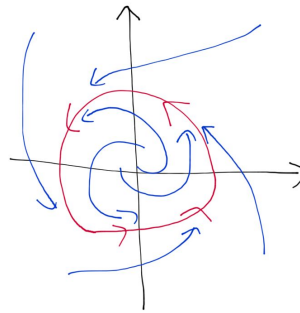


1. Synchronization Phenomena

In nature synchronization happens all the time. In mechanical systems, in biological systems, in epidemiology, basically everywhere. When we talk about synchronization we usually assume that some sort of cyclical dynamics is going on in the units which then synchronize. This means, we need to understand first that usually at the basis of synchronization we are talking about units that if left along perform periodic motion. We have already discussed that this can happen in the form of limit cycles in two-dimensional activator inhibitor systems for example. Now let's assume that we have such an isolated system that performs dynamics in form of a limit cycle in its own state space.

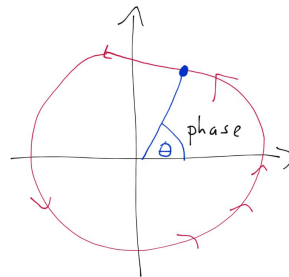


Now effectively we can describe the system by a phase θ the position on its limit cycle. Clearly this phase variable θ is periodic

$$\theta(t) = \theta(t + T).$$

and this phase may have different phase velocity at different times along its period

$$\dot{\theta}(t) = \omega(t)$$



In the simplest form, we have a system that has a constant phase velocity

$$\dot{\theta} = \omega$$

1.1. Phase coupled oscillators

Now, clearly if we have many such oscillators, labeled n , each one can have its own internal ω_n and if the oscillators are uncoupled then each one is going to happily move around in a circle at its own velocity

$$\begin{aligned}\dot{\theta}_n &= \omega_n \\ \theta(t) &= \omega_n t \pmod{2\pi}\end{aligned}$$

From now on, we are not going to write this mod 2π any more and assume that this is always the case in these systems. Now the question is, how can these oscillators synchronize? Clearly they need to be coupling in some way, to one oscillator can change the phase of another oscillator, or increase or decrease its speed. To generally we would have a situation

$$\dot{\theta}_n = \omega_n + f_n(\theta_1, \dots, \theta_{n-1}, \theta_{n+1}, \dots, \theta_N)$$

if we have a total of N oscillators. The key question is, what kind of couplings f_n can induce synchrony, and what do we mean by synchrony anyway?

1.1.1. Possible flavors of synchronization

What do we really mean by synchronization? In its simplest form, a multi-oscillator system will evolve into a system in which every unit does exactly the same, i.e.

$$\theta_n(t) = \theta_m(t)$$

for all n, m . This also implies that

$$\dot{\theta}_n = \dot{\theta}_m$$

which means that in the synchronous state, the angular velocities are also identical.

We can, however, also encounter situations in which only the velocities are the same but the individual pairs of oscillators possess a phase difference that is constant

$$\theta_n(t) = \theta_m(t) + \alpha_{nm}$$

We will see examples of both.

1.1.2. Two phase coupled oscillators

Let's look at a system of two oscillators that influence each other

$$\begin{aligned}\dot{\theta}_1 &= \omega_1 + f_1(\theta_1, \theta_2) \\ \dot{\theta}_2 &= \omega_2 + f_2(\theta_1, \theta_2)\end{aligned}$$

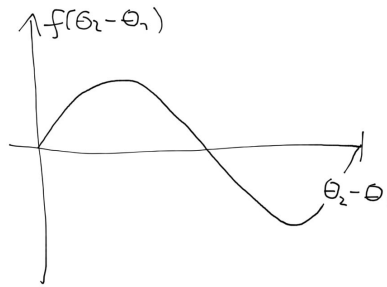
Let's simplify this a bit. Let's assume that the coupling functions are the same so

$$\begin{aligned}\dot{\theta}_1 &= \omega_1 + f(\theta_1, \theta_2) \\ \dot{\theta}_2 &= \omega_2 + f(\theta_2, \theta_1)\end{aligned}$$

Another assumption is that the coupling depends on the phase difference, so

$$\begin{aligned}\dot{\theta}_1 &= \omega_1 + f(\theta_2 - \theta_1) \\ \dot{\theta}_2 &= \omega_2 + f(\theta_1 - \theta_2)\end{aligned}$$

and because the phases are periodic we would like to use a function f that is periodic, too. Now let's assume that $\theta_2(t) > \theta_1(t)$, which means that the second oscillator is ahead. If the function $f(\theta_2 - \theta_1)$ is positive for a positive difference then this will accelerate the first oscillator and decelerate the second, moving them closer.



So let's assume

$$f(x) = \frac{K}{2} \sin(x)$$

so

$$\begin{aligned}\dot{\theta}_1 &= \omega_1 + \frac{K}{2} \sin(\theta_2 - \theta_1) \\ \dot{\theta}_2 &= \omega_2 + \frac{K}{2} \sin(\theta_1 - \theta_2)\end{aligned}$$

where $K > 0$. This is a simple version of the so called Kuramoto model. Let's see what happens to the phase difference

$$x = \theta_2 - \theta_1$$

$$\begin{aligned}\dot{x} &= \mu + K/2 [\sin(-x) - \sin(x)] \\ &= \delta\omega - K \sin x\end{aligned}$$

where $\delta\omega = \omega_2 - \omega_1$. This dynamical system has a solution on the interval $x \in [0, 2\pi]$ if we can find a solution to

$$\sin x = \frac{\delta\omega}{K}$$

1.1.2.1. $\omega_1 = \omega_2$

Let's first consider this. In this case we have solutions

$$x_1^* = 0 \quad \text{and} \quad x_2^* = \pi$$

so that means the oscillators are in phase or anti-phase. Because the derivative of $-\sin x$ is negative at the first fixed point, this one is stable the other is unstable. This means that for any value of the coupling K (arbitrarily small) the oscillators will go into phase synchrony,

$$\theta_1(t) = \theta_2(t)$$

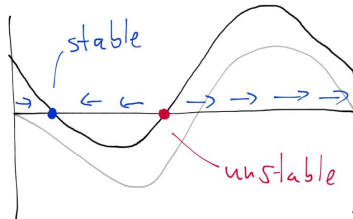
and they will move around in their natural identical frequency $\omega_1 = \omega_2$. So, two identical oscillators will synchronize in the Kuramoto model for any coupling strength K

1.1.2.2. $\omega_1 \neq \omega_2$

This is of course the more interesting case. Let's assume that $\omega_2 > \omega_1$. Looking at the above equation

$$\sin x = \frac{\delta\omega}{K}$$

we see that this has only solutions if $|\delta\omega/K| \leq 1$. so if either the coupling is sufficiently strong, or the difference in natural frequencies sufficiently small. Let's assume that we are in this regime, the the above equation has solutions where the constant $\delta\omega/K$ intersects the curve $f(x) = \sin(x)$



That happens at two points. One is α the other is $\pi - \alpha$ and

$$\alpha = \sin^{-1} \delta\omega/K$$

That means, the system will evolve into a state

$$\theta_2(t) = \theta_1(t) + \alpha$$

that means the faster oscillator (referring to its natural frequency) is leading the other one by a constant phase. What are their frequencies?

$$\begin{aligned}\dot{\theta}_1 &= \omega_1 + \frac{K}{2} \sin \alpha \\ \dot{\theta}_2 &= \omega_2 - \frac{K}{2} \sin \alpha\end{aligned}$$

which is

$$\begin{aligned}\dot{\theta}_1 &= \omega_1 + \frac{\omega_2 - \omega_1}{2} = \frac{1}{2}(\omega_1 + \omega_2) = \bar{\omega} \\ \dot{\theta}_2 &= \omega_2 - \frac{\omega_2 - \omega_1}{2} = \frac{1}{2}(\omega_1 + \omega_2) = \bar{\omega}\end{aligned}$$

so they both compromise and move around at the mean frequency.

We can look at the problem this way. Given two oscillators with ω_1 and ω_2 we need at least a coupling strength

$$K > K_c = \omega_2 - \omega_1$$

such that these two oscillators go into sync.

1.1.3. Many phase coupled oscillators

In most applications we have many oscillators that are coupled, each one interacting with some or all the other ones at a different strength. We can generalize the above approach directly to many oscillators labeled n , each one with its own internal frequency ω_n in which case we would have a

$$\dot{\theta}_n = \omega_n + \frac{1}{N} \sum_m K_{nm} \sin(\theta_m - \theta_n)$$

The entire complexity of what this system can do is hidden in the coupling K_{nm} . And depending on this coupling, lots of different things can happen. Before we discuss these we need to develop ways to measure synchrony in oscillator systems.

1.1.3.1. Measuring the degree of synchrony

The common way of doing this is based on tricks borrowed from complex variables. A complex variable is essentially a 2D vector that has a length r and a phase θ and can be expressed as

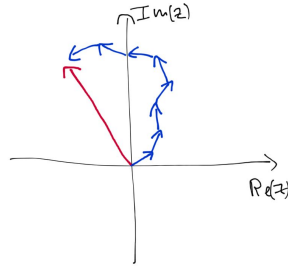
$$z = r e^{i\theta} = x + iy$$

Sum's of complex variables are just sums of little vectors:

$$z = \sum_{i=1}^N z_i$$

The resulting sum, also has a length and a total phase

$$Z = \sigma e^{i\psi}$$



Now for our system we can assume that every oscillator has a fixed length $r = 1/N$ and its phase continuously changes over time according to $\theta_n(t)$. And we can write

$$\sigma(t)e^{i\Psi(t)} = \frac{1}{N} \sum_{n=1}^N e^{i\theta_n(t)} = \langle e^{i\theta_n(t)} \rangle$$

If the system evolves into a state in which $\theta_n(t) = \Omega t + \alpha_n$ then

$$\sigma e^{i\Psi(t)} = e^{i\Omega t} \langle e^{i\alpha_n} \rangle$$

which means that

$$\Psi(t) = \Omega t + \Psi_0$$

is the overall movement of all oscillators and Ω their synchronized frequency. In this case the prefactor is

$$\sigma = \left| \langle e^{i\alpha_n} \rangle \right|$$

This means that the constant σ is a measure for the phase coherence in the synchronized state.

1.1.3.2. All to all coupling of identical oscillators

Now let's assume that all N oscillators influence each other by the same amount and have the same frequency

$$\dot{\theta}_n = \omega_0 + \frac{K}{N} \sum_m \sin(\theta_m - \theta_n)$$

Now let's assume that we find a solution in which

$$\theta_n(t) = \omega t + \alpha_n$$

That means that

$$0 = \delta\omega + \frac{K}{N} \sum_m \sin(\alpha_m - \alpha_n)$$

We can see that $\omega = \omega_0$ and $\alpha_n = \alpha_m$ for all oscillators is a solution to the dynamical system. Is it stable? It turns out that this is indeed a stable solution for all initial conditions as long as the oscillators have identical natural frequencies.

1.1.3.3. Some results on more general cases

If we have identical oscillators but variability in the coupling strength K_{nm} one can show that as long as the coupling is symmetric

$$K_{nm} = K_{mn}$$

the dynamics will also always converge to a synchronous state. However, in this case the oscillators have constant phase deviations. Note that the above equation does not imply that all the couplings are the same, only pairwise they are. This means that there can be some spatial heterogeneity, for example the oscillators can be coupled in a network topology. And indeed, in scenarios like that, oscillators synchronize but with a phase distribution.

There are a bunch of more results for the Kuramoto model but they go too deep to discuss them here. Essentially, if one has a distribution of natural frequencies one can expect that synchronization breaks down if the coupling is too weak. If all oscillators are identical then they all synchronize but with a potential distribution of phase differences.

1.2. Pulse-coupled oscillators

The above model is phenomenological and assumes that the force by which individual oscillators influence one another is a smooth function of their phase difference which is largest when a phase-difference of a pair of oscillators is $\pi/2$. In many natural systems oscillators only interact in small periods of time and in form of short pulses. These oscillators are called pulse-coupled oscillators. For example the fire-flies only emit a light pulse which is perceived by the other flies. Another example are neurons which integrate their inputs and then generate an action-potential which is a short pulse that is transported via the neuron's axon and synapses to the receiving neurons which then integrate this input to generate a spike themselves. The simplest model for a neuron is the integrate and fire neuron where the quantity of interest is a membrane potential that follows a dynamics given by

$$\dot{x} = S_0 - \gamma x$$

where S_0 is a constant input and γ models the decay of the membrane potential, which is why these neurons are called leaky integrate and fire neurons. The clue is now if the membrane potential reaches a threshold $x_c = 1$ the neuron fires an action potential and the membrane potential is immediately reset to the resting potential of $x = 0$. If we start the membrane potential at $t = 0$ at $x(0) = 0$ the above dynamical system can be solved

$$x(t) = \frac{S_0}{\gamma}(1 - e^{-\gamma t})$$

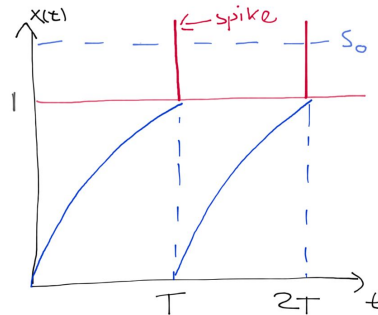
as long as $x(t) < 1$ if $S_0/\gamma > 0$ this solution will hit the critical value $x_c = 1$ when

$$1 = \frac{S_0}{\gamma}(1 - e^{-\gamma T})$$

so at time

$$T = \frac{1}{\gamma} \log \left(\frac{S_0}{S_0 - \gamma} \right)$$

at which time the membrane is reset to zero and the system emits a pulse. Such an oscillator left alone will emit pulses continuously at a period T . The curve of the membrane potential looks like this:



and we can write it

$$x(t) = \frac{1 - e^{-\gamma t}}{1 - e^{-\gamma T}}$$

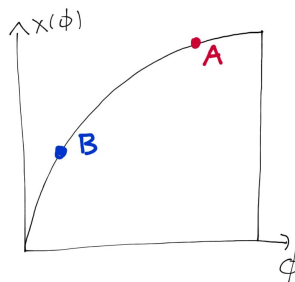
We can express time in units T in which the equation becomes

$$x(\theta) = \frac{1 - e^{-\gamma \theta}}{1 - e^{-\gamma}}$$

Now we have to specify what an oscillator's pulse does to another oscillator. Let's first discuss a system of two such oscillators.

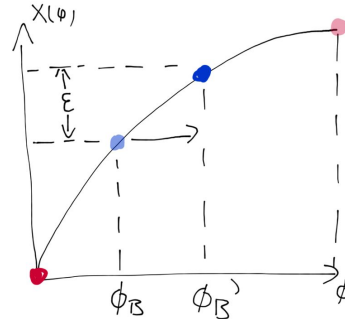
1.2.1. Two pulse-coupled oscillators

Let's look at two oscillators A and B each one being in some phase ϕ . So let's call these states ϕ_A and ϕ_B . Let's assume that A is closer to its firing time, so $\phi_A > \phi_B$. We can visualize this by drawing dots on the curve in the x, ϕ plane:



If A reaches the firing threshold it's phase is reset to 0 and the membrane potential of B gets boosted by a value $\epsilon > 0$. This boost in membrane potential x is equivalent to an advance in the phase of B

$$\phi_B \rightarrow \phi'_B.$$



How do we compute the new phase ϕ'_B ? We have

$$x = f(\phi) = \frac{1 - e^{-\gamma\phi}}{1 - e^{-\gamma}}.$$

so the new phase is

$$\phi'_B = g(x + \epsilon)$$

where the function $g(x)$ is the inverse of $f(\phi)$. We can see that under some very general assumptions this kind of system can synchronize oscillators of the pulse of a firing oscillator advances the other oscillator sufficiently. However that second oscillator when it fires will advance the first and in principle they could be racing one another forever. This is why the function $f(\phi)$ has to be concave down. So that the first oscillator advances the second one more than vice versa. One the both fire together, they will stay in synchrony.

1.2.2. Many pulse-coupled oscillators

Now let's look at N such identical oscillators that are all coupled to one-another. One can show that if the oscillators are identical then they will eventually all synchronize. An intuitive explanation is that they can never desynchronize once they are in synchrony and that eventually clusters of synchronized oscillators emerge that will continue to form larger clusters.

1.3. Diffusively coupled oscillators and patterns

Let's get back to phase coupled oscillators and imagine that each oscillator is on a site in a 1D lattice: Recall that the dynamic equation is given by

$$\dot{\theta}_n = \omega_n + \frac{1}{N} \sum K_{nm} \sin(\theta_m - \theta_n).$$

Now let's assume that each oscillator only interacts with its neighbors and that these interactions are all of the same strength, in this case we have

$$\theta_n = \omega_n + \frac{K}{2} \sum_{m \in G_n} \sin(\theta_m - \theta_n)$$

where G_n is the set of 2 neighbors of n . Explicitly we can write

$$\dot{\theta}_n = \omega_n + K \left[\frac{\sin(\theta_{n+1} - \theta_n) + \sin(\theta_{n-1} - \theta_n)}{2} \right]$$

Now let's assume we have very many of those guys and that as we go from grid to the next grid the phase doesn't change so much. In this case we can use the series expansion of the sin

$$\sin(x) = x - \frac{1}{3}x^3 \dots$$

so the equation is approximately governed by

$$\dot{\theta}_n = \omega_n + K \left[\frac{\theta_{n+1} - 2\theta_n + \theta_{n-1}}{2} \right]$$

If we now identify n with a spatial coordinate $x_n = n\Delta x$ and let $K = D/\Delta x$ this becomes

$$\partial_t \theta(x, t) = \omega(x) + D \partial_x^2 \theta(x, t)$$

where we interpret $\theta(x, t)$ as a continuous array of oscillators that are now diffusively coupled. This means that the phase "diffuses" to the neighboring locations. The function $\omega(x)$ determines the local natural frequency density of oscillators.

This system also develops synchrony and the spatial pattern is determined by the strength of diffusion. Depending on the variability of $\omega(x)$ we can see that the oscillator field converges to oscillatory behavior with a uniform frequency but with a phase decoherence, just like in the original phase coupled system.

1.4. Coupled Limit cycle systems

Let's now investigate a system that helped us motivate the phase model as well as the pulse coupled system. We discussed that systems, e.g. activator inhibitor systems, that naturally yield limit cycle behavior are candidates for being modelled just by focusing on the phase. Let's see what happens if we model a full activator inhibitor system in the sense that we explicitly model each oscillator by

$$\begin{aligned} \dot{u} &= f(u, w) \\ \dot{w} &= g(u, w) \end{aligned}$$

where the variables u, w are the state variables of one oscillator. A simple system that generates limit cycles is given by

$$\begin{aligned} \dot{\theta} &= \Omega \\ \dot{r} &= \lambda r(1 - r) \end{aligned}$$

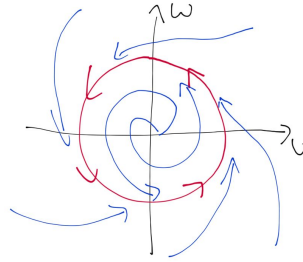
where $r = \sqrt{u^2 + v^2}$ and $\theta = \tan^{-1} w/u$, or $u = r \cos \theta$ and $w = r \sin \theta$. We can relate both coordinate systems by

$$\begin{aligned}\dot{u} &= \dot{r} \cos \theta - r \dot{\theta} \sin \theta \\ \dot{w} &= \dot{r} \sin \theta + r \dot{\theta} \cos \theta\end{aligned}$$

so

$$\begin{aligned}\dot{u} &= \lambda(1 - \sqrt{u^2 + w^2})u - \Omega w \\ \dot{w} &= \lambda(1 - \sqrt{u^2 + w^2})w + \Omega u\end{aligned}$$

This means that u is the activator and w is the inhibitor and trajectories go to a limit cycle $\dot{\theta} = \Omega$ and $r = 1$.



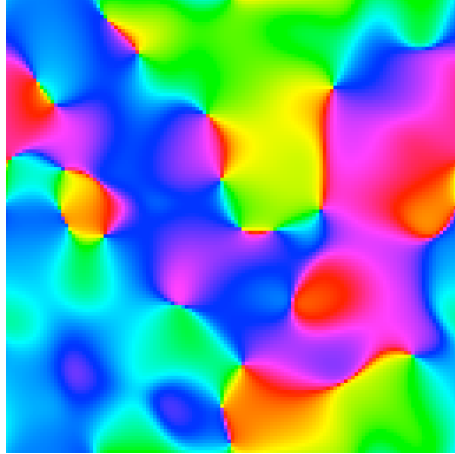
Now lets assume that both, u and w are concentrations of a chemical or a species on some site n . and both concentrations and diffusively change the concentration on neighboring sites so

$$\begin{aligned}\dot{u}_n &= \lambda(1 - \sqrt{u_n^2 + w_n^2})u_n - \Omega w_n + \frac{D_u}{2} [u_{n+1} + u_{n-1} - 2u_n] \\ \dot{w}_n &= \lambda(1 - \sqrt{u_n^2 + w_n^2})w_n + \Omega u_n + \frac{D_w}{2} [w_{n+1} + w_{n-1} - 2w_n]\end{aligned}$$

which means that if the concentration w_{n+1} and w_n are very different the last term is going to make them closer. Effectively coupling the dynamics at each site. If we now consider the spatially continuous model this reads

$$\begin{aligned}\partial_t \dot{u}(x, t) &= \lambda(1 - \sqrt{u^2(x, t) + w^2(x, t)})u(x, t) - \Omega w(x, t) + D_u \partial_x^2 u(x, t) \\ \partial_t \dot{w}(x, t) &= \lambda(1 - \sqrt{u^2(x, t) + w^2(x, t)})w(x, t) + \Omega u(x, t) + D_w \partial_x^2 w(x, t)\end{aligned}$$

Patterns generated by this model also exhibit synchronization but what interesting is the emergence of locations where the phase θ exhibits a singularity. These are pinwheels. Locations in the fields where oscillators can't decide what to do. In the long time limit these singularities can annihilate by moving towards one another. This only can happen if two of these singularities have the opposite charge.

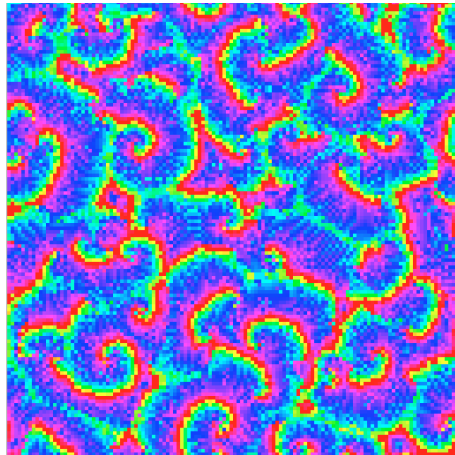


1.5. Spatially distributed pulse coupled oscillators

The above system, that produces these beautiful pinwheel patterns motivates us to ask what kind of patterns can emerge in pulse coupled oscillators in which each oscillator is governed by the equation

$$\dot{x} = S_0 - \gamma x$$

when below the threshold $x_{th} = 1$ and in the regime $S_0/\gamma > 1$. In this regime every oscillator fires at a constant period. Now let's assume that on a lattice each oscillator receives input only from its metric neighbors in the lattice. This system generates non-equilibrium patterns that consists either of target or spiral waves. Here's an example:



Why is this happening. The spirals are rotating regions of repetitive activation. This happens because in the pulse coupled scenario, even though the coupling is symmetric between oscillators in terms of strength, the pulse occur only in one direction which introduces a temporal asymmetry. These spiral patterns are very generic in excitable systems in which individual units can be pushed above threshold and become active and

feed-forward activation throughout the system. We will talk more about these patterns in the next chapter.