Mathematical Foundations of Neuroscience - Lecture 13. Coupled oscillators.

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- Recall that any system

$$\frac{dx}{dt} = f(x)$$

having a stable limit cycle can be mapped into a simple phase model

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

Defined on a circle $\mathbb{S}^1$. The mapping is a simple stretching on the cycle itself (a cycle is a deformed circle), but can also be defined off the cycle via isochrons.

- We will show how to make such a transformation when the system is coupled with some input signal. In particular we are interested in networks of oscillators coupled in some way, and the conditions under which then synchronize.

Example - circadian rhythm

- There is a certain piece of the brain which provides a 24 hour cycle that influences sleeping etc.
- It turns out that it is an oscillator, which can be reset by bright light stimulus (Charles A. Czeisler 2003)
- The phase resetting curve of the oscillator looks much like a sinusoid with period $[-12h, 12h]$ the origin at T_0 which is the minimum body temperature time. It turns out that

$$T_{\text{wake}} = \frac{2}{3} T_0 + 5.4h$$

- Assume I'm flying to California, the time shift is $-9h$. When should I get out to the bright light in order to efficiently reset by circadian oscillator assuming my $T_{\text{wake}} = 8\text{am}$?

- We have

$$8:00\text{am} = \frac{2}{3}T_0 + 5.4h \Rightarrow T_0 = \frac{3}{2}2.6 = 3.9 = 3:54\text{am}$$

- My rhythm is 9 hours ahead of that in California, so I need to delay my oscillator. That is I have to get as much sun as possible before T_0
- $T_0 = 3:54$ am CET $= 6:54$ pm Pacific
- So I need to get out before 6:54pm on the first day (preferably $\approx$ 1pm, not earlier that $6:54$am though). 6h spent in bright sunlight shifts the oscillator by about 2 hours. So the next day my $T_0 \approx 8:54$pm.
- At the third day my $T_0 \approx 10:54$pm, fourth $T_0 \approx 12:54$am. After the fifth day my rhythm should be completely reset.

- Assume wa have a system

$$\frac{dx}{dt} = f(x) + \varepsilon p(t)$$

  where $p(t)$ is time dependent input, ε is small but not zero. Whenever ε is sufficiently small, we call $\varepsilon p(t)$ a weak coupling.
- $p(t)$ can be any waveform (we do not impose any restrictions on it). It may be a continuous synaptic input, or a pulse train. In particular it may have the form

$$p(t) = \sum_s g_s(x(t), x_s(t))$$

  (sum of synaptic inputs from a set of other oscillators).
- The interesting question is whether such a coupled system can be decomposed into a phase model.

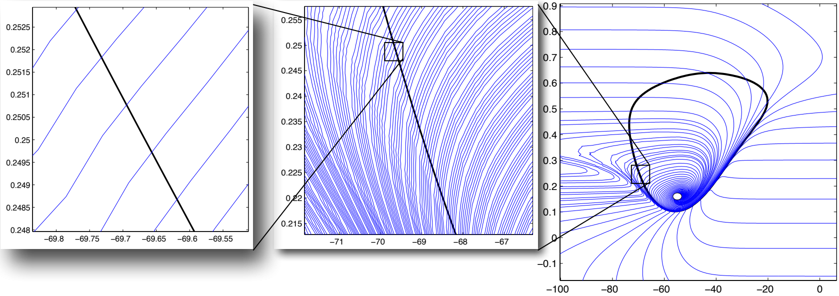


Figure: Even though isochrons can have a complex form, sufficiently near the cycle they are collinear and equally spaced.

- Assume that ε is sufficiently small to assume, that the isochrons near the point x on the cycle are collinear and equally spaced.
- Collinearity means, that the phase resetting of any point y on the same isochron as x is the same as that of x
- Equal spacing means, that phase resetting scales linearly with the strength of the pulse.
- Since PRC scales linearly with the strength of the pulse, we can substitute the PRC by its linear approximation:

$$\mathrm{PRC}(\vartheta, A) \approx \left.\frac{\partial \mathrm{PRC}(\vartheta, \mathcal{A})}{\partial \mathcal{A}}\right|_{\mathcal{A}=0} \cdot A = \mathrm{iPRC}(\vartheta) \cdot A$$

- iPRC stands for infinitesimal PRC, sometimes called linear response (sometimes denoted $Z(\vartheta)$).

- Lets now discretize the the input signal $\varepsilon p(t)$, such that $A = \varepsilon p(t_n)h$ where h is the small time interval (we change the continuous signal into a step signal, with the step width equal h).
- We write the Poincaré phase map:

$$\vartheta(t_{n+1}) = [\vartheta(t_n) + \mathrm{PRC}\left(\vartheta(t_n), \varepsilon p(t_n)h\right) + h] \mod T$$

$$\vartheta(t_{n+1}) = [\vartheta(t_n) + \mathrm{iPRC}\left(\vartheta(t_n)\right) \cdot \varepsilon p(t_n)h + h] \mod T$$

$$\frac{\vartheta(t_n + h) - \vartheta(t_n)}{h} = \mathrm{iPRC}\left(\vartheta(t_n)\right) \cdot \varepsilon p(t_n) + 1$$

Finally we obtain:

$$\frac{d\vartheta}{dt}(t_n) = \lim_{h\to 0} \frac{\vartheta(t_n+h) - \vartheta(t_n)}{h} =$$

$$= \lim_{h\to 0} \mathrm{iPRC}\left(\vartheta(t_n)\right) \cdot \varepsilon p(t_n) + 1$$

so

$$\frac{d\vartheta}{dt} = 1 + \varepsilon \cdot \mathrm{iPRC}\left(\vartheta\right) \cdot p(t)$$

which is the phase model for the coupled system!

Kuramoto's model

- Consider another approach. Let $\vartheta : U \subset \mathbb{R}^n \to \mathbb{S}^1$ be the mapping that assigns a phase to points near the limit cycle. Note that isochrons are level contours of that function, since the phase is constant along any isochron.
- Differentiating $\vartheta(x)$ with respect to time, using the chain rule gives:

$$\frac{d\vartheta(x)}{dt} = \nabla\vartheta \cdot \frac{dx}{dt} = \nabla\vartheta \cdot f(x)$$

where $\nabla\vartheta$ is the gradient of ϑ (the direction highest slope of isochrons).
- But on (and near) the limit cycle

$$\frac{d\vartheta(x)}{dt} = 1$$

(the phase advances constantly as time passes)

- We therefore get:

$$\nabla\vartheta \cdot f(x) = 1$$

- Now applying the chain rule to the perturbed system:

$$\frac{d\vartheta(x)}{dt} = \nabla\vartheta \cdot \frac{dx}{dt} = \nabla\vartheta \cdot (f(x) + \varepsilon p(t)) =$$

$$= \nabla\vartheta \cdot f(x) + \nabla\vartheta \cdot \varepsilon p(t) = 1 + \nabla\vartheta \cdot \varepsilon p(t)$$

we obtain a phase model which has the same form as previously. We note that:

$$\nabla\vartheta(x) = \mathrm{iPRC}(\vartheta) = \left.\frac{\partial \mathrm{PRC}(\vartheta, \mathcal{A})}{\partial \mathcal{A}}\right|_{\mathcal{A}=0}$$

so Kuramoto's approach is equivalent to that of Winfree.

- Another approach is the most general is by Ioel Gil'evich Malkin.
- Assume as above that the uncoupled oscillator has an exponentially stable limit cycle. The the phase equation of the weakly coupled system has the form:

$$\frac{d\vartheta}{dt} = 1 + \varepsilon Q(\vartheta) \cdot p(t)$$

where the function $Q : \mathbb{S}^1 \to \mathbb{R}^n$ is the solution of the adjoint equation:

$$\frac{dQ}{d\vartheta} = -\left(Df\left(x(\vartheta)\right)\right)^\top Q(\vartheta)$$

with the condition $Q(0) \cdot f(x(0)) = 1$. $Df(x(t))$ is the Jacobian matrix of f.

- It turns out that the three approaches are all equivalent and:

$$\nabla\vartheta(x) = \mathrm{iPRC}(\vartheta) = Q(\vartheta)$$

- In order to derrive the phase equation of coupled oscillators we therefore need to obtain the infinitesimal PRC either from ordinary PRC normalized by the amplitude of stimuli, analyzing isochrons or solving the adjoint equation.

- Let us now derive the models for coupled oscillators, that is:

$$\frac{dx_i}{dt} = f_i(x_i) + \varepsilon \sum_{j=1}^{n} g_{ij}(x_i, x_j), \quad x_i \in \mathbb{R}^m$$

for $i = 1...n$. Assume for simplicity that uncoupled oscillators $(\varepsilon = 0)$ have equal periods $T_i = T$.

- Applying any of the methods we get the phase model

$$\frac{d\vartheta_i}{dt} = 1 + \varepsilon \mathrm{iPRC}(\vartheta_i) \cdot \overbrace{\sum_{j=1}^{n} g_{ij}(x_i(\vartheta_i), x_j(\vartheta_j))}^{p_i(t)}$$

- The original model is defined in $\mathbb{R}^{mn}$, while the phase model is defined on the torus $\mathbb{T}^n$, $x(\vartheta)$ is the position on the cycle in $\mathbb{R}^m$ of a point whose phase is ϑ

- We are mostly interested with phase deviations from the original periodicity, it therefore useful to make a substitution and represent $\vartheta = t + \varphi$ where t is the uniform time, while φ is de deviation from the original phase. In consequence we get:

$$\frac{d\varphi_i}{dt} = \varepsilon \mathrm{iPRC}(t + \varphi_i) \cdot \sum_{j=1}^{n} g_{ij}(x_i(t + \varphi_i), x_j(t + \varphi_j))$$

- The system can be further reduced by averaging out t (which is fast compared to φ):

$$\frac{d\varphi_i}{dt} = \varepsilon \cdot \sum_{j=1}^{n} \int_{\tau=0}^{T} \mathrm{iPRC}(\tau) g_{ij}(x_i(\tau), x_j(\tau + \varphi_j - \varphi_i))d\tau$$

- Denote:

$$H_{ij}(\varphi_j - \varphi_i) = \int_{\tau=0}^{T} \mathrm{iPRC}(\tau) g_{ij}(x_i(\tau), x_j(\tau + \varphi_j - \varphi_i)) d\tau$$

  Note that this interaction function depends only on the phase difference of oscillator i and j. iPRC in the integral accounts for the intrinsic oscillators phase resetting properties, while g_{ij} accounts for the coupling properties (whether it is a synapse of some response profile, gap junction, delta pulse etc).

- Moreover

$$\omega_i = H_{ii}(\varphi_i - \varphi_i) = H_{ii}(0)$$

  describes the constant frequency deviation from the uncoupled oscillations due to a self interaction.

- All in all we get the system

$$\frac{d\varphi_i}{dt} = \varepsilon\omega_i + \varepsilon \sum_{j \neq i} H_{ij}(\varphi_j - \varphi_i)$$

  a phase model for coupled oscillators.
- A particularly useful special case is the Kuramoto phase model

$$\frac{d\varphi_i}{dt} = \omega_i + \sum_{j \neq i} c_{ij} \sin(\varphi_j - \varphi_i)$$

  in which the interaction function has a simple sinusoidal form. The model is nice for analytical studies, but the lack of any even component in the interaction function is rather degenerate.

Two coupled oscillators

- Consider two coupled oscillators in the most general form:

$$\frac{d\vartheta_1}{dt} = h_1(\vartheta_1, \vartheta_2)$$
$$\frac{d\vartheta_2}{dt} = h_2(\vartheta_1, \vartheta_2)$$

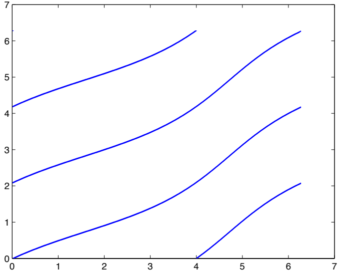
- Since $\vartheta_1, \vartheta_2 \in \mathbb{S}^1$, the joint state of the system falls on a 2-torus $\mathbb{T}^2 = \mathbb{S}^1 \times \mathbb{S}^1$
- The trajectories on the torus cannot cross, and can be periodic or quasiperiodic. A periodic orbit on a torus is called a torus knot.

Two coupled oscillators

- We say that two oscillators are frequency locked if their joint trajectory is a $p:q$ periodic orbit on the torus ($p:q$ knot). $1:1$ frequency locking is called entrainment.
- Moreover we say that two oscillators are $p:q$ phase locked if they are $p:q$ frequency locked and

$$q\vartheta_1(t) - p\vartheta_2(t) = l_{\vartheta_1,\vartheta_2} = \text{const}$$

  for any t where $l_{\vartheta_1,\vartheta_2}$ is called a phase lag.
- $1:1$ phase locking is synchronization. Moreover synchronization is in phase if $l_{\vartheta_1,\vartheta_2} = 0$, anti-phase if $l_{\vartheta_1,\vartheta_2} = T/2$ and off-phase otherwise.



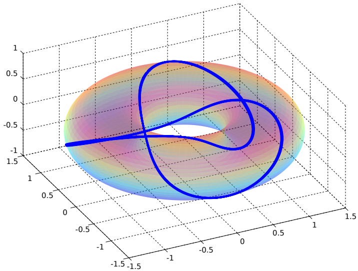


Figure: 2/3 frequency locking and the corresponding torus knot.

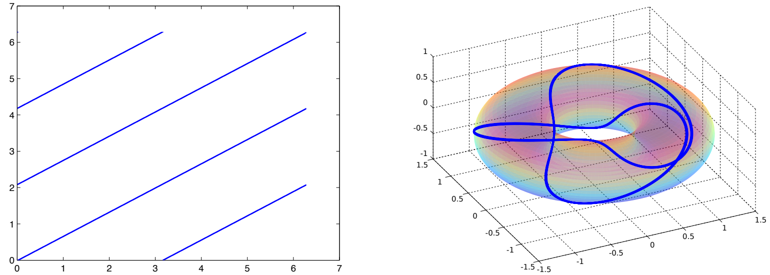
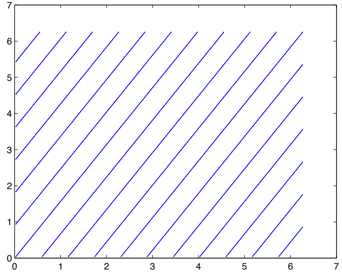


Figure: $2/3$ phase locking ($3\vartheta_1 + 2\vartheta_2 = \text{const}$) and the corresponding torus knot.



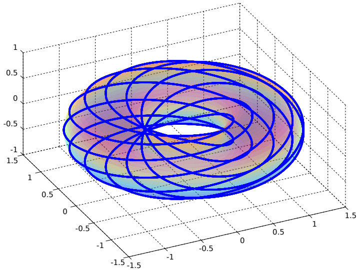
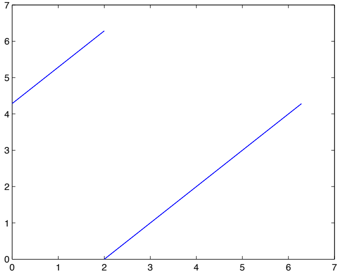


Figure: 7/11 phase locking and the corresponding torus knot.



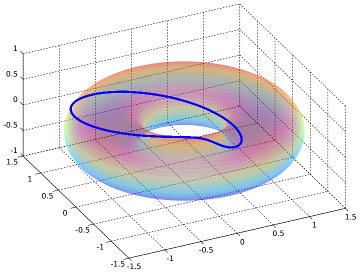


Figure: Off-phase synchronization.

- Now lets get back to the phase model

$$\frac{d\varphi_i}{dt} = \varepsilon\omega_i + \varepsilon \sum_{j \neq i} H_{ij}(\varphi_j - \varphi_i)$$

in the case of two oscillators. It is convenient to rewrite the model in slow time $\tau = \varepsilon t$ to obtain:

$$\varphi_1' = \omega_1 + H_1(\varphi_2 - \varphi_1)$$
$$\varphi_2' = \omega_2 + H_2(\varphi_1 - \varphi_2)$$

- Let $\chi = \varphi_2 - \varphi_1$, subtracting the equations we obtain a 1d model:

$$\chi' = \omega + G(\chi)$$

where $\omega = \omega_2 - \omega_1$ and $G(\chi) = H_2(\chi) - H_1(-\chi)$

- Any stable equilibrium of:

$$\chi' = \omega + G(\chi)$$

  corresponds to a phase locking solution of the coupled oscillators.

- All equilibria are solutions to $G(\chi) = -\omega$. When the oscillators are identical then $G(\chi) = H(\chi) - H(-\chi)$ is an odd function while $\omega = 0$ and consequently $\chi = 0$ and $\chi = T/2$ are always solutions. $\chi = 0$ is stable when $G'(0) = -2H'(0) < 0$

- The range of values taken by G established the tolerance to frequency mismatch ω. When ω becomes too large, all equilibria vanish via a saddle node bifurcation, leaving the ghost attractor that results in cycle slipping (drifting).

- So far we derived a phase model for generally all to all coupled oscillators. In its most general form the model is hard to analyze.
- Interesting things may happen when the coupling reflects some topological structure like a chain or a grid.
- Consider a chain:

$$\varphi_i = \omega_i + H^+(\varphi_{i+1} - \varphi_i) + H^-(\varphi_{i-1} - \varphi_i)$$

if all ω_i are equal and $H^+(0) = H^-(0) = 0$ then obviously synchrony is a solution (all φ_i equal). But when $\omega_i \neq \omega_j$ other solutions are possible.

- Any phase locked solution of

$$\varphi_i' = \omega_i + H^+(\varphi_{i+1} - \varphi_i) + H^-(\varphi_{i-1} - \varphi_i)$$

has the form $\varphi_i(\tau) = \omega_0\tau + \phi_i$ where ω_0 is the common frequency of oscillation and ϕ_i are phase shifts satisfying:

$$\begin{aligned} \omega_0 &= \omega_1 + H^+(\phi_2 - \phi_1) \\ \omega_0 &= \omega_i + H^+(\phi_{i+1} - \phi_i) + H^-(\phi_{i-1} - \phi_i) \\ \omega_0 &= \omega_n + H^-(\phi_{n-1} - \phi_n) \end{aligned}$$

- One can check easily by differentiating $\varphi_i(\tau) = \omega_0\tau + \phi_i$ with respect to τ that is satisfies the chain model.
- Any solution with a monotonic sequence ϕ_i is called a traveling wave.

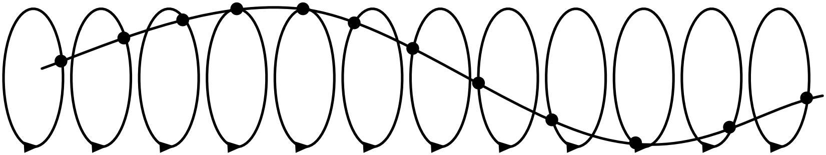


Figure: Traveling wave solution to a chain of coupled oscillators.

- The traveling wave exists when the frequencies ω_i are not equal. Assume the phase shift is constant, that is $\chi = \phi_{i+1} - \phi_i$
- Subtracting all of the conditions imposed on the solution from the second we get

$$0 = \omega_2 - \omega_1 + H^{-}(-\chi)$$
$$0 = \omega_2 - \omega_i$$
$$0 = \omega_2 - \omega_n + H^{+}(\chi)$$

and since

$$\omega_0 = \omega_1 + H^{+}(\chi)$$

we have

$$\omega_0 = \omega_1 + \omega_n - \omega_2$$

- The wave should appear when $\omega_1 \leqslant \omega_2 = \ldots = \omega_{n-1} \leqslant \omega_n$, that is the two extreme oscillators are tuned up and down.
- When the sequence of frequencies is monotonic, the wave may also occur, but the case is harder to analyze.
- A wave can also occur when all the frequencies are equal with $H^+(0) \neq 0$ or $H^-(0) \neq 0$. For example:

$$\varphi_i' = \omega + H^+(\varphi_{i+1} - \varphi_i)$$

(descending coupling, with $\omega_0 = \omega$). If $\chi = \varphi_{i+1} - \varphi_i$ is the phase shift along the wave, then we have $n-1$ conditions

$$H^+(\chi) = 0$$

and the traveling wave exists when H^+ has a stable root at χ. Note that the sign of χ, not the direction of coupling determines the direction of the wave.

Networks

- Now consider a general network with the possibly all-to-all coupling:

$$\frac{d\varphi_i}{dt} = \varepsilon\omega_i + \varepsilon \sum_{j \neq i} H_{ij}(\varphi_j - \varphi_i)$$

- The system has a stable solution if the phase deviation φ remains constant, that is:

$$0 = \omega_i + \sum_{j \neq i} H_{ij}(\varphi_j - \varphi_i)$$

- Assume we have a solution $(\phi_1, \phi_2, \ldots \phi_n)$. How to determine whether it is stable?

- The general condition is that the Jacobian matrix at ϕ has negative real parts of the eigenvalues, except for one zero eigenvalue which corresponds to the direction of constant phase shift (phase shifted solution is still a solution since phase difference $\phi_j - \phi_i$ is not affected).

Theorem (Bard Ermentrout 1992)

Assume

- $a_{ij} = H'_{ij}(\phi_j - \phi_i) \geqslant 0$
- *the weighted, directed graph with adjacency matrix $A = [a_{ij}]$ is strongly connected*

then equilibrium ϕ is neutrally stable and the corresponding cycle $x(t + \phi)$ is asymptotically stable.

- Now consider a planar grid of identical oscillators coupled via sine (Kuramoto model):

$$\frac{d\varphi_i}{dt} = 1 + \sum_{j \sim i} \sin(\varphi_j - \varphi_i)$$

where $j \sim i$ means that j is a neighbor of i in the grid.
- Synchrony is a solution since $\sin(0) = 0$. Moreover it is stable, since following Ermentrout condition $\sin'(0) = \cos(0) = 1 > 0$ and the grid graph is strongly connected.
- It turns out however, that it not the only stable solution! The other solutions are rotating waves! Such waves are frequently observed in cortical recordings...

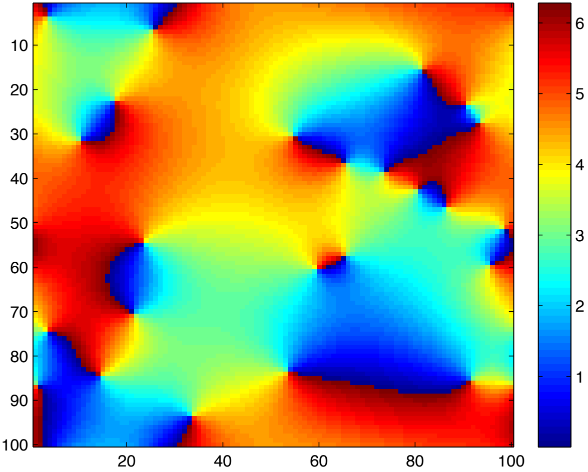


Figure: Rotating waves.

- Coupling via sin is a little degenerate since it is an odd function and all the even components in the Fourier series are zero.
- Lets add some even component to the model:

$$\frac{d\varphi_i}{dt} = 1 + \sum_{j \sim i} \left(\sin(\varphi_j - \varphi_i) + \beta(\cos(\varphi_j - \varphi_i) - 1) \right)$$

  for some $\beta < 1$. Synchrony remains the solution since $\cos'(0) = 0$
- The rotating waves solutions though get a little curl and become spiral waves! Compare with http://www9.georgetown.edu/faculty/wuj/propagationwave.html

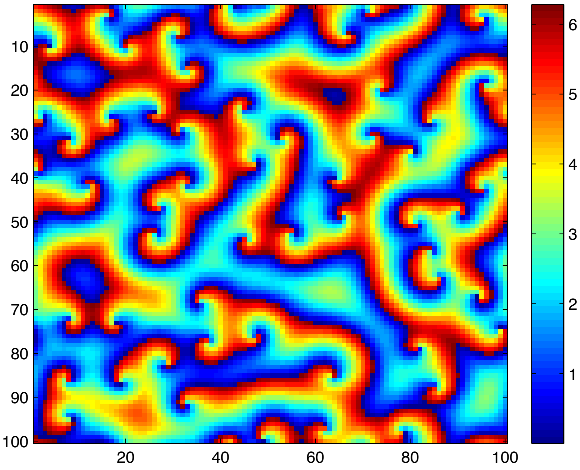


Figure: Spiral waves.

Recapitulation

- iPRC (infinitesimal PRC or linear response function) can be derived using Winfree, Kuramoto and Malkin approach.
- Knowing the *iPRC* one can create phase models of coupled oscillators
- Phase models can be further reduced to phase deviation equations, with interaction functions being the coupling profiles weighted by the iPRC over the whole period.
- Phase models operate on a torus, where each torus knot corresponds to a frequency locked solution.
- Chains an grids of oscillators, even when the coupling is synchronizing and the synchronous solution is stable, can have other interesting solutions like rotating waves and spiral waves.