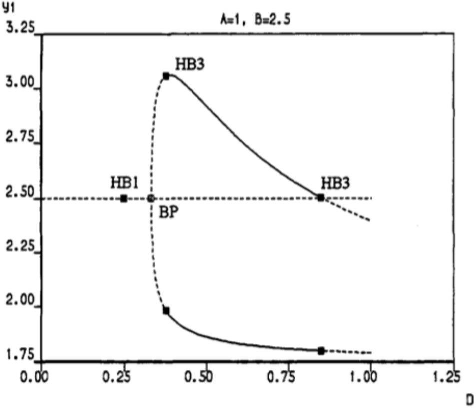


$$A = 1,\ B = 2.5,\ D = 0.57$$

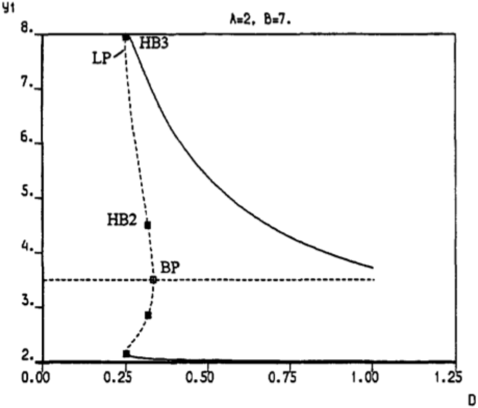


In-homogeneous dynamical regimes

$A = 1,\ B = 2.5$



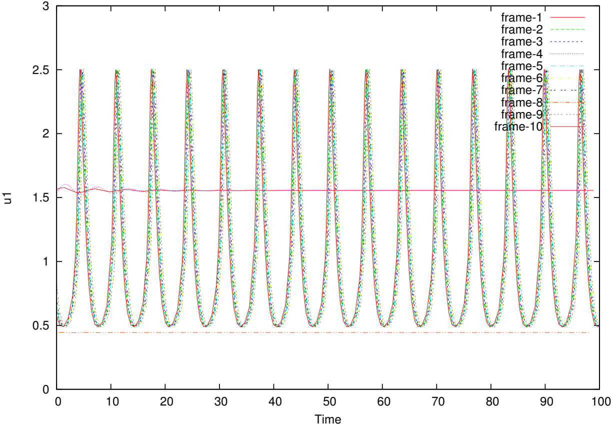
$A = 2,\ B = 7$



E. Volkov and V. Romanov, *Physica Scripta*, **51**, 19–28, 1995.

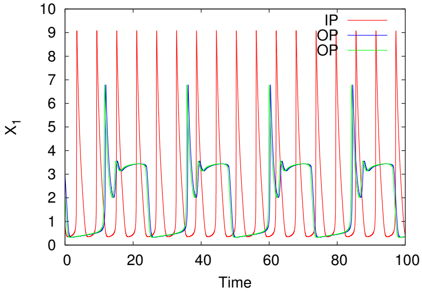
Trying to find in-homogeneous steady state

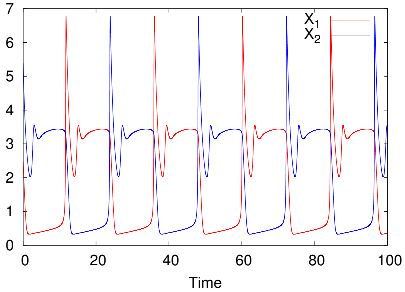
$A = 1,\ B = 2.5,\ D = 0.57$



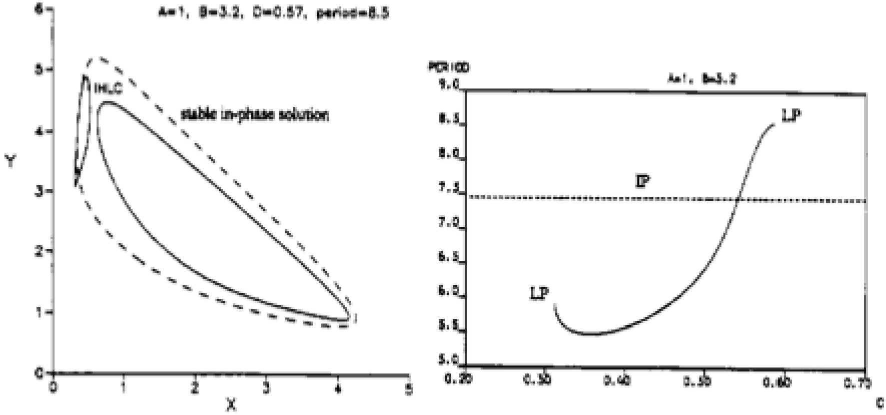
Trying to find out-of-phase oscillations

$A = 2, \; B = 7, \; D = 0.24$





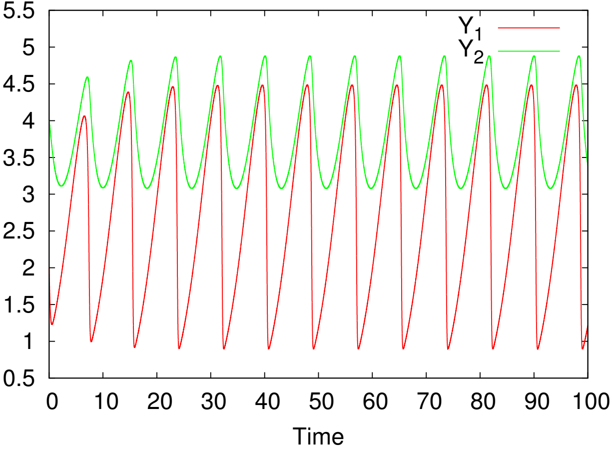
In-homogeneous limit cycle



E. Volkov and V. Romanov, *Physica Scripta*, **51**, 19–28, 1995.

In-homogeneous limit cycle

$A = 1,\ B = 3.2,\ D = 0.57$



In-homogeneous limit cycle→chaos

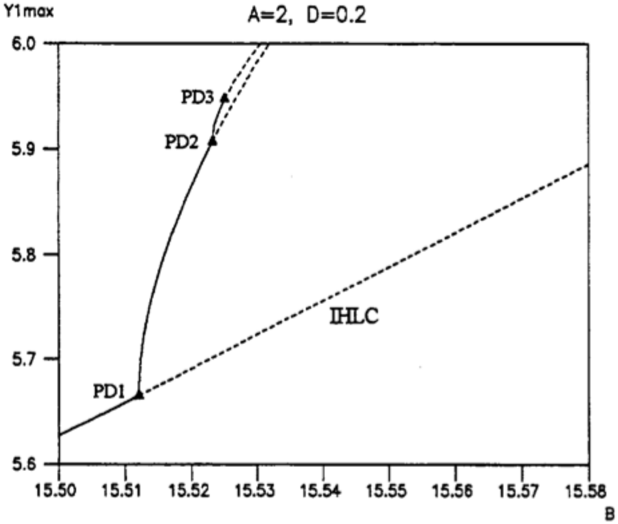


Fig. 9. Period-doubling cascade of IHLC at $A = 2$, $D = 0.2$.

Three coupled brusselators

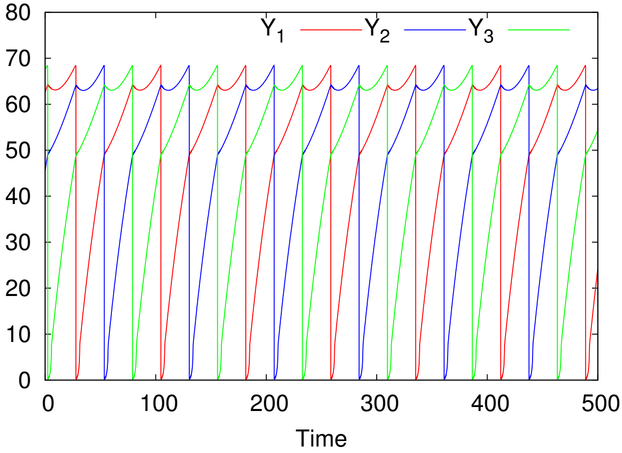
- Global coupling, i.e. all-to-all.
- Similar to 2 coupled Brusselators.

$$\frac{dx_i}{dt} = A - (B+1)x_i + x_i^2 y_i$$

$$\frac{dy_i}{dt} = Bx_i - x_i^2 y_i + D(\frac{1}{N}\sum_{j=1}^{N} y_j - y_i)$$

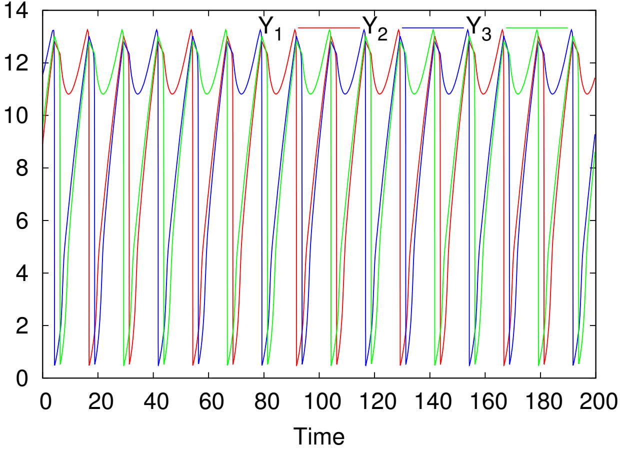
Wave-solution: out-of-phase homogeneous oscillations

$A = 1,\ B = 15.4,\ D = 0.046$

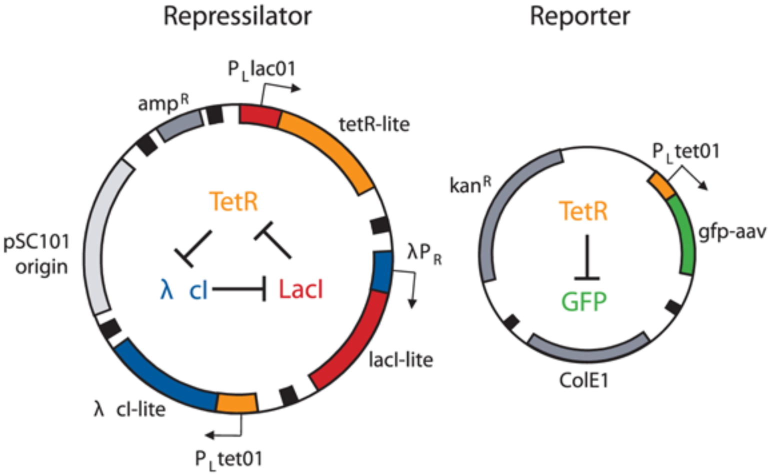


Other out-of-phase homogeneous oscillations

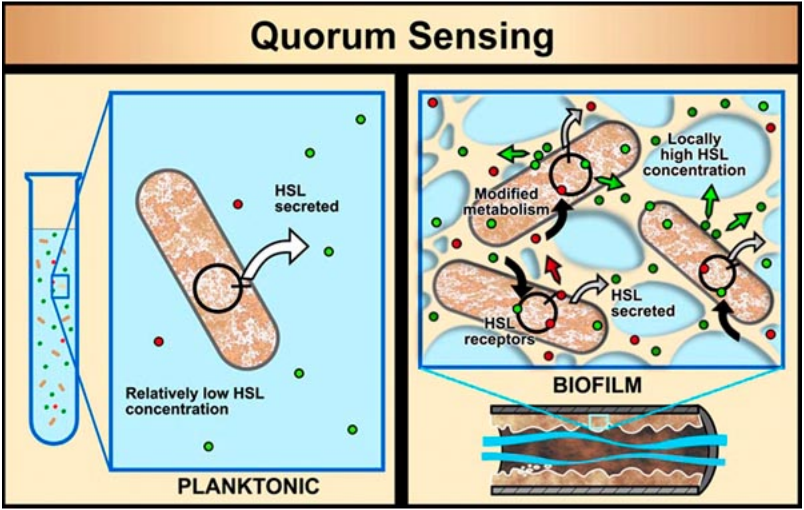
$A = 1,\ B = 6,\ D = 0.234$



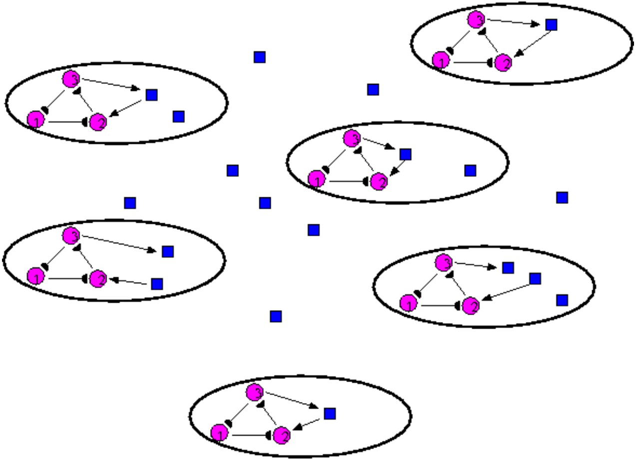
Repressilator



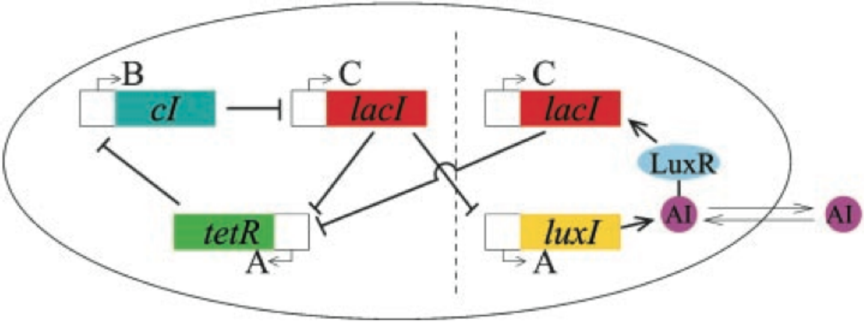
Quorum Sensing (QS)



Repressilator + QS



Repressilator + QS: phase-attractive coupling



J. Garcia-Ojalvo, M. Elowitz, and S. Strogatz, *PNAS*, **101**:10955-10960, 2004.

Repressilator + QS: phase-attractive coupling

$$\frac{da_i}{dt} = \frac{\alpha}{1 + C_i^n} - a_i \qquad \frac{dA_i}{dt} = \beta_a(a_i - A_i)$$

$$\frac{db_i}{dt} = \frac{\alpha}{1 + A_i^n} - b_i \qquad \frac{dB_i}{dt} = \beta_b(b_i - B_i)$$

$$\frac{dc_i}{dt} = \frac{\alpha}{1 + B_i^n} - c_i + \kappa \frac{S_i}{1 + S_i} \qquad \frac{dC_i}{dt} = \beta_c(c_i - C_i)$$

$$\frac{dS_i}{dt} = -k_{s0} S_i + k_{s1} A_i - \eta(S_i - Q\bar{S}) \,,$$

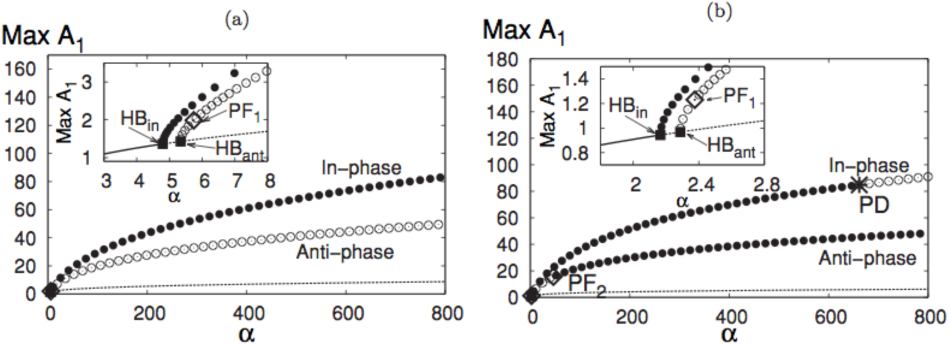
where $\bar{S} = \dfrac{1}{N} \sum_{j=1}^{N} S_j$.

J. Garcia-Ojalvo, M. Elowitz, and S. Strogatz, *PNAS*, **101**:10955-10960, 2004.

Repressilator + QS: phase-attractive coupling

Hill-cooperativity (n) and mRNA/protein life time ratio (β):

$n = 2,\ \beta = 1.0$ $\qquad\qquad$ $n = 2.6,\ \beta = 1.0$

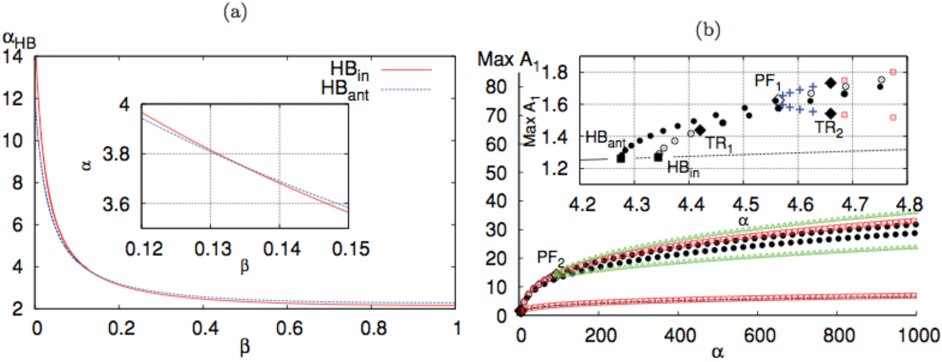


I. Potapov, E. Volkov, and A. Kuznetsov, *Phys Rev E*, 031901, 2011.

Repressilator + QS: phase-attractive coupling

- β determines which comes first: HB_{in} or HB_{ant}.

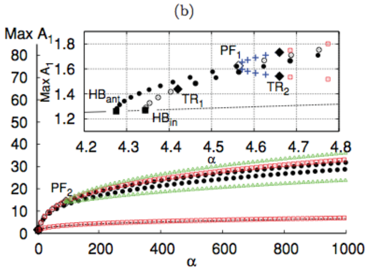
$n = 2.6$ $\qquad\qquad$ $n = 2.6,\ \beta = 0.1$



I. Potapov, E. Volkov, and A. Kuznetsov, *Phys Rev E*, 031901, 2011.

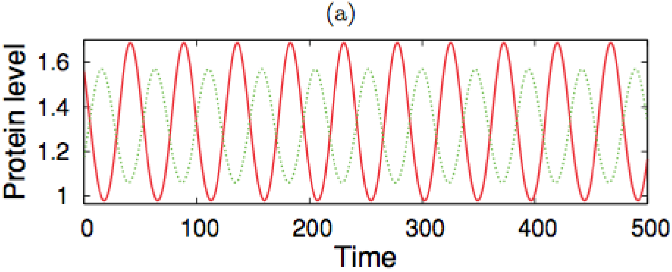
Repressilator + QS: phase-attractive coupling

- There are dynamical behaviors not predicted by the bifurcation analysis.
- In-homogeneous anti-phase solution changes its properties after the “torus” bifurcation (TR_2). The resulting solutions are not seen in the bifurcation analysis.



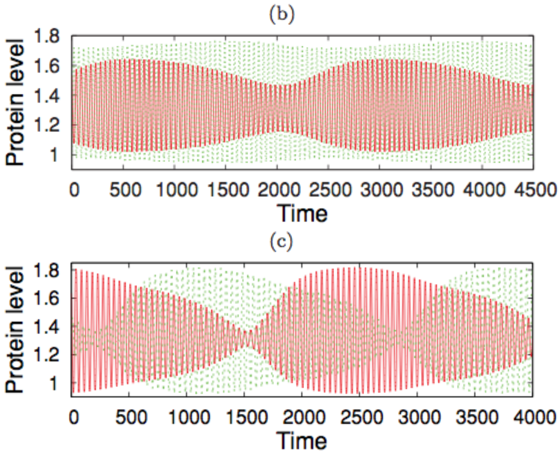
I. Potapov, E. Volkov, and A. Kuznetsov, *Phys Rev E*, 031901, 2011.

Repressilator + QS: In-homogeneous limit cycle



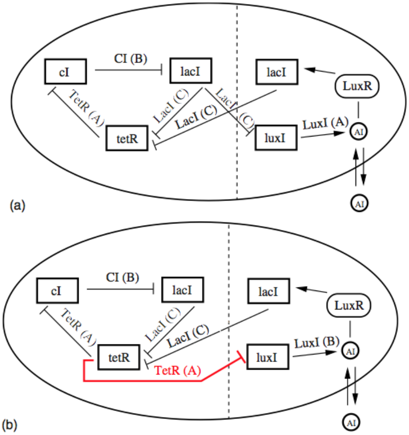
I. Potapov, E. Volkov, and A. Kuznetsov, *Phys Rev E*, 031901, 2011.

Repressilator + QS: after torus bifurcation (TR_2)



I. Potapov, E. Volkov, and A. Kuznetsov, *Phys Rev E*, 031901, 2011.

Repressilator + QS: attractive vs. repulsive coupling



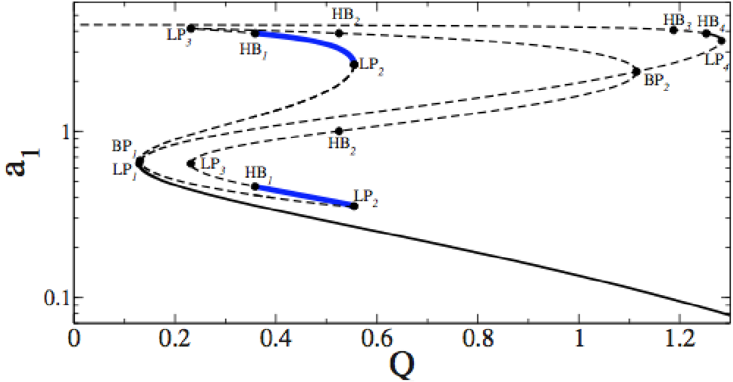
- The same equations except for the AI.
- Phase-repulsive coupling has AI equation:

$$\frac{dS_i}{dt} = -k_{s0}S_i + \underline{k_{s1}B_i} - \eta(S_i - Q\bar{S}),$$

$$\text{where } \bar{S} = \frac{1}{N}\sum_{j=1}^{N} S_j.$$

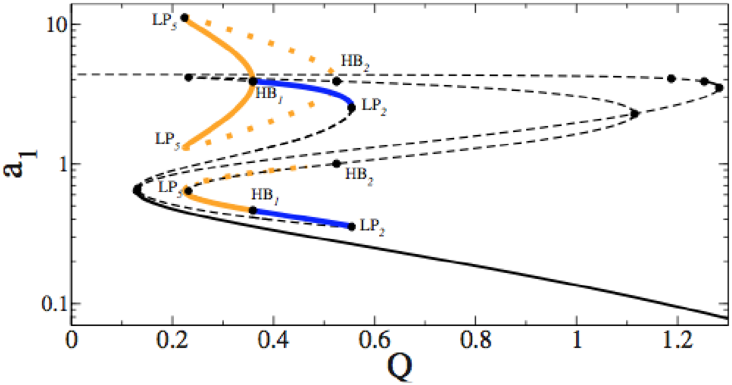
E. Ullner et al., *Phys Rev E*, 031904, 2008.

Phase-repulsive coupling: steady state diagram



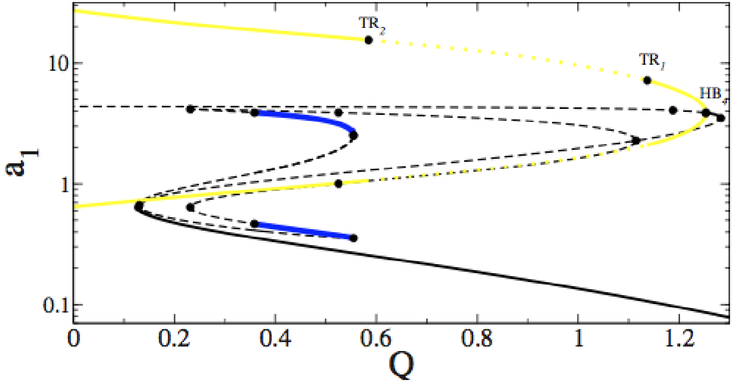
E. Ullner et al., *Phys Rev E*, 031904, 2008.

Phase-repulsive coupling: in-homogeneous oscillations



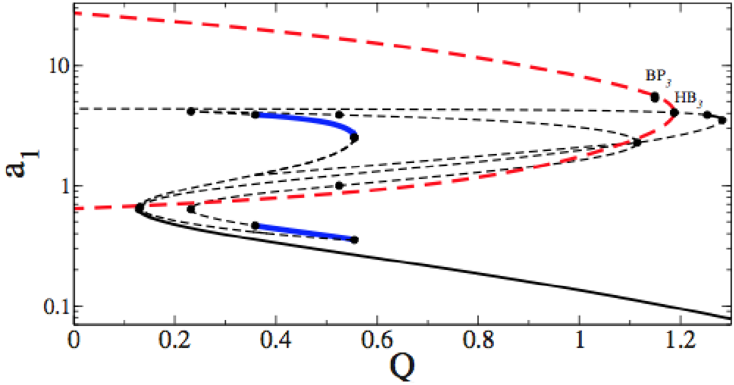
E. Ullner et al., *Phys Rev E*, 031904, 2008.

Phase-repulsive coupling: anti-phase solution branch



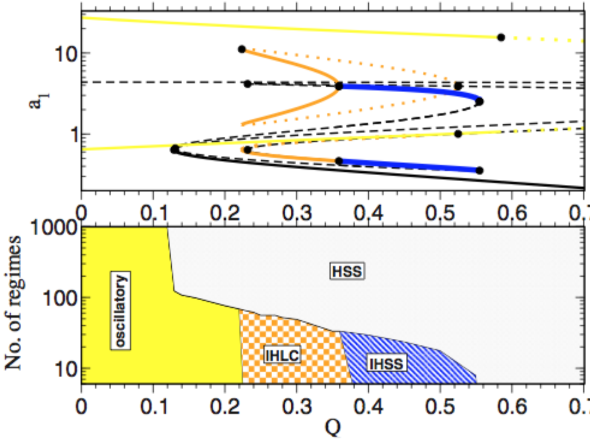
E. Ullner et al., *Phys Rev E*, 031904, 2008.

Phase-repulsive coupling: in-phase solution unstable



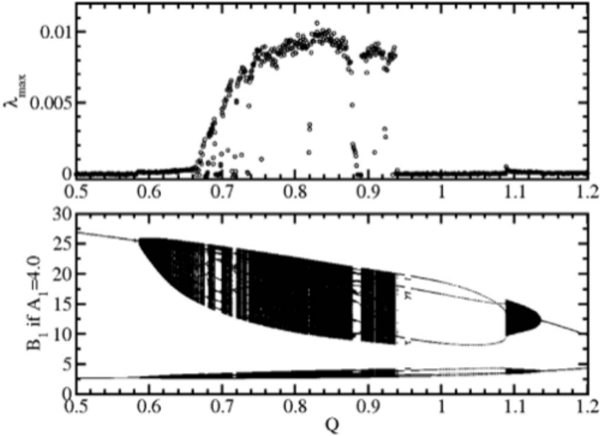
E. Ullner et al., *Phys Rev E*, 031904, 2008.

Phase-repulsive coupling: quantitative analysis



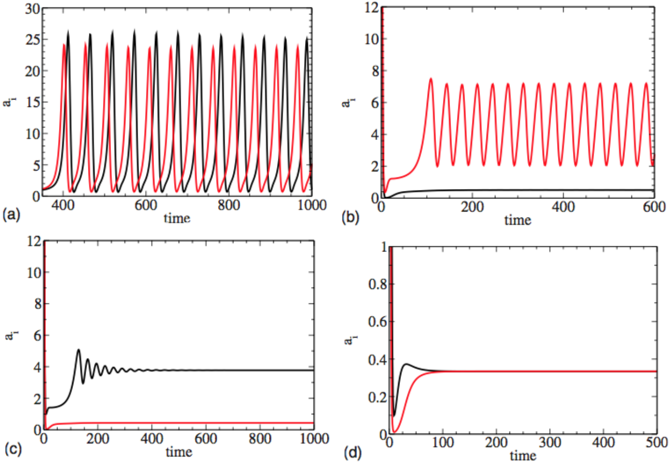
E. Ullner et al., *Phys Rev E*, 031904, 2008.

Phase-repulsive coupling: chaos



E. Ullner et al., *Phys Rev E*, 031904, 2008.

Phase-repulsive coupling: variety of kinetics



E. Ullner et al., *Phys Rev E*, 031904, 2008.

Summary

- Coupling between mathematically similar systems is plausible assumption of a population of "identical" (genetically, morphologically etc.) cells.
- Coupling increases the dynamical complexity of models, that is the dynamics of the coupled systems is much more complex (in many cases) than that of an isolated system.
- Coupling increases the mathematical complexity of models, since dimension grows with increasing number of coupled systems.
- Type of coupling is essential, for example, all-to-all (diffusion coupling, QS etc.), one-to-one (neurons), pulsed coupling...
- Dynamical behaviors in coupled systems are classified roughly by homogeneity and synchronization, that is amplitude and temporal characteristics are compared.

Further reading

- Non-technical presentation of the synchronization phenomenon:
  Coupled oscillators and Biological Synchronization by Steven Strogatz and Ian Stewart, in Scientific American, December 1993, p. 102.
- Scholarpedia pages on synchronization:
  `http://www.scholarpedia.org/article/Synchronization`
- Scholarpedia pages on phase models (more neuronal dynamics oriented):
  `http://www.scholarpedia.org/article/Phase_model`