
The essential character of an action potential is the corresponding limit cycle. If the neuron stays on the limit cycle, its dynamics are one dimensional. An important reduction to one-dimensional dynamics uses the concept of phase. The reduction to phase dynamics and incorporating coupling to study networks is the topic of this lecture. For further reading consult the books by Ermentrout & Terman [1], and Pikovsky et al [2], where the derivations below are given.

Consider a circular trajectory (Figure 1) defined by
\[ x(t) = r \cos \phi(t) \]
\[ y(t) = r \sin \phi(t) \]
It can equivalently be written as \( \phi(t) = \omega t \) and \( r \) is constant, or as a pair of differential equations \( \dot{\phi} = \omega \) and \( \dot{r} = 0 \). Hence the entire trajectory is well described by the phase, which varies at a constant rate, hence phase and time are equivalent.

When the limit cycle is not a circle (Figure 2), but the origin lies inside, one can still define a phase via \( \tan \theta = y/x \), but now time and phase are not equivalent (Figure 3), because the rate of phase change with time may depend on the phase itself: \( \dot{\theta} = f(\theta) \). One can still define a phase with this equivalence property:
\[ \phi = \omega_0 \int_{0}^{\phi(t)} 1/f(\theta) d\theta, \]
in which case \( \dot{\phi} = \omega_0 \).

This allows one to describe the effect of a perturbation. Consider an oscillation (e.g. a neuron spiking) that starts on \( t=0 \) at zero phase, \( \theta=0 \). At a later time, with phase \( \theta=\phi \) a perturbation is applied that makes the neuron spike earlier. That means that just after the perturbation the phase has changed to \( \theta=\phi' \). The phase remains constant.
transition curve (PTC), describes the relation between the two phases \( \phi' = P(\phi) \), whereas the phase reset curve (PRC) describes the change in phase \( \Delta(\phi) = \phi - \phi' = P(\phi) - \phi \). Let’s for the moment assume that phase and time are the same. In the unperturbed situation we have that the time to spike at phase \( \phi \) is \( T-\phi \), but after the perturbation the neuron spikes after \( T-\phi' \) which is at the new time \( T' \). Hence \( T'=\phi+(T-\phi')=T-(\phi'-\phi)=T-\Delta(\phi) \) yielding \( \Delta(\phi)=T-T' \) and \( \phi'=\phi+T-T'=P(\phi) \).

The question is now to determine the new \( \phi' \), or equivalently the new \( T' \). The simplest approach, which will only work for the simplest systems, is to calculate the asymptotic phase for all positions in the phase plane. We will illustrate this for the following example

\[
\dot{R} = R(1 - R^2) \\
\dot{\theta} = \eta - \alpha R^2
\]

Here \( \alpha \) and \( \eta \) are parameters. As you will be able to confirm using the analysis of the previous lectures, this system has a stable limit cycle at \( R=1 \).

**Self-test 1**: Show that the above system has a stable limit cycle at \( R=1 \).

As the equation for \( R \) is uncoupled from the phase, the convergence to the limit cycle of a system that was at \( R_0 \) on \( t=0 \), can be calculated directly by performing the following integral:

\[
t = \int_{R_0}^{R} \frac{dR}{R(1 - R^2)} \Rightarrow R^2 = \frac{1}{1 + e^{-2t(1-R_0^2/R_0^2)}}
\]

**Self-test 2**: Provide the details of the above calculation and show that \( R \) converges back to the limit cycle.

Given the solution for \( R(t) \), one can determine the corresponding phase variation by direct integration also:

\[
\dot{\theta} = \eta - \alpha R(t)^2 \Rightarrow \theta_0 + \eta t - \alpha \int_0^t \frac{dt}{1 + e^{-2t(1-R_0^2/R_0^2)}}
\]

**Figure 5**: The phase for an unperturbed trajectory is shown at two instances (black circles), at the time of perturbation, and some time later. The perturbation pushes the system off the limit cycle (first red circle), but after a while it returns to the limit cycle, but at a different position (second red circle), hence phase, compared to the unperturbed trajectory.

**Figure 6**: Different initial \( R \) values lead to different asymptotic phases.
\[ \theta = \theta_0 + (\eta - \alpha)t - \frac{1}{2} \alpha \ln(R_0^2 + (1 - R_0^2)e^{-2t}) = \theta_0 + \omega_0 t + \phi_0 \]

\[ \phi_0 = -\alpha \ln R_0 \]

This means that any point initially of the limit cycle, \((\theta_0,R_0)\) \(\to\) \(((\theta_0 + \phi_0) + \omega_0 t,1)\), but picking up an additional phase \(\phi_0\).

**Self-test 3:** Fill in the details of the above calculation.

The effect of a perturbation can now also be understood. A system on the limit cycle is characterized by \((\theta(\iota),R(\iota)) = (\phi_0 + \omega_0 \iota,1)\), a perturbation moves it off the limit cycle via \((\theta,R) \to (\theta + \Delta \theta,R + \Delta R) \to (\phi' + \omega_0 \iota,1)\), but after some time it returns to the limit cycle at a different phase. The PTC is given by determining the mapping \(\phi_0 \to \phi'_0\). This mapping can be determined for perturbations of all size, even big ones. For the more general case, this analysis is not possible and we will need to consider small perturbations of order \(\varepsilon\).

When there is only one stable limit cycle (and no other stable fixed points), each vector \(\dot{X}\) corresponds to an asymptotic phase \(\phi(\dot{X})\), corresponding to the phase when it ends up on the limit cycle, sometimes after a long time. The dynamics of the system is given by \(\dot{X} = \bar{f}(\dot{X})\), but for a trajectory \(\dot{X}(\iota)\) on the limit cycle the phase so defined should increase at a constant rate

\[ \frac{d\phi(\dot{X}(\iota))}{dt} = \sum_k \frac{\partial \phi}{\partial x_k} \frac{dx_k}{dt} = \sum_k \frac{\partial \phi}{\partial x_k} f_k(\dot{X}(\iota)) = \omega_0 \]

This is also be true for trajectories off the limit cycle, because each point has an asymptotic phase that also varies with a constant rate! A perturbation can be described as the addition of a function \(\rho\) to the dynamics \(\dot{f} \to \bar{f} + \varepsilon \rho(\dot{X},\iota)\), its effect on the phase dynamics is

\[ \frac{d\phi(\ddot{X}(\iota))}{dt} = \omega_0 + \varepsilon \sum_k \frac{\partial \phi(\ddot{X}(\iota))}{\partial x_k} p_k(\ddot{X}(\iota),\iota) \]

\[ = \omega_0 + \varepsilon \sum_k \frac{\partial \phi(\dot{X}_0(\iota))}{\partial x_k} p_k(\dot{X}_0(\iota),\iota) \]

\[ = \omega_0 + \varepsilon \sum_k \frac{\partial \phi(\dot{X}_0(\phi))}{\partial x_k} p_k(\dot{X}_0(\phi),\iota) \]

In the first line, \(X\) denotes the perturbed trajectory, but in the second line it is replaced by the limit cycle \(X_0\) in the term that is already of order \(\varepsilon\), in the third line we replace time with phase, except for in the perturbation term. Taken together this gives:

\[ \frac{d\phi}{dt} = \omega_0 + \varepsilon Q(\phi,\iota) \]
where \( Q \) is a \( 2\pi \) periodic function of the phase, and a \( T \) periodic function of the time (\( T \) is the period of the applied periodic perturbation, \( T_0 \) is the period of the oscillation corresponding to the limit cycle. We chose this setup to be able to study phase locking to an external periodic perturbation).

**Self-test 4:** Write out the formula for \( Q \).

Let’s apply this formula to the above example for which we know the answer already. First we convert the radial coordinates to Cartesian ones.

\[
\begin{align*}
\dot{R} &= R(1 - R^2) \\
\dot{\theta} &= \eta - \alpha R^2
\end{align*}
\]

which gives for the asymptotic phase

\[
\phi(x, y) = \theta - \alpha \ln R = \arctan \frac{y}{x} - \frac{1}{2} \alpha \ln(x^2 + y^2)
\]

For simplicity we now consider a perturbation in the \( x \)-direction (for instance, corresponding to voltage) comprised of a oscillatory current with a different frequency than the limit cycle itself.

\[
\frac{d\phi}{dt} = (\eta - \alpha) + \varepsilon \frac{\partial \phi}{\partial x} \cos \omega t = \omega_0 - \varepsilon (\sin \phi + \alpha \cos \phi) \cos \omega t = \omega_0 - \varepsilon \sqrt{1 + \alpha^2} \cos(\phi - \phi_0) \cos \omega t
\]

where we used \( \omega_0 = \eta - \alpha \) and \( \tan \phi_0 = 1/\alpha \).

We can bring this in a form more conducive for analysis by considering the goniometric identity

\[
2 \cos \gamma \cos \beta = \cos(\gamma + \beta) + \cos(\gamma - \beta)
\]

with \( \gamma + \beta = \phi - \phi_0 + \omega t \) (fast, averages out) and \( \gamma - \beta = (\phi - \omega t) + \phi_0 \) (slow when intrinsic and driving frequency are close). Hence we can simplify the dynamics by only considering the slow dynamics of the phase

\[
\frac{d\phi}{dt} = \omega_0 + \varepsilon Q(\phi, t) \to \omega_0 + \varepsilon q(\phi - \omega t)
\]

This can be rewritten into the phase difference \( \psi = \phi - \omega t \) between external and intrinsic phase and the difference \( v = \omega - \omega_0 \) in the corresponding frequencies:

\[
\frac{d\psi}{dt} = -v + \varepsilon q(\psi)
\]

Figure 7. Phase-locking: Arnold tongues
As we are looking for a $2\pi$ periodic function, which is odd around zero for stability reasons, we should start with $q(\psi) = \sin(\psi)$, because more realistic functions could be accounted for by adding the appropriate higher order harmonics. The resulting dynamics can be studied using the methods exposed in Lecture 1.

Fixed points: $\dot{\psi} = -v + \varepsilon \sin \psi = 0 \Rightarrow n \sin \psi = v / \varepsilon$. When $|v| < \varepsilon$, then there are two solutions, one of which is stable, which will be denoted by $\psi_s$. This corresponds to the solution $\phi(t) = \omega t + \psi_s$, that is, the oscillator is entrained to the external drive, but at the cost of a phase shift. This area of phase-locking forms a triangle in parameter space, which is named ‘Arnold Tongue’ (Figure 7).

There is one solution when $v = \pm \varepsilon$, and none otherwise. In the latter case there is no phase-locking, and the phase difference between external and intrinsic oscillation keeps increasing: $\dot{\psi} = -v + \varepsilon \sin \psi \neq 0$, $\langle \dot{\psi} \rangle = \Omega_\psi = \frac{2\pi}{T_\psi}$, with $T_\psi = \int_0^{2\pi} \frac{d\psi}{-v + \varepsilon \sin \psi}$ (apart from the sign). Hence, $\dot{\phi} = \omega + \dot{\psi} = \omega + \Omega_\psi$. The result is shown in Figure 8.

Self-test 4: If you remember how to do contour integrals from the class on complex functions, you can find the analytical expression for $T_\psi$.

Networks of phase-coupled oscillators.

For a single oscillator, the following equation describes the effect of a perturbation $\dot{X} = \ddot{f}(X)$, which for the phase means

$$\frac{d\phi(X(t))}{dt} = \omega_0 + \varepsilon \sum_k \frac{\partial \phi(X_0(\phi))}{\partial x_k} p_k(X_0(\phi), t)$$

If instead of coming from an external source, the perturbation comes from another neuron, we get a perturbation that depends on the state of that second neuron:

$$\dot{X}_1 = \ddot{f}_1(X_1) + \varepsilon \ddot{G}(X_1, X_2).$$

If each of them is on a limit cycle, and the interaction does not move them too far away from their respective limit cycles, we can describe this interaction in terms of the phase variables corresponding to each oscillator $j$:

$$\frac{d\phi_j}{dt} = \omega_0 + \varepsilon \sum_k \frac{\partial \phi_j}{\partial x_k} G_k(X_j, X_{\text{not},j}) = \omega_0 + \varepsilon H(\phi_{\text{not},j} - \phi_j)$$

This can be extended for more than a pair of oscillators, and by taking a sinusoidal interaction function for $H$, it leads to the Kuramoto system of $N$ oscillators:
\[
\frac{d\phi_k}{dt} = \omega_k + \frac{\varepsilon}{N} \sum_j \sin(\phi_j - \phi_k)
\]

Let \(\bar{\omega} = \frac{1}{N} \sum_{k=1}^{N} \omega_k\) and redefine zero mean frequencies \(\omega_k \rightarrow \omega_k - \bar{\omega}\), and further define the order parameters \(Z = Ke^{i\Theta} = \frac{1}{N} \sum_{k=1}^{N} e^{i\phi_k}\), then, a calculation (see practice hours) shows

\[
\frac{d\phi_k}{dt} = \omega_k + \varepsilon K \sin(\Theta - \phi_k)
\]

Hence for a fixed value of \(K\) and \(\Theta\), those oscillators \(k\) that satisfy \(\omega_k < \varepsilon K\) are phase locked according to our calculation to determine the Arnold Tongues. In this case, however, the value of \(K\) depends on all the other oscillators, and needs to be obtained self-consistently. Kuramoto did this and you can find the corresponding derivations in Pikovsky et al.