An example of a limit cycle is provided by the Fitzhugh-Nagumo model for a neuron:

\[
\begin{align*}
\dot{V} &= V(a - V)(V - 1) - w + I \\
\dot{w} &= bV - cw
\end{align*}
\]

Here \( V \) represents the membrane potential of the neuron, which has fast dynamics because it displays action potentials and \( w \) represents a slower variable, for instance representative for a potassium or calcium current. \( I \) is the depolarizing current. The other parameters are \( a, b \) and \( c \), whose role will become clear later.

The null clines are given by

\[
\begin{align*}
\dot{V} &= 0 \Rightarrow w = I + V(a - V)(V - 1) \\
\dot{w} &= 0 \Rightarrow w = \frac{b}{c}V
\end{align*}
\]

The first one is a third order polynomial (blue) with zeros at \( V=0, V=a \) and \( V=1 \), which gets translated in the \( w \) direction by the level of depolarizing current \( I \). The second one is a linear function going through the origin (red).

The fixed point (FP) is determined by the intersection(s) of the null clines. We expect either 1 or 3 real solutions because the FPs are given by a third order polynomial:

\[
I + V(a - V)(V - 1) - \frac{b}{c}V = 0
\]

In order to make sketches we consider the case \( I=0, b=0.01, c=0.02 \) and \( a=0.1 \). Hence the origin \( V^* = w^* = 0 \) is a fixed point. For the sketch it is useful to determine the maxima of \( w(V) \) for the \( V \) null cline by setting \( dw/dV=0 \). This yields \( V \) values near zero and around 0.73. In Figure 1, I show a sketch without ticks (On the exam points will be subtracted for that). I drew in a limit cycle (green) by connecting the derivative arrows. The question is, whether it actually exist? For this we need to appeal to Poincaré-Bendixson: If the trajectory stays inside a particular region and there is no stable fixed point, then there is a limit cycle, otherwise there is not.
The Hessian, denoted by $\nabla F$ in part A of this lecture, comprised of the matrix of partial derivatives, is given by

$$\nabla F = \left( \frac{\partial F_j}{\partial x_i} \right) = \begin{pmatrix} -a + (2a + 1)V - 3V^2 & -1 \\ b & -c \end{pmatrix}$$

Its trace and determinant are given by $\tau = -(a + c) < 0$ and $\Delta = ac + b > 0$, which means for the parameters chosen that $\tau^2 - 4\Delta < 0$. Appealing to Figure 15 in part A this implies that we have stable spiral. Hence, according to Poincaré-Bendixson there is no limit cycle.

**Self-test 1**: Find the parameter values $a$, $b$ and $c$ for which there is a stable limit cycle, by following the same steps as in the preceding analysis.

The bifurcation diagrams of part A of lecture 1 dealt mostly with changes in stability of the fixed point. For neural dynamics it is important to determine how limit cycles emerge or become stable. There are the following generic mechanisms.

**Supercritical Hopf.** In polar coordinates ($r > 0$ is the radius) the generic example reads

$$\dot{r} = \mu r - r^3$$
$$\dot{\theta} = \omega + br^2$$

The limit cycle corresponds in this case to $\dot{r} = 0$ that is $r(\mu - r^2) = 0$ or $r = 0$ and $r = \sqrt{\mu}$ (the negative solution is excluded because the radius is always positive). For the stability of the limit cycle we study $f(r) = \mu r - r^3$ with $f'(r) = \mu - 3r^2$, which yields $f'(0) = \mu$ (stable for negative $\mu$) and $f'(\sqrt{\mu}) = -2\mu$ (stable for positive $\mu$). Key properties are that the oscillation starts at a finite frequency $\omega$ and its amplitude increases smoothly with $\mu$.

**Subcritical Hopf.** The generic example is

$$\dot{r} = \mu r + r^3$$
$$\dot{\theta} = \omega + br^2$$

The main change is the $+$ sign in front of the third order term. This makes that the nonzero $r$ fixed points occur for negative $\mu$, hence that when
the stable r=0 fixed point becomes unstable for positive μ, the system ‘explodes’, because all that is left is an unstable FP.

\[ f(r) \]

\[ \mu < -\frac{1}{4} \]

\[ \mu = -\frac{1}{4} \]

\[ -\frac{1}{4} < \mu < 0 \]

Figure 4. (top) SNLC bifurcation; (bottom) representative orbits.

This instability can be remedied by adding a fifth order term in r with a minus sign, which also serves to introduce a new bifurcation: **saddle-node of a limit cycle** (SNLC):

\[ \dot{r} = \mu r + r^3 - r^5 \]
\[ \dot{\theta} = \omega + br^2 \]

It is instructive to analyze the dynamics. Fixed points are given by the roots of \( f(r) = \mu r + r^3 - r^5 = r(\mu + r^2 - r^4) \), which has three allowed solutions r=0 and \( r_s^2 = \frac{1}{2} \pm \frac{1}{2} \sqrt{1 + 4 \mu} \). The latter requires that \( \mu > -\frac{1}{4} \) for the + solution and \( 0 > \mu > -\frac{1}{4} \) for − solution. Stability is determined by \( f'(r) = \mu + 3r^2 - 5r^4 \), hence we get \( f'(0) = \mu \). Let \( \alpha = \sqrt{1 + 4 \mu} \) which is between 0 and 1 for the minus solution, then \( f'(r_s) = -\alpha^2 \mp \alpha \), which means that \( r_+ \) is always stable and \( r_- \) is always unstable. Figure 4 illustrates the bifurcation.

A bifurcation that occurs in the angle variable is the **saddle-node of an invariant circle** (SNIC) bifurcation. The generic example is given by

\[ \dot{r} = r(1 - r^2) \]
\[ \dot{\theta} = \mu - \sin \theta \]
The bifurcation variable ($\mu$) does not change the stability of the circle. It is given by $f(r) = r(1 - r^2) = 0$, that is $r=0$ or $r=1$. The stability is determined by $f'(r) = 1 - 3r^2$, which yields $f'(0)=1$ for the origin (unstable), and $f'(1)=-2$ for the circle (stable).

The FPs are given by $f(\theta) = \mu - \sin \theta = 0$. There is no fixed point for $|\mu| > 1$. There is one for $|\mu| = 1$ (saddle point) and 2 for $|\mu| < 1$, one of which is stable and one of which is unstable (please check). Hence a bifurcation occurs at $\mu=1$ or $-1$, we illustrate only the case for positive $\mu$.

In the **homoclinic** bifurcation a saddle point merges with a limit cycle (p. 263 of Strogatz). For example:

\[
\begin{align*}
\dot{x} &= y \\
\dot{y} &= \mu y + x - x^2 + xy
\end{align*}
\]

for which at $\mu_c = -0.8645$ a homoclinic bifurcation occurs. This chain of events is captured in Figure 6.
**The Morris-Lecar model**

All of these bifurcations have been illustrated use simple generic examples. In neural systems they are not that simple, but near the bifurcation point the generic dynamics are visible. The Morris-Lecar model is two-dimensional but already displays many types of bifurcations. It is given by

\[
\begin{align*}
C \frac{dV}{dt} &= -g_{Ca} m_{\infty}(V)(V - V_{Ca}) - g_K w(V - V_K) - g_L (V - V_L) + I \\
\frac{dw}{dt} &= \frac{w_{\infty}(V) - w}{\tau_w(V)}
\end{align*}
\]

\[
\begin{align*}
m_{\infty}(V) &= \frac{1}{2} \left( 1 + \tanh \left( \frac{V - V_1}{V_2} \right) \right) \\
w_{\infty}(V) &= \frac{1}{2} \left( 1 + \tanh \left( \frac{V - V_3}{V_4} \right) \right) \\
\tau_w(V) &= 1/\cosh^2 \left( \frac{V - V_3}{2V_4} \right)
\end{align*}
\]

With the parameter values: \( V_1 = -1.2, \ V_2 = 18, \ V_3 = 2, \ V_4 = 30, \ V_K = -84, \ V_L = -60, \ V_{Ca} = 120 \) (in mV), \( g_{Ca} = 4.4, \ g_K = 8.0, \ g_L = 2 \) (in mS/cm²), \( C = 20 \ \mu F/cm² \), \( \phi = 0.2 \).

We now illustrate a few of the behaviors of the Morris-Lecar equations.

(Figure 7) For a current of \( I = 84 \) (µA/cm²), there is only one stable FP. On the left we show the time traces of \( V \) and \( n \) (the same as \( w \)). They converge to a constant value, just as expected for a fixed point. The same can also be illustrated in the phase plane where \( n \) is plotted versus \( V \). The \( V \) nullcline is shown in red and the \( n \) nullcline in green. They intersect at the fixed point. All the trajectories end up there, some directly, some indirectly, only after going through one orbit.
(Figure 8) For a current of I=90, there is both a stable limit cycle and a stable fixed point – a bistable system. Left-top: V, Left-bottom: n The initial conditions for the black and cyan curve lead to the limit cycle, whereas as the rest go to the fixed point via a few low amplitude orbits. Right: the same but with different color convention in the phase plane.

(Figure 9) In a bistable system with a stable FP and limit cycle you can switch from the limit cycle to the FP by applying a current pulse.
(Figure 10) The transition from one stable FP to a system with a stable FP and a limit cycle is indicated in a bifurcation diagram where the $V$ is plotted as a function of driving current. The black dots indicate the position of the FP and the two red dots for each current value indicate the minimum and maximum voltage of the LC. The transition is a supercritical Hopf bifurcation.

(Figure 11) An example of SNLC. For $I=30.0$, there is a stable FP, saddle point and unstable FP. The left panel shows their location as an intersection of the null clines. The most leftwards FP is stable. Left: starting at the saddle-point, one reaches the stable FP either after one orbit or directly.
(Figure 12). Left: Starting from the unstable FP the trajectories also end up near the stable FP. Right: Above the bifurcation (I=40.8) the stable FP and saddle-point have disappeared, and a stable LC has emerged.

(Figure 13). Summary of the above events in terms of a bifurcation diagram. Conventions as in Figure 10.

(Figure 14) Illustration of a homoclinic bifurcation. We start out with two stable FP, an unstable FP, stable LC and unstable LC. Left: trajectories near the most-left stable FP, converge there. Right: trajectories near the unstable LC either spiral in towards the right most stable FP or spiral out towards the stable LC.
(Figure 15) Homoclinic bifurcation continued. (Left) Trajectories near the unstable FP end up in the left-most FP or the stable LC. (Right) Bifurcation diagram. At higher current a saddle-node touches the limit cycle and then disappears.