Mathematical Foundations of Neuroscience - Lecture 12. Synchronization.

Filip Piękniewski

Faculty of Mathematics and Computer Science, Nicolaus Copernicus University, Toruń, Poland

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Introduction

- An oscillator is any entity that exhibits periodic behavior
- The features of an oscillator can be captured by a mathematical model (dynamical system), that has a limit cycle in his phase space
- World is full of oscillators, ranging from pendulum, neutron stars (pulsars), biological cells etc. In particular neurons (when they spike or burst) exhibit oscillations.
- A lot of mathematical biology (and computational neuroscience) is in fact the study of coupled oscillators.
- Next two lectures follow Izhikevich "Dynamical systems is neuroscience" chapter 10, which is available on the web.

Assume we have a dynamical system

$$\frac{d\vec{x}}{dt} = f(\vec{x})$$

with exponentially stable limit cycle (that is any deviation from the cycle converges to the cycle as e^{-t}). Furthermore lets assume the system receives additional inputs at times t_s, that instantaneously increase the variable $\vec{x}$ by vector $\vec{A}$:

$$\frac{d\vec{x}}{dt} = f(\vec{x}) + \vec{A}\delta(t - t_s)$$

where $\delta(t)$ is the Dirac delta. We will usually assume that $\vec{A}$ has got only one nonzero component (that is the reset is performed along one of the variables, usually voltage like).

The system

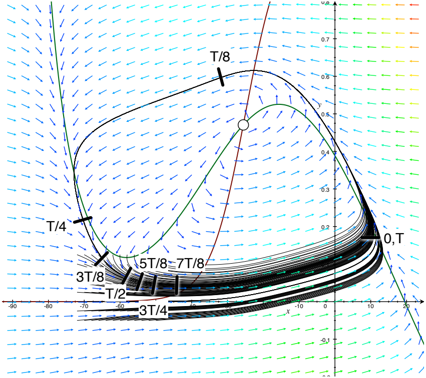
$$\frac{d\vec{x}}{dt} = f(\vec{x})$$

can be replaced with a simpler phase model

$$\frac{d\vartheta}{dt} = 1$$

where the phase variable $\vartheta \in [0, T]$ where T is the period of oscillations of the original system. We therefore replace the original limit cycle with a $\mathbb{S}^1$ circle.

Phase of oscillation is the distance (with respect to vector field f) along the cycle from any fixed point on the cycle. We have to choose the point of zero phase, which can be for example the peak of the spike (since it is very simple to track).



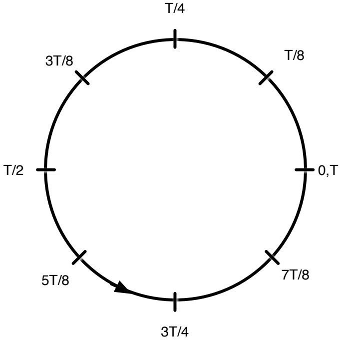


Figure: Phase model.

Isochrons

- The concept of a phase is well defined on the limit cycle. However, since the cycle is attracting, phase can be extended to some (possibly large) neighborhood of the cycle
- Assume we choose some point x. In order to attribute a phase we study the forward trajectory $x(t)$ which approaches the cycle exponentially. Say at some time t_ε the trajectory is closer that ε from the cycle. The nearest point on the cycle has phase $\vartheta_{t_\varepsilon}$.
- We may therefore approximate the phase of original point x as $\vartheta - t_\varepsilon$. Generally:

$$\vartheta(x) = \lim_{\varepsilon \to 0} \vartheta_{t_\varepsilon} - t_\varepsilon$$

Isochrons

- Consequently we have a mapping $\vartheta : U \subseteq \mathbb{R}^n \to [0, T] \subset \mathbb{R}$ which ascribes phase to any point of the phase space sufficiently near the limit cycle.
- The mapping is as continuous as the vector field, and so for smooth systems it makes sense to define the sets for which $\vartheta = \text{const}$, that is for any $\alpha \in [0, T]$ we have $\vartheta^{-1}(\alpha)$
- Any such set of a constant phase is called an isochron (iso - constant, chronos - time/phase). Isochrons are mapped to isochrons by the flow f. Furthermore for any isochron I

$$\Phi_T(I) \subset I$$

(the image of I under the flow of the vector field falls to itself after making one cycle of length T)

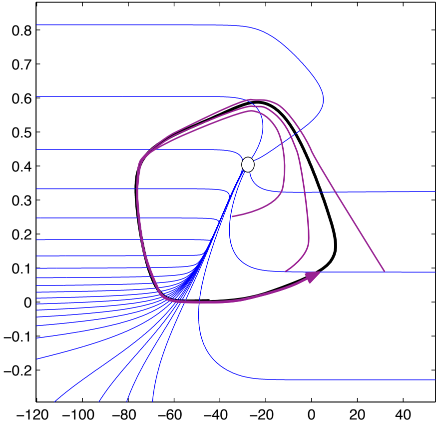


Figure: Isochrons extend the notion of a phase away from the limit cycle.

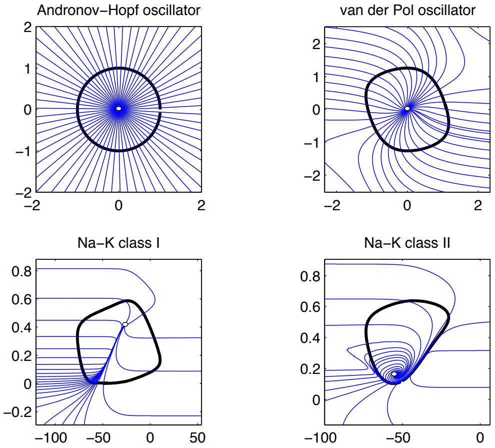


Figure: Phase portraits of various oscillators with isochrons.

Andronov-Hopf oscillator in complex coordinates:

$$\frac{dz}{dt} = (1 + i)z - z|z|^2$$

is sometimes called radial isochron clock (for obvious reasons). Van der Pol oscillator:

$$\begin{aligned}\frac{dx}{dt} =& x - x^3 - y \\ \frac{dy}{dt} =& x\end{aligned}$$

named for Dutch physicist Balthasar van der Pol was originally defined as

$$\frac{d^2x}{dx^2} - \epsilon(1 - x^2)\frac{dx}{dt} + x = 0$$

Phase resetting curve

- The phase is defined on a significant portion of the phase space using isochrons
- When the oscillator is stimulated with the brief pulse, the state of the system jumps suddenly (possibly out of the limit cycle), but to some new isochron (new phase).
- Consequently the input of the system resets the phase. Given the stimulus $\vec{A}$ we can get the curve that shows how the phase changes with respect to the original phase of the system at the time of stimulus. The curve is called a phase resetting curve (PRC for short).

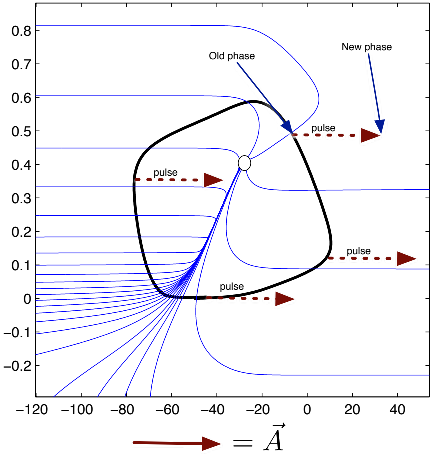


Figure: Phase resetting by a brief pulse.

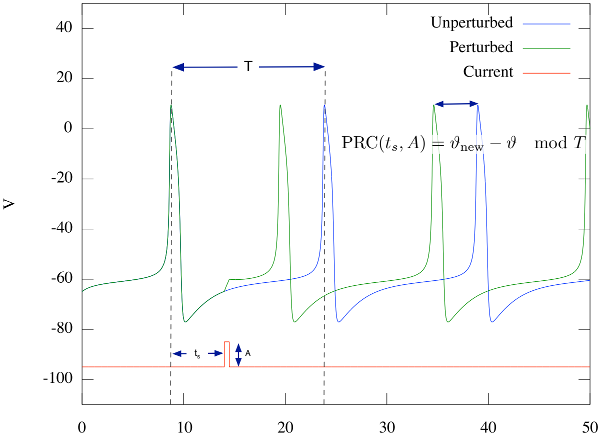


Figure: Phase resetting by a brief pulse.

- By definition the new phase after reseting by vector $\vec{A}$:

$$\vartheta_{\text{new}} = \vartheta + \text{PRC}_{\vec{A}}(\vartheta)$$

- When $|\vec{A}| \to 0$ then

$$\frac{\text{PRC}_{\vec{A}}(\vartheta)}{|\vec{A}|} = \frac{\vartheta_{\text{new}} - \vartheta}{|\vec{A}|} \to \frac{\partial\vartheta}{\partial\vec{A}}$$

- Consequently

$$\frac{\partial\text{PRC}_{\vec{A}}(\vartheta)}{\partial\vec{A}} = \nabla\vartheta$$

at $\vec{A} = 0$

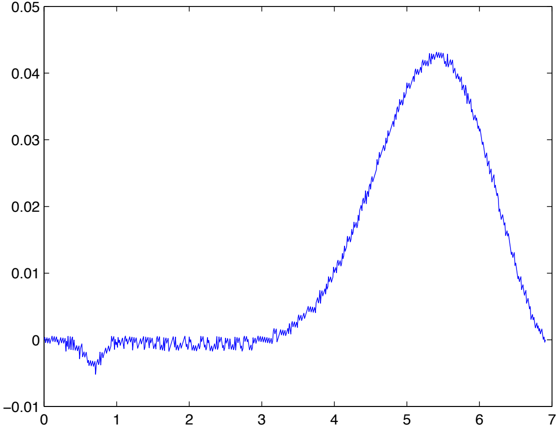


Figure: PRC of the $I_{Na,p} + I_K$ model with class I excitability (stimulus amplitude 0.2 in voltage).

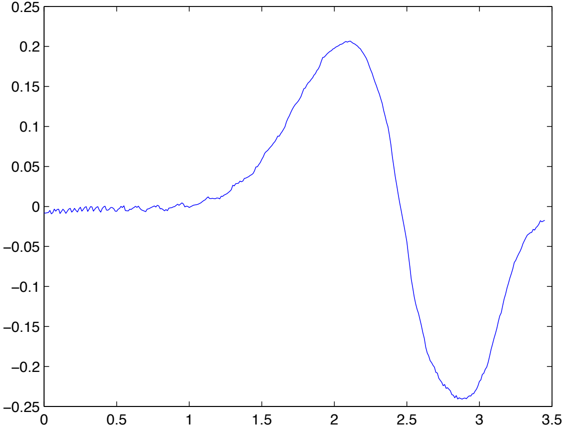


Figure: PRC of the $I_{Na,p} + I_K$ model with class II excitability (stimulus amplitude 0.2 in voltage).

Strong/weak resetting

- Whenever the vector $\vec{A}$ is small, the resetting is straightforward and nothing very surprising can happen.
- However if $\vec{A}$ is long enough that the reset can reach the equilibrium point inside the cycle, strange things may happen.
- When the reset hits the equilibrium exactly, the oscillation halts.
- If it hits further than the equilibrium, the oscillation continues but the new phase skips a lot of isochrons, resulting in a discontinuity in PRC.
- Sometimes instead of PRC researchers use PTC (phase transition curve). Both approaches are equivalent.

$$\mathrm{PTC}(\vartheta) = (\vartheta + \mathrm{PRC}(\vartheta)) \mod T$$

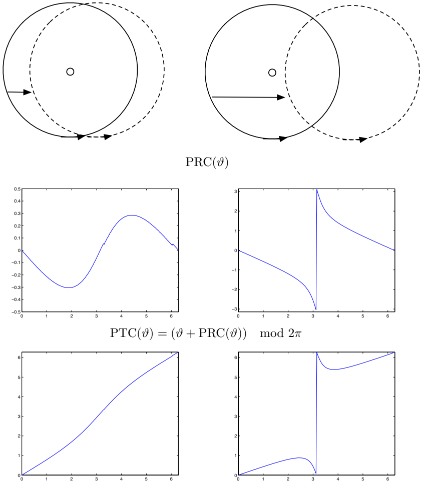


Figure: Strong and weak resetting in Andronov-Hopf oscillator.

Time crystals

- PRC and PTC are defined for a vector $\vec{A}$, but not only the direction of $\vec{A}$ influences the curve but also its amplitude (recall strong/weak resetting)
- The combined PTC plotted against phase and amplitude of $\vec{A}$ is called a *time crystal*.
- Time crystals can have very complex shapes depending on the properties of the oscillator (structure of nearby bifurcations etc).

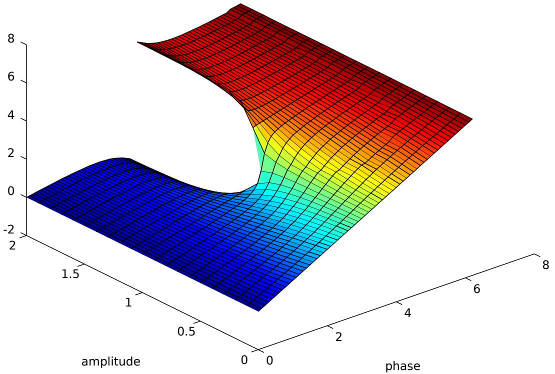


Figure: Time crystal of the Andronov-Hopf oscillator.

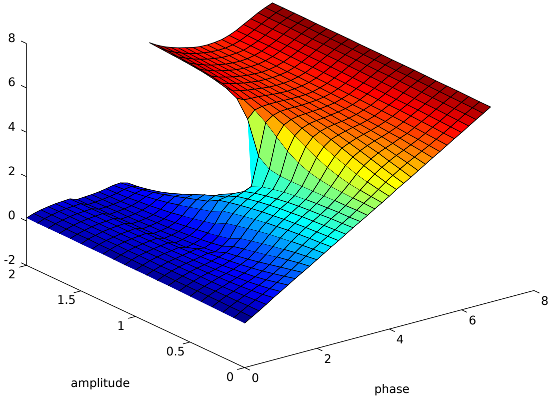


Figure: Time crystal of the van der Pol oscillator

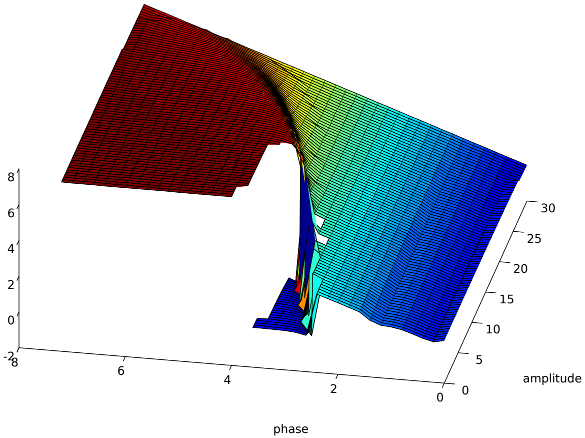


Figure: Time crystal of the $I_{Na,p} + I_K$ model with class I excitability

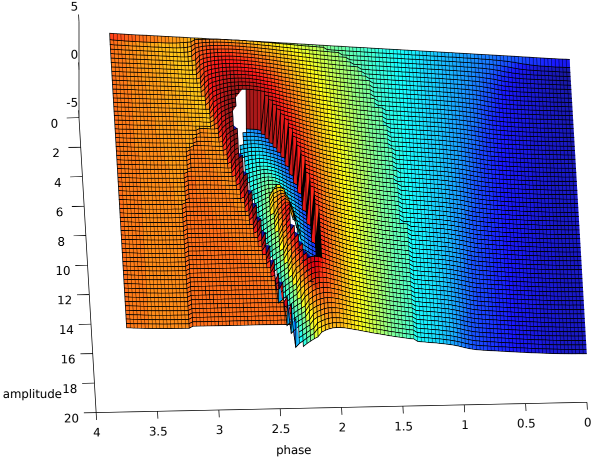


Figure: Time crystal of the $I_{Na,p} + I_K$ model with class II excitability

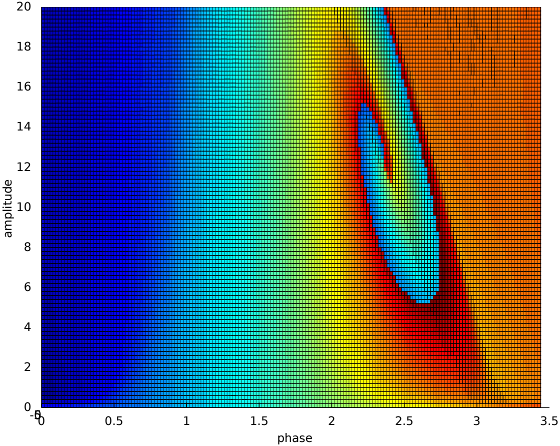


Figure: Time crystal of the $I_{Na,p} + I_K$ model with class II excitability

Poincaré phase maps

- Assume we have an oscillator with intrinsic period T stimulated with pulses with period T_s
- Knowing the PRC we can derive the phase just before the $n+1$ pulse:

$$\vartheta_{n+1} = (\vartheta_n + PRC(\vartheta_n) + T_s) \mod T$$

- We obtain a iterative map, called Poincaré phase map. By studying properties of the map, we can decide wether two oscillators will synchronize, phase lock etc.
- Note for example that a fixed point of the map means that the forced oscillator synchronizes with with forcing signal!

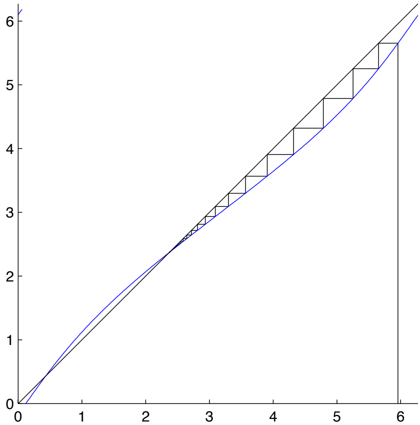
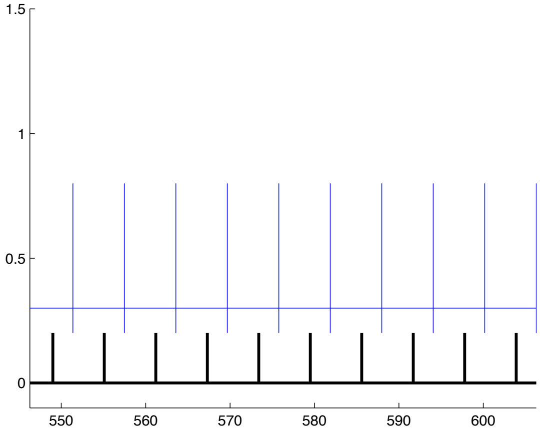


Figure: Poincare phase map for Andronov-Hopf oscillator (puse 0.3 on first variable, forcing $T_s = 6.1$) and the corresponding pulse train.



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- Iteration maps have a lot in common with differential equations (to some extent an iteration map is a discrete analog of a differential equation)
- Much like dynamical systems, iteration maps may have a fixed points (equilibria) whenever:

$$\vartheta = f(\vartheta)$$

- The fixed point may either be stable or unstable, it may appear and disappear via bifurcations. Geometrically equilibria appear at intersections of $f(\vartheta)$ and identity function,

$$0 = \vartheta - f(\vartheta)$$

- The stability of a fixed point depends on the derivative of f !

- The stability of fixed points of a map f depends on the derivative $m = f'$ called *Floquet multiplier* of a mapping.
- When $|m| < 1$ the point is stable while with $|m| > 1$ the point is unstable.
- The derivation is fairly simple - the fixed point is at the intersection of the diagonal (slope 1) and the map. The map itself can be locally approximated with a linear function $f_l(x) = m(x - x_0) + f(x_0) = f'(x_0)(x - x_0) + f(x_0)$
- If $|m| < 1$ the sequence of points will converge to x_0 while iterating the linearized map above (easy to check!)
- The analogy with continuous dynamical systems is such that $|m| = e^{\lambda}$, so $|m| < 1$ $(\lambda < 0)$ is stable, $|m| > 1$ $(\lambda > 0)$ is unstable and $|m| = 1$ $(\lambda = 0)$ is a bifurcation point.

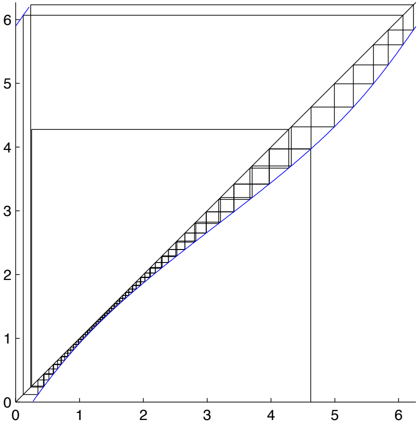
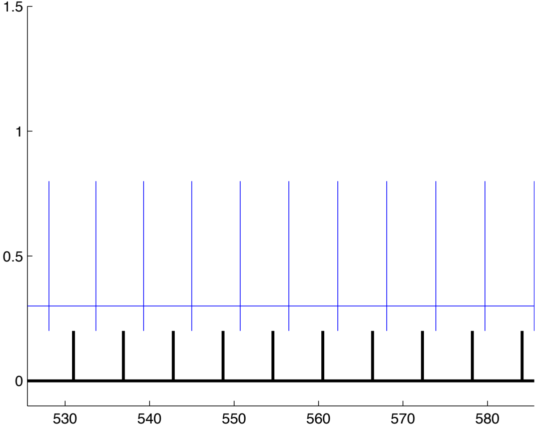


Figure: Poincare phase map for Andronov-Hopf oscillator (puse 0.3 on first variable, forcing $T_s = 5.9$) and the corresponding pulse train.



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Bifurcations of maps

- Equilibria of maps appear and disappear via a fold bifurcation - discrete analog of saddle-node bifurcation (two equilibrium point - stable and unstable collide)
- An equilibrium may also loose stability via a flip bifurcation - discrete analog of Andronov-Hopf bifurcation. In that case a periodic cycle emerges.
- The fold bifurcation leaves a ghost attractor (much like with continuous systems) resulting in a slow transition.
- Equilibria may coexist with cycles resulting in rich synchronization regimes of two oscillators.

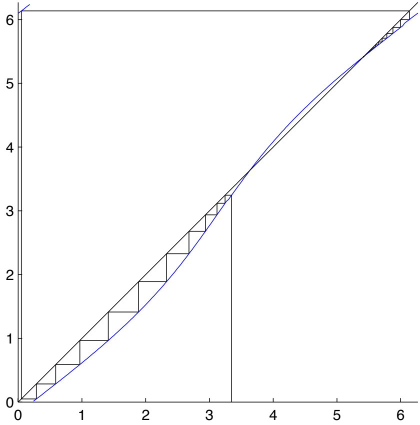
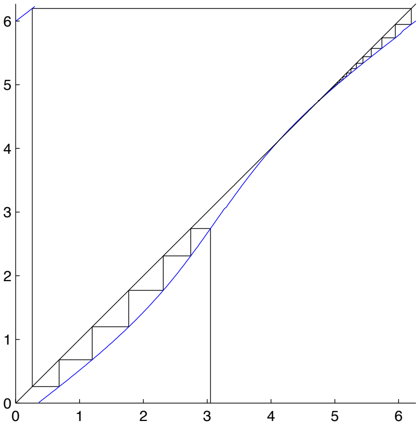


Figure: Changes to the Poincare phase map for Andronov-Hopf oscillator for $T_s = 6.2 \ldots 5.7$, pulse 0.3



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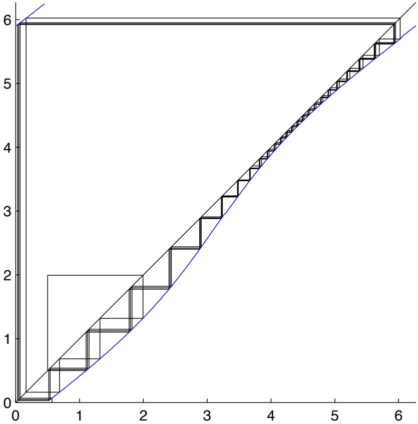

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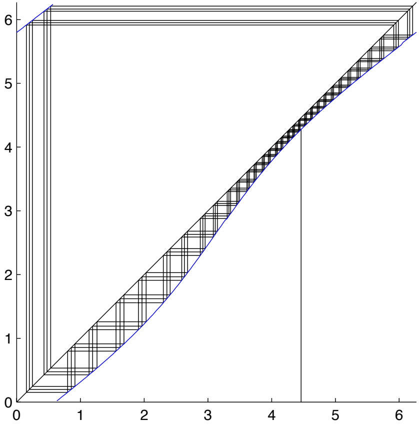


Figure: Changes to the Poincare phase map for Andronov-Hopf oscillator for $T_s = 6.2...5.7$, pulse 0.3

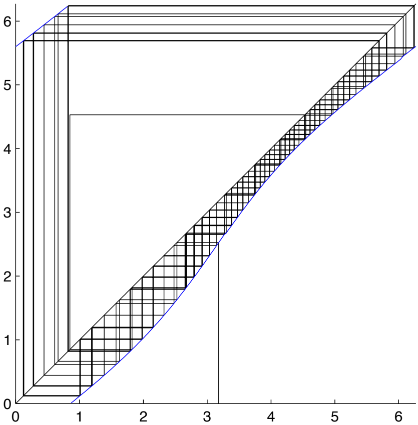


Figure: Changes to the Poincare phase map for Andronov-Hopf oscillator for $T_s = 6.2 \ldots 5.7$, pulse 0.3

Synchronization

A forced oscillator may either:

- Synchronize to the forcing signal - this corresponds to a fixed point of the Poincaré phase map. Synchronization may either be stable or unstable.
- p/q phase lock - every p cycles of the oscillator and every q cycles of the forcing signal the trains meet. Phase locking corresponds to periodic cycles of phase maps.
- fail to synchronize - the failure can be complete (the trajectory of the map becomes purely chaotic), but there can also be cycle slipping in which the oscillator seems to synchronize with the forcing signal, but then after possibly significant time, the cycle slips and synchronization fails. This corresponds to slow transitions near fold bifurcation of the map.

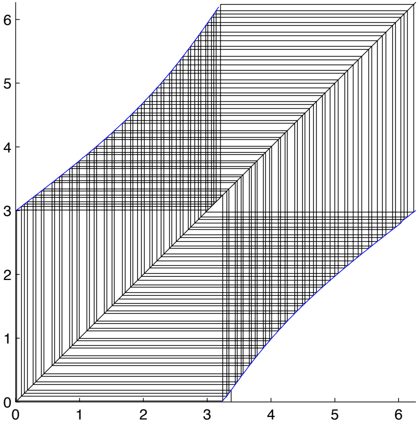
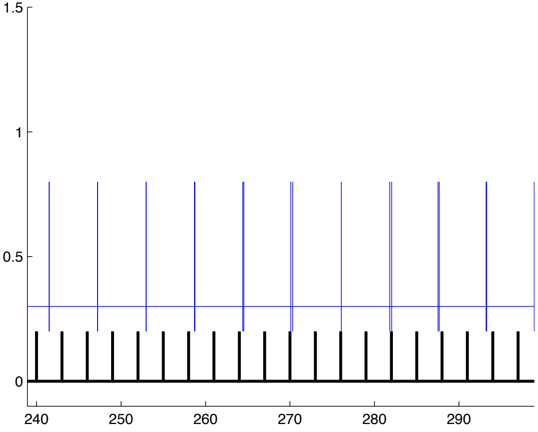


Figure: Failure to synchronize - Andronov-Hopf oscillator for $T_s = 3$ pulse 0.3



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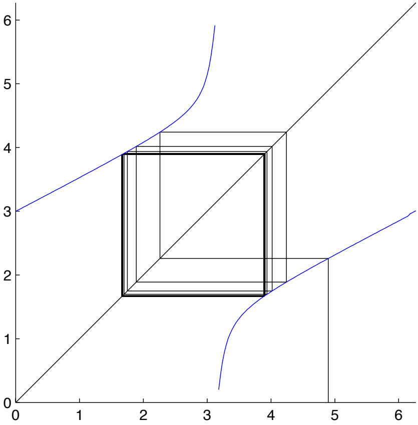
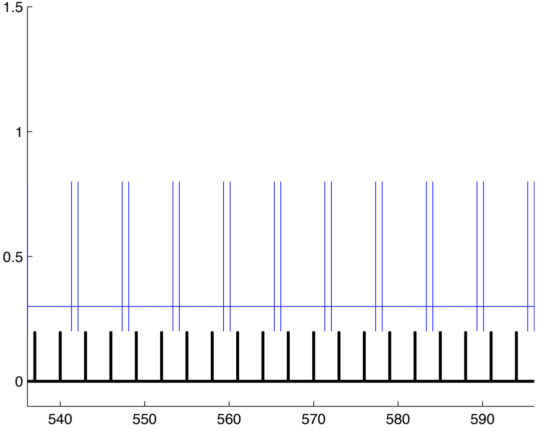


Figure: 2/2 phase locking - Andronov-Hopf oscillator for $T_s = 3$ pulse 0.9



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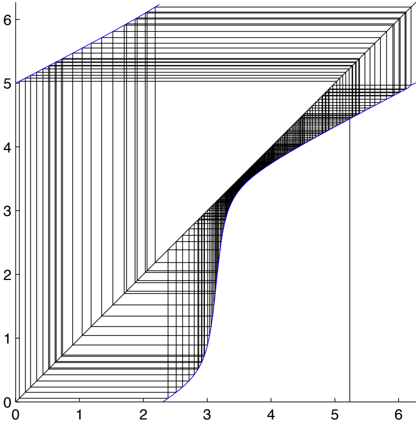

Figure: Cycle slipping - Andronov-Hopf oscillator for $T_s = 3$ pulse 0.9

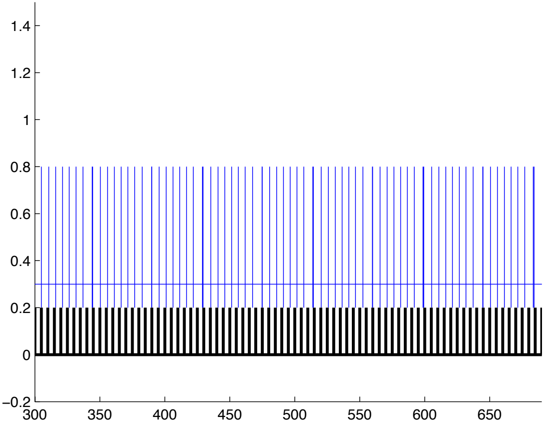

Figure: Cycle slipping - Andronov-Hopf oscillator for $T_s = 3$ pulse 0.9

Phase locking

- p/q phase locking typically occurs when $pT \approx qT_s$
- Synchronization corresponds to 1/1 phase locking
- p/q phase locking solution corresponds to a periodic orbit of the map $\vartheta_n = \vartheta_{n+q}$. Such periods are equilibria of iterations, that is

$$\vartheta_{n+1} = f^q(\vartheta_n)$$

  where $f^q = f \circ f \circ f \circ \ldots \circ f$
- Phase locking and synchronized solutions may coexists for the same input pulse train. The oscillator may converge to either one depending on the initial phase shift and be switched to a different regime by a clever pulse.

Arnold Toungues

- To synchronize an oscillator the phase map has to interest the diagonal (so that there could be a fixed point).
- When the amplitude of the stimulus decreases, also $|\mathrm{PRC}_A(\vartheta)|$ decreases, and so the range of T_s such that the map

$$\vartheta_{n+1} = (\vartheta_n + PRC(\vartheta_n) + T_s) \mod T$$

  intersects diagonal shrinks.
- When plotted on $T_s \times A$, the regions of synchronization and phase locking look like tongues, shrinking as $|A| \to 0$
- These regions are called Arnold Tongues after Vladimir Arnold, Russian mathematician born 12 June 1937 in Odessa.

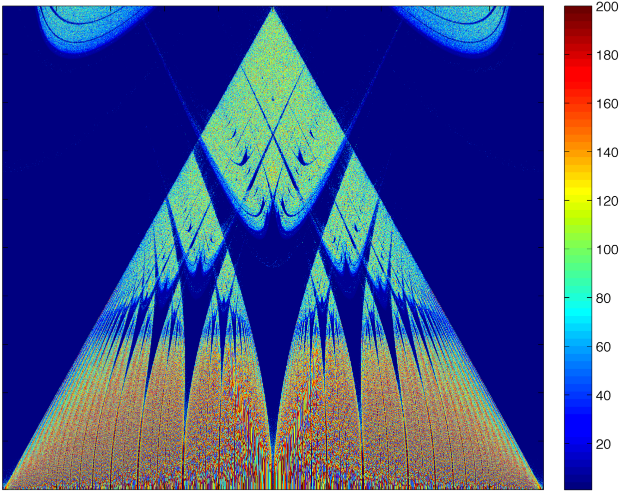

Figure: Arnold tongues for Andronov-Hopf oscillator, horizontal axis is the phase of stimulus $(0 - 1)$, vertical amplitude $(0 - \frac{\pi}{2})$

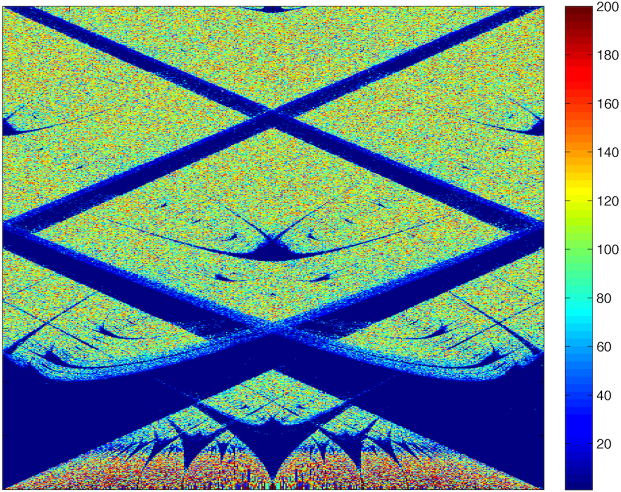

Figure: Arnold tongues for Andronov-Hopf oscillator, horizontal axis is the phase of stimulus $(0-1)$, vertical amplitude $(0-2\pi)$

The above pictures were plotted for

$$\vartheta_{n+1} = \left(\vartheta_n + T_s - \frac{A}{2\pi} \sin(2\pi\vartheta_n) \right) \mod 1$$

where ϑ, $T_s \in [0, 1]$. The map is called a circle map. The term

$$-\frac{A}{2\pi} \sin(2\pi\vartheta_n) = \mathrm{PRC}_A(\vartheta_n)$$

is the PRC. Arnold tongues for other oscillators may look differently.

Phase map may not be a reliable determinant of the behavior of oscillators if the amplitude of the input is too large (the trajectories are pushed away from the limit cycle).

Farey fractions

- The figures above have a very peculiar mathematical properties. First of all, Arnold tongues form a fractal.
- Secondly, an Arnold tongue emerges from every rational number on the $A = 0$ line. Therefore the set of elements in the tongues for $A = 0$ has (Lebesgue) measure zero, whereas for any $A > 0$ it has measure grater than zero.
- When sorted by size (and the phase of stimulus is scaled to $[0, 1]$), Arnold tongues hit the so called Farey fractions, a very mysterious and emerging in many aspects of computer science sequence.
- n-th Farey sequence contains sorted all reduced fractions with denominator at most n, e.g.:

$$F_5 = \{\frac{0}{1}, \frac{1}{5}, \frac{1}{4}, \frac{1}{3}, \frac{2}{5}, \frac{1}{2}, \frac{3}{5}, \frac{2}{3}, \frac{3}{4}, \frac{4}{5}, \frac{1}{1}\}$$

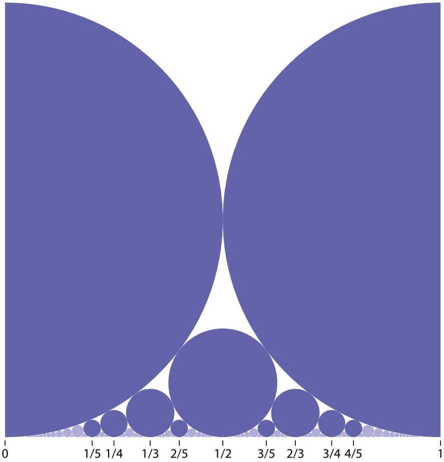

Figure: Ford Circles are touching the axis in Farey fractions. Farey sequence is surprisingly frequent in computer science.

Recapitulation

- Synchronization of coupled oscillators is a problem frequently found in biological sciences and engineering.
- The theory of coupled oscillators is rich and full of elegant mathematical insights.
- Complex oscillators like neurons, can be reduced to their phase models. Together with the PRC (phase resetting curve) the phase model is sufficient to determine synchronization properties via a Poincaré phase maps
- The methodology is only valid if the limit cycles are exponentially stable, and the resetting was not too strong!
- Phase maps themselves are an interesting subject, resulting in Fractal Arlond tongues, Farey sequences etc.
- PRC can be useful for dealing with the jet-lag!