Synchronization and Phase Oscillators

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Synchronization occurs often in biological systems. For example, neurons of the region of the hypothalamus called the suprachiasmatic nucleus exhibit circadian oscillations in electrical activity. These rhythms are synchronized, so that the peak of activity occurs simultaneously in all or most of the neurons.

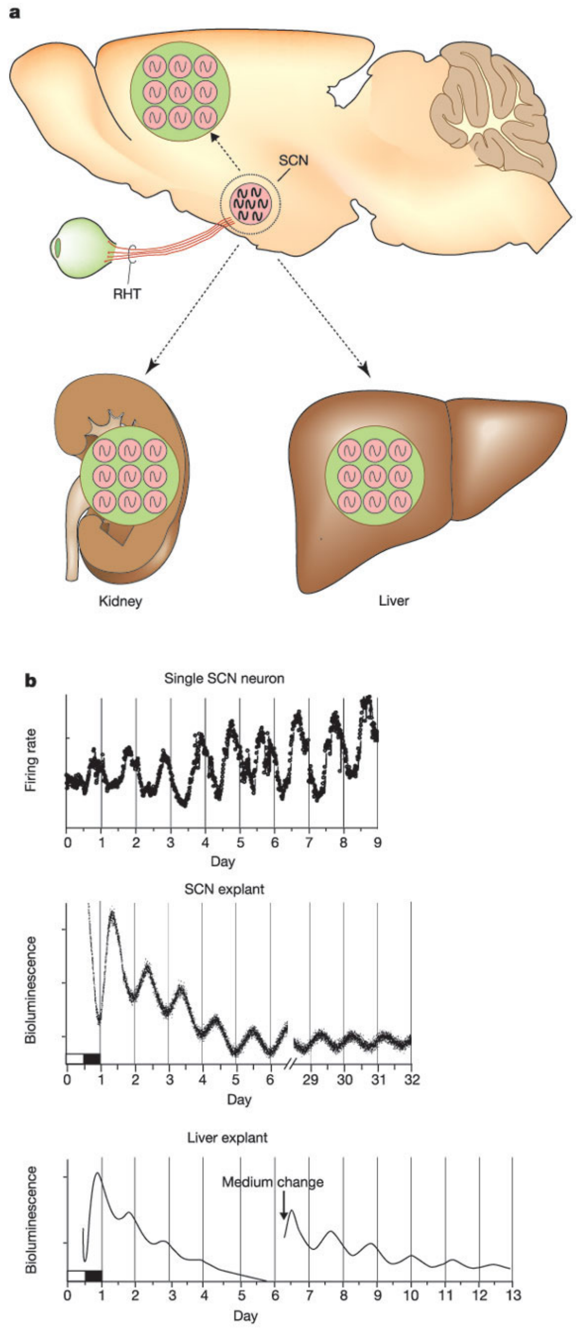


Figure 1: From Repper and Weaver, Nature, 418:935, 2002

As another physiological example, the β-cells within a pancreatic islet all burst in synchrony, resulting in coordinated insulin release from all the β-cells in an islet.

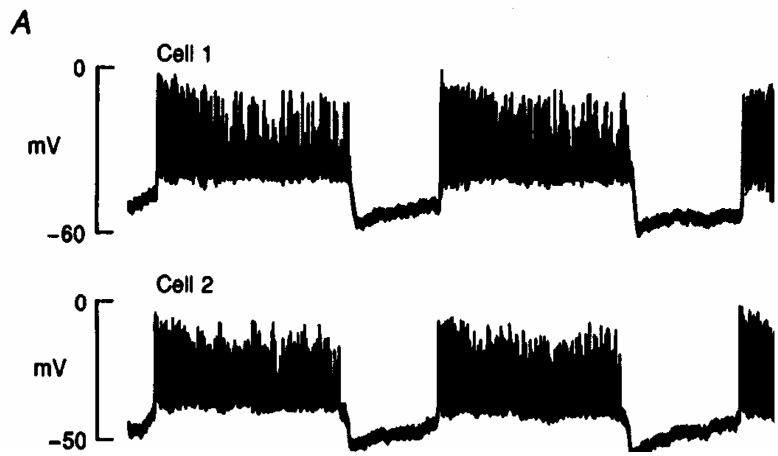
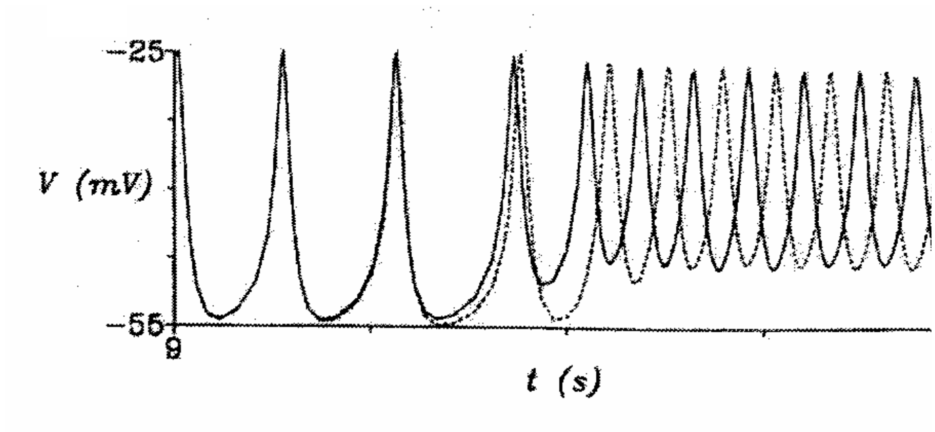


Figure 2: From Valdeolmillos et al., J. Physiol., 493:9, 1996

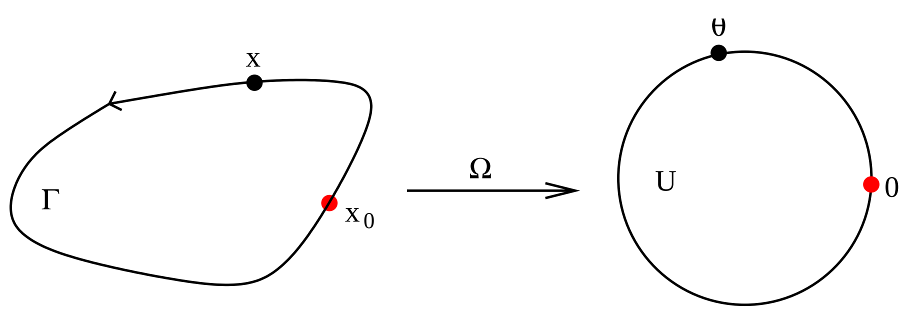
In some cases, the oscillators are in antiphase with one another. That is, their phases differ by 180^o. One example of this is when two model neurons are electrically coupled and the coupling strength is weak. This electrical coupling occurs through gap junctions.



-25
V (mV)
-55
9
t (s)

Phase Oscillators

The biological mechanisms through which oscillators are coupled and can become synchronized differ from situation to situation. However, mathematical descriptions of coupled oscillators can reveal some general principles. This area of mathematics is quite well developed, largely due to the efforts of **Bard Ermentrout**, **Nancy Kopell**, **Arthur Winfree**, **Yoshiki Kuramoto**, and **Eugene Izhikevich**. We will just touch on some of this theory, beginning with the description of a phase oscillator.



Let Γ denote a stable limit cycle for some system of differential equations. Then there exists a continuous function Ω that maps each point on Γ to a point on the unit circle U. That is, one can pick a point on Γ, call it x_0, and map it to $\theta = 0$. Then every other point on Γ is mapped to another point θ on U in a continuous fashion.

The dynamics of the original stable limit cycle are replicated by the phase oscillator

$$\frac{d\theta}{dt} = \omega \tag{1}$$

θ is the **phase** relative to x_0 and ω is the **phase speed**. The period of the limit cycle oscillation, and the period of one complete loop around the unit circle U, is then $T = \frac{2\pi}{\omega}$.

Entrainment of Fireflies

The following example comes from Strogatz (1994). In one species of southeast Asian fireflies the males gather in trees at night and begin flashing. Different flies flash at different frequencies when in isolation, and if they did this as a group then flashing in the trees would be continuous. However, periodic flashing is what is actually observed. This indicates that the fireflies synchronize their activity. This observation motivated experiments in the 1970's in which a flashlight was used to entrain flies to the flashing period of the flashlight.

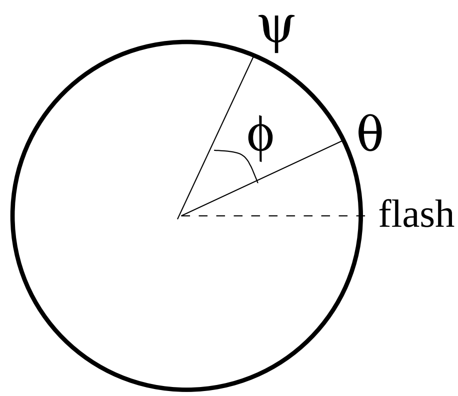
Represent the flashing of the flashlight as a uniform phase oscillator:

$$\dot{\psi} = \Omega \tag{2}$$

where Ω is a constant. Represent the firefly flashing as a nonuniform phase oscillator:

$$\dot{\theta} = \omega + A \sin(\psi - \theta) \tag{3}$$

where ω is the natural frequency of the firefly and A is the **coupling strength** (assume that $A > 0$). If $\psi > \theta$, then $A \sin(\psi - \theta) > 0$ and the firefly speeds up, trying to catch up to the flashlight.



Define the **phase difference** as $\phi \equiv \psi - \theta$. Then

$$\begin{aligned} \dot{\phi} &= \dot{\psi} - \dot{\theta} && (4) \\ &= \Omega - \omega - A \sin \phi \quad . && (5) \end{aligned}$$

The 3 parameters (Ω, ω, and A) can be replaced by a single parameter μ by **non-dimensionalizing** the system:

t has units of seconds

Ω, ω, and A have units of radians per second.

Define the dimensionless variables $\tau \equiv At$ and $\mu \equiv \frac{\Omega-\omega}{A}$. Then

$$\begin{aligned} \frac{d\phi}{dt} &= \frac{d\phi}{d\tau}\frac{d\tau}{dt} && (6) \\ &= \frac{d\phi}{d\tau} \cdot A && (7) \end{aligned}$$

and

$$\Omega - \omega - A\sin\phi = A\mu - A\sin\phi \ \ . \qquad (8)$$

Combining, we get the phase equation in **dimensionless form**:

$$\frac{d\phi}{d\tau} = \mu - \sin\phi \qquad (9)$$

Parameter Exploration

In parametric systems it is typical to explore parameter space to get a better understanding of the range of behaviors that the system of equations can exhibit. In our dimensionless equation the parameter space is one-dimensional (unlike the 3-dimensional space of the original dimensional phase equation).

Case 1: $\mu = 0$

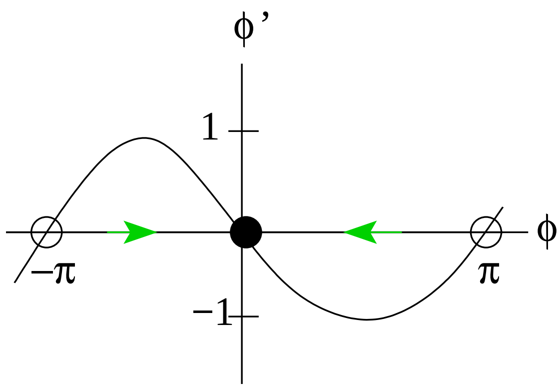
The phase difference equation is

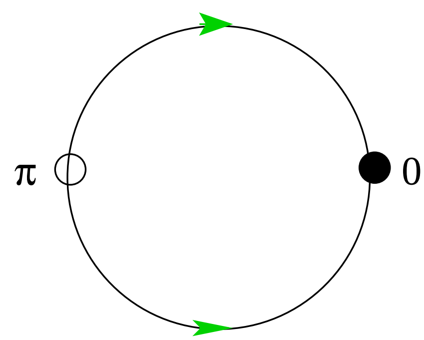
$$\frac{d\phi}{d\tau} = -\sin\phi \tag{10}$$

Steady state: $\phi^* = 0$ (and mutliples of 2π).

Since $\phi = 0$ corresponds to $\theta = \psi$, the firefly synchronizes with the flashlight. That is, it is **entrained** and the **phase difference** is 0. So even though the phase of the firefly may initially be different from that of the flashlight, it will eventually synch up.

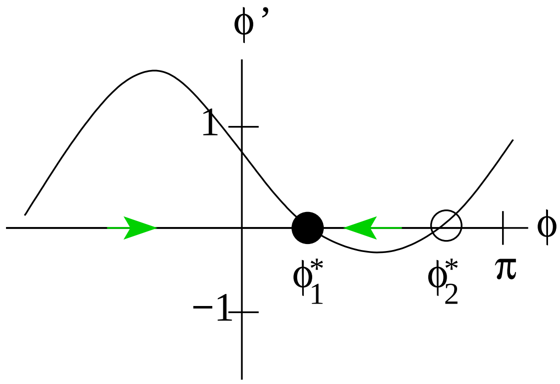
We can view the phase portraits of the phase difference on either the number line or the circle diagram.

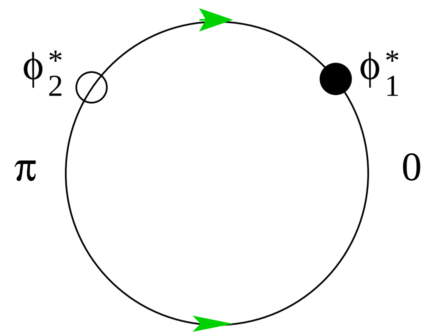




Case 2: $0 < \mu < 1$

When μ is increased beyond 0 it translates the velocity curve upward. The new stable steady state ϕ_1^* is at a non-zero values, so the firefly and flashlight will be phase locked but not synchronized.

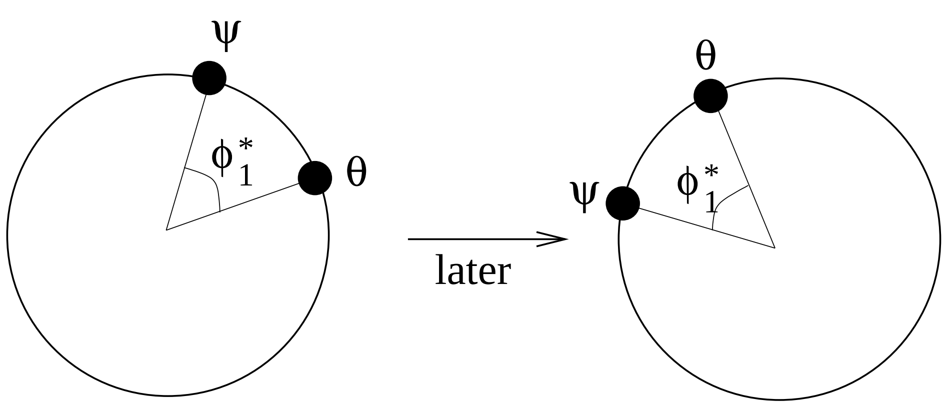




The two steady states (stable and unstable) satisfy

$$\phi^* = \arcsin(\mu) \tag{11}$$

and the smaller of the two solutions is the stable one. In terms of the phase circle diagram (not the phase difference circle diagram):

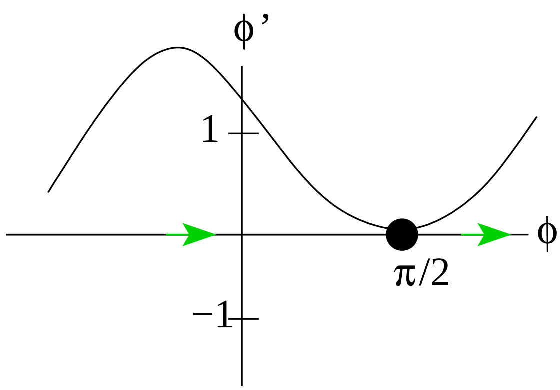


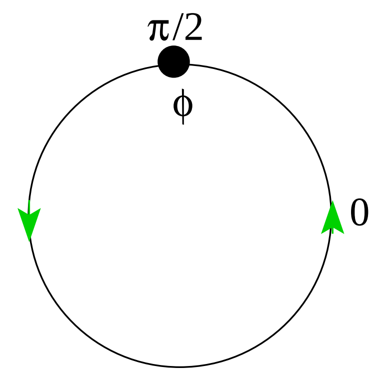
Case 3: $\mu = 1$

In this case there is a single steady state,

$$\phi^* = \arcsin(1) = \frac{\pi}{2} \tag{12}$$

and the velocity curve is tangent to the ϕ-axis. The system has gone through a saddle node bifurcation.

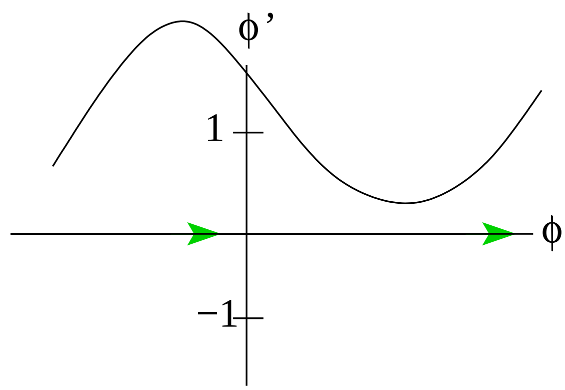


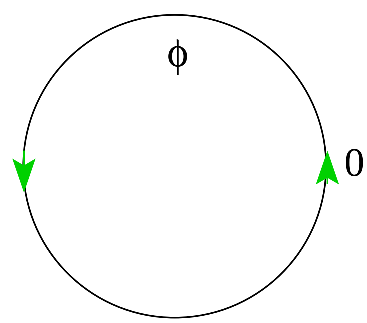


The steady state is **half stable** since it attracts on one side and repels on the other.

Case 4: $\mu > 1$

Now the velocity curve never intersects the ϕ-axis, so the phase difference continues to change over time. This is called phase drift. In this case, the flashlight fails to entrain the firefly.





If $\mu < 0$ the cases are similar to these, except that the firefly leads the flashlight ($\phi^* < 0$). We can then give the entrainment window, the range of μ over which the system is entrained. In terms of the dimensionless parameter μ this is:

While in terms of the original parameters (dimensioned) it is:

$\boxed{\text{Isochrons}}$

Previously we defined a phase for each point on a limit cycle. If the limit cycle is stable, then we can extend this idea to all points within the basin of attraction of the limit cycle. We do this through the use of isochrons. An isochron is a set of points that all have the same **asymptotic phase**. That is, all points on an isochron will approach the same phase on the limit cycle as $t \to \infty$. There will be an isochron for each phase value, and thus each point in the basin of attraction will lie on an isochron. In this way, we define the phase of each point in the basin according to which isochron it lies on.

Example (Winfree, 2001)

Consider the polar system of equations:

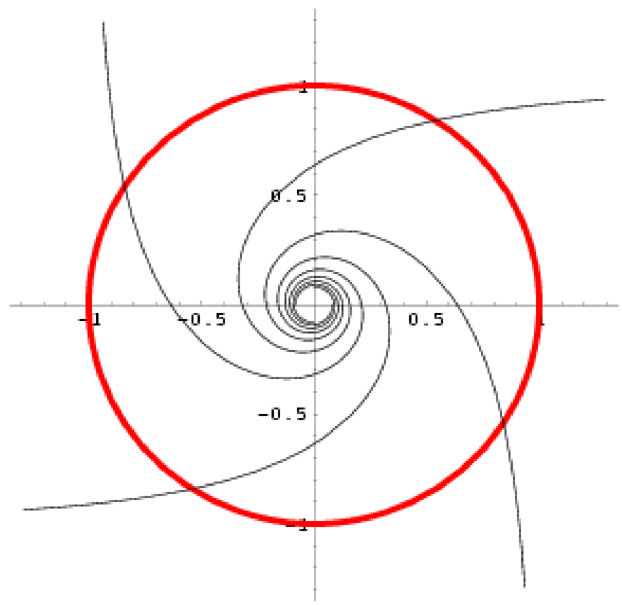
$$\frac{dr}{dt} = (1-r)r^2 \tag{13}$$

$$\frac{d\phi}{dt} = r \quad . \tag{14}$$

There is a stable solution of $r = 1$, which is a circular limit cycle. It can be shown that the isochrons are:

$$\phi = \theta + \frac{1}{r} - 1 \tag{15}$$

where θ is the phase associated with the isochron. Four isochrons and the limit cycle are shown below.



1
0.5
-1
-0.5
0.5
1
-0.5
-1

Isochrons are useful for understanding phase transition curves and phase response curves. Suppose that a phase point moving along a limit cycle is given an instantaneous perturbation, knocking it off the limit cycle but not out of the basin of attraction of the limit cycle. Then the point will land on an isochron, which tells us the phase of the point once it comes back to the limit cycle. The phase transition curve (PTC) plots the new phase of the point as a function of the stimulus phase. The phase response curve (PRC) plots the phase difference as a function of the stimulus phase.

Example

Consider a planar system with the following circular stable limit cycle and radial isochrons:

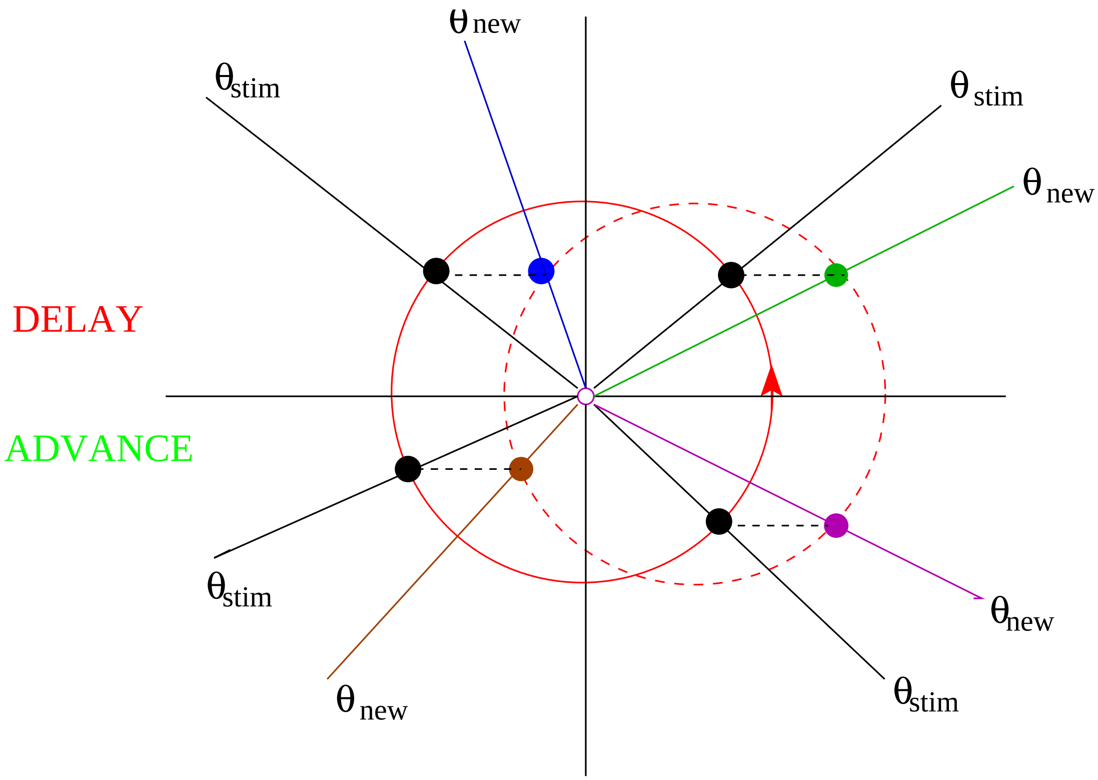


Figure 4: Limit cycle, isochrons, and image for weak perturbations.

The solid circle is the limit cycle. The dashed circle is the result of a small horizontal perturbation applied to any point on the limit cycle. Consider the case illustrated with a black horizontal line. The isochron intersecting the solid circle at point a defines the original phase, while the isochron intersecting the dashed circle at point b defines the new phase. The phase transition curve for this example is shown below.

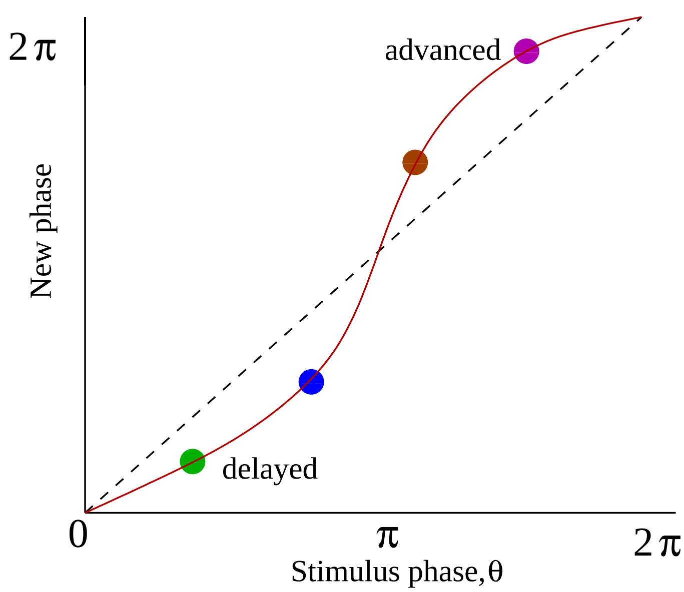


Figure 5: Type 1 Phase Transition Curve (PTC) for weak perturbations

For values of θ at which the PTC is below the dashed 45^o line the phase is **delayed** by the perturbation, while for values at which the PTC is above the line the phase is **advanced**.

The **phase response curve (PRC)** is formed by computing the difference between the dashed line and the PTC at each θ, as shown below.

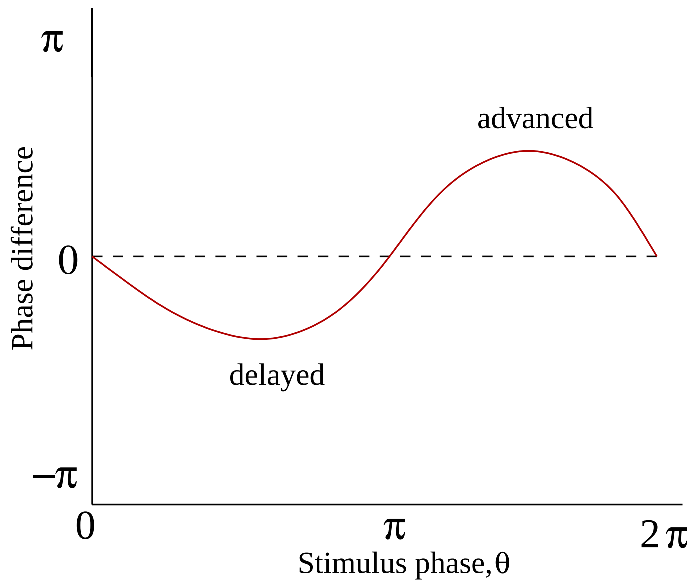


Figure 6: Type 1 Phase Response Curve (PRC) for weak perturbations

In this last example the perturbations were weak, and this is called Type 1 phase resetting. For large perturbations the situation is quite different:

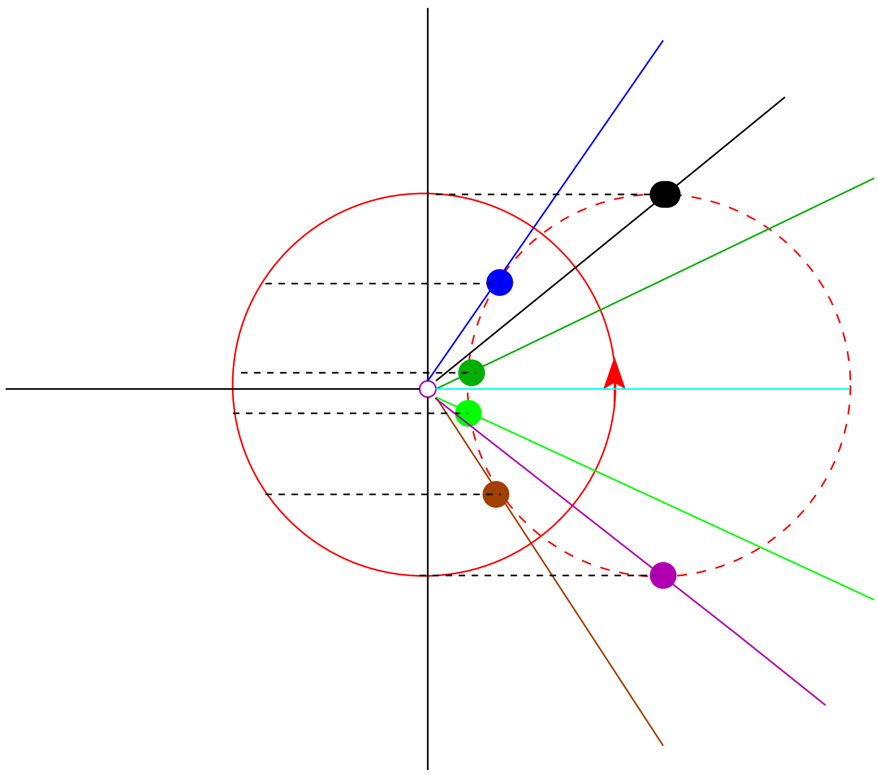


Figure 7: Limit cycle, isochrons, and image for strong perturbations.

When a perturbation is applied at $\theta \in (0, \pi)$ the response is delayed, just as before. However, while the new phase was previously a monotonic increasing function of the old phase, it now first increases but then decreases on the interval $\theta \in (0, \pi)$. The blue isochron corresponds to the maximal new phase value. At $\theta = \pi$ the new phase is 0 (light blue isochron) and for larger θ becomes negative. The new phase grows in magnitude initially, but then at some point (brown isochron) begins to decline toward 0. This is called a Type 0 PTC.

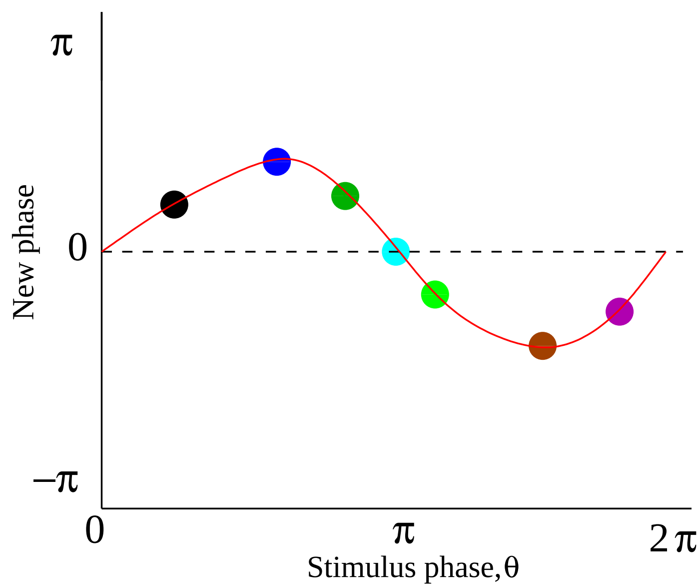


Figure 8: Type 0 PTC for strong perturbations

If one restricts the phase to the interval $[0, 2\pi)$, then the Type 0 PTC can be represented as follows:

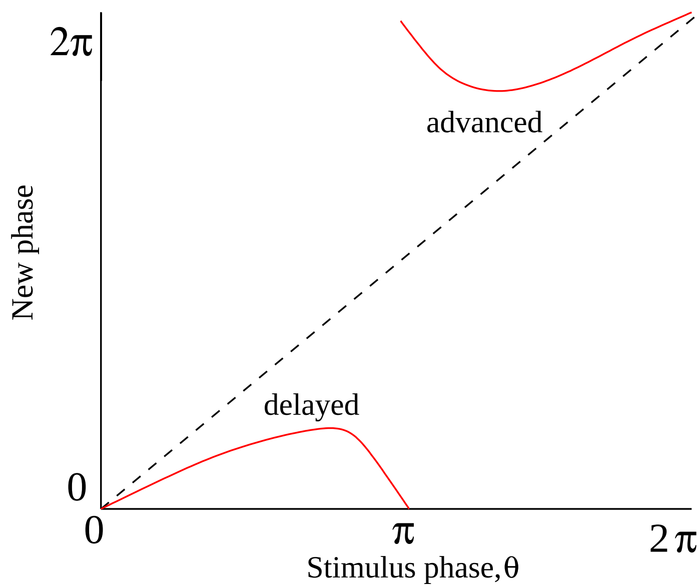


Figure 9: Alternate form of Type 0 PTC

What does the Type 0 PRC look like?

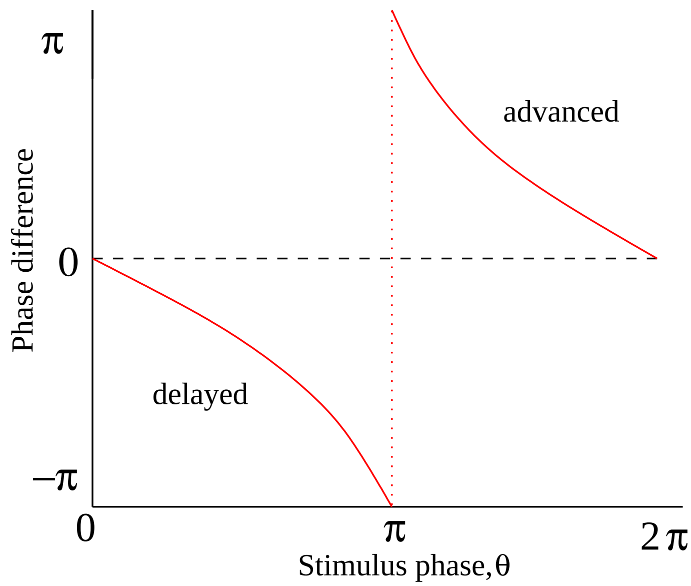


Figure 10: Type 0 PRC for strong perturbations

The type 1 and type 0 PRCs are fundamentally different. In the first case the curve is continuous, while in the second case it has a discontinuity.

Phase transition and response curves are important both in understanding synchronization properties of weakly coupled oscillators and for understanding something about an actual biological oscillator. In the latter case, it is often possible to determine PTCs and PRCs experimentally. These give insight into how sensitive the system is to perturbations, and place constraints on mathematical models of the system (i.e., the model PRC should look similar to the experimental one).

Synchronization of Weakly Coupled Oscillators

Here we see how the PRC can help in the analysis of two endogenous oscillators that are mutually coupled. The mathematical theory is most developed for the case where coupling is weak.

Consider the two coupled oscillators

$$\begin{aligned}\frac{d\vec{x}_1}{dt} &= f_1(\vec{x}_1) + \vec{g}_{12}(\vec{x}_1, \vec{x}_2) \\ \frac{d\vec{x}_2}{dt} &= f_2(\vec{x}_2) + \vec{g}_{21}(\vec{x}_1, \vec{x}_2) \qquad (16)\end{aligned}$$

where f is the oscillator's velocity function and g is the coupling function. Also, $\vec{x} \in \Re^n$ where $n \geq 2$. The corresponding phase model is

$$\begin{aligned}\dot{\theta}_1 &= \omega_1 + Q_1(\theta_1) g_{12}(\theta_1, \theta_2) \\ \dot{\theta}_2 &= \omega_2 + Q_2(\theta_2) g_{21}(\theta_1, \theta_2) \qquad (17)\end{aligned}$$

where ω is a natural frequency of the oscillator and $Q(\theta)$ is the infinitesimal PRC. How does this come about? Basically, by the chain rule,

$$\frac{d\theta}{dt} = \frac{d\theta}{dx}\frac{dx}{dt} \tag{18}$$

and $\frac{dx}{dt}$ is equivalent to g, while $\frac{d\theta}{dx}$ describes how the phase responds to a small perturbation in x. This $\frac{d\theta}{dx}$ is Q, which is the PRC normalized by the amplitude of the pertubation, A, in the limit as $A \to 0$:

$$Q(\theta) = \lim_{A\to 0} \frac{\text{PRC}}{A} \quad . \tag{19}$$

Equation 17 can be rewritten as

$$\begin{aligned} \dot{\theta}_1 &= \omega_1 + h_{12}(\theta_1, \theta_2) \\ \dot{\theta}_2 &= \omega_2 + h_{21}(\theta_1, \theta_2) \end{aligned} \tag{20}$$

where $h_{12} = Q_1 g_{12}$ describes the influence of oscillator 2 on oscillator 1.

One can then average the influence of one oscillator on the other by averaging h over all time. This gives the H-function:

$$\boxed{H_{12}(\chi) = \lim_{T\to\infty} \frac{1}{T} \int_0^T h_{12}(t, t+\chi)\, dt} \tag{21}$$

where $\chi = \theta_2 - \theta_1$. Then the phase equation becomes

$$\dot{\theta}_1 = \omega_1 + H_{12}(\theta_2 - \theta_1) \tag{22}$$

$$\dot{\theta}_2 = \omega_2 + H_{21}(\theta_1 - \theta_2) \tag{23}$$

The H-function is a constant unless the oscillators are **nearly resonant**, i.e., $T_1/T_2 \approx p/q$ where $p + q$ is small.

- H constant $\Longrightarrow$ oscillators phase drift.
- If the oscillators are nearly resonant then it is possible for the oscillators to phase lock.

Example

Consider two coupled oscillators with nearly equal natural frequencies:

$$\dot{\theta}_1 = \omega_1 + H_{12}(\theta_2 - \theta_1) \tag{24}$$

$$\dot{\theta}_2 = \omega_2 + H_{21}(\theta_1 - \theta_2) \quad . \tag{25}$$

Let $\chi = \theta_2 - \theta_1$, then

$$\boxed{\dot{\chi} = \omega + H(\chi)} \tag{26}$$

where $\omega = \omega_2 - \omega_1$ and $H(\chi) = H_{21}(-\chi) - H_{12}(\chi)$. To determine a phase locked solution (χ^*) one finds the steady state solutions to this phase difference ODE. These satisfy

$$\boxed{H(\chi^*) = -\omega} \quad . \tag{27}$$

This can be done graphically by plotting $y = H(\chi)$ and $y = -\omega$ and looking for intersections of the two curves.

In the Kuramoto model $H(\chi) = -\sin(\chi)$. To find phase locked solutions in this case, one plots $y = -\sin(\chi)$ and $y = -\omega$. The solution is **stable** if the slope of the graph of H is negative at the intersection.

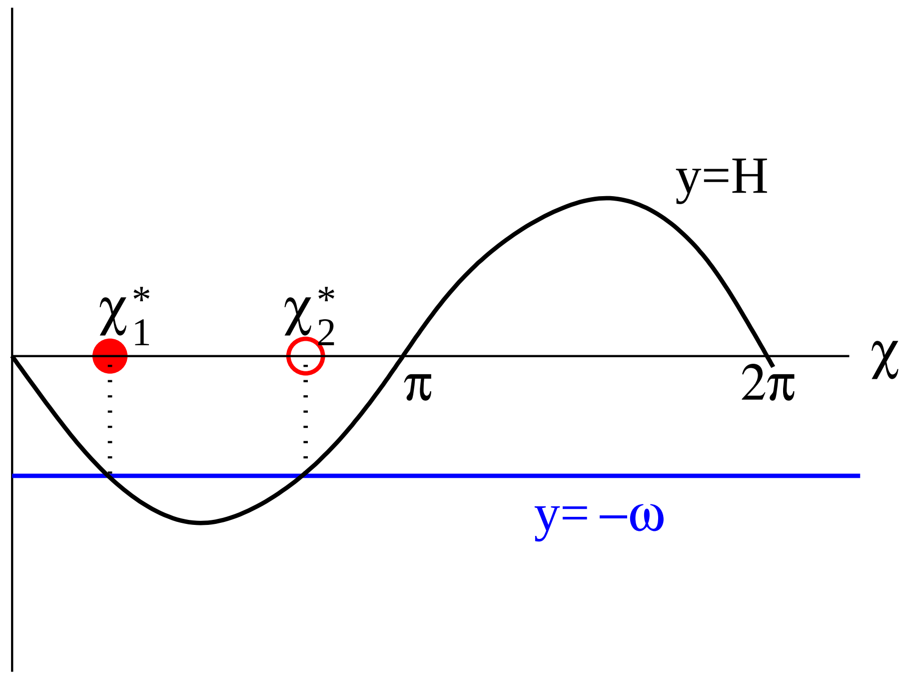


Figure 11: Two phase locked solutions, one stable and the other unstable.

In the stable phase-locked steady state oscillator 2 **leads** oscillator 1 by a phase angle of χ_1^*. The opposite would occur if $w < 0$.

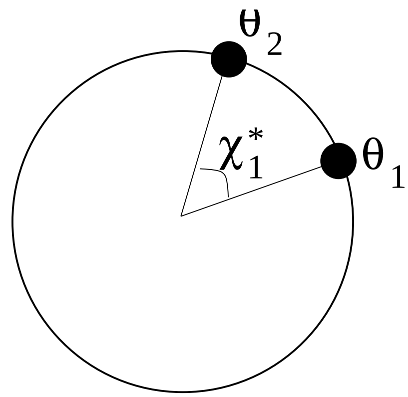


Figure 12: When phase locked, oscillator 2 leads oscillator 1 by a phase angle χ_1^* .

If the oscillators are actually identical, then $w = 0$ and the two phase locked solutions are at $\chi = 0$ (the **synchronous solution**) and $\chi = \pi$ (the **antiphase solution**). The synchronous solution is stable.

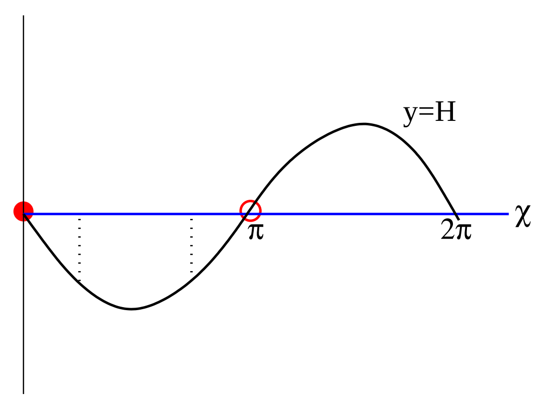


Figure 13: For identical oscillators the synchronous solution is stable.

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