

Oscillations

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3 Oscillations [Limit Cycles and Hopf bifurcation]

If you consider a linear 2D system with purely imaginary eigenvalues

$$\dot{x} = \begin{bmatrix} 0 & \beta \\ -\beta & 0 \end{bmatrix} x \tag{1}$$

($\implies \lambda_{1,2} = \pm i\beta$), then the equilibrium point $x^* = 0$ is a center (see Fig. 2 of previous notes), i.e., the trajectories are concentric ellipses (or circles), meaning that the system oscillates forever. However, this is not a “strong” notion of oscillation, in the sense that if a trajectory is perturbed infinitesimally (for instance adding a very small quantity to the right hand side of (1)), then the system moves away from the current ellipse and never goes back to it.

What we would like to have is an equivalent for periodic trajectories of the concept of asymptotic stability. For that we need to define first the notion of limit cycle.

A *limit cycle* is an *isolated* periodic trajectory (i.e., such that in a neighbourhood around it there is no other periodic trajectory). When periodic trajectories are isolated then they can attract/repel nearby trajectories. We say that a limit cycle is *stable* if it attracts all nearby trajectories. It is *unstable* if it repels nearby trajectories, see Fig. 1. Notice that unstable limit cycles can be *half-stable* i.e., stable e.g. on the outside and unstable in the inside (in 2D of course).

Stable limit cycles provide a stronger notion of “sustained oscillation” than centers of linear systems, because they are robust to small perturbations. A limit cycle is however an intrinsically nonlinear concept: a linear system cannot have a limit cycle.

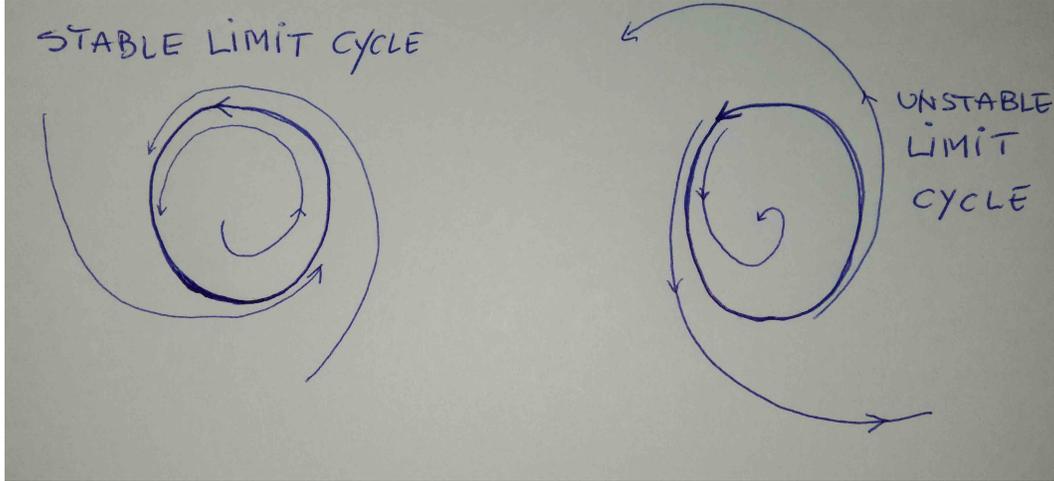


Figure 1: Left: stable limit cycle (solid line) in 2D. Right: unstable limit cycle (solid line) in 2D.

3.1 Conditions for existence of periodic orbits in 2D [Poincaré-Bendixson theorem]

In 2D it is possible to give testable conditions for the existence of periodic trajectories. The most important is the Poincaré-Bendixson theorem.

Theorem 3.1 (*Poincaré-Bendixson theorem*) Consider the system $\dot{x} = f(x)$, $x \in \mathbb{R}^2$. Assume there exists a bounded region $D \subset \mathbb{R}^2$ such that D is forward-invariant for the system (i.e., $x(0) \in D \implies x(t) \in D \forall t > 0$, see Fig. 2). Assume also that the system either does not have any equilibrium point in D or it has at most a single equilibrium point which is a repeller (i.e., the linearization has two eigenvalues with positive real part). Then there must be a periodic orbit in D . If D contains only one periodic orbit then this must be a stable limit cycle.

The verification that the periodic orbit is indeed a limit cycle may not be immediate (often one looks at simulations). Notice that if instead D contains two limit cycles then necessarily one must be half stable. Notice further that D can have holes, see Fig. 2.

A necessary but not sufficient condition for existence of periodic orbits is given by the Bendixson criterion.

Theorem 3.2 (*Bendixson criterion*) Consider the system $\dot{x} = f(x)$, $x \in \mathbb{R}^2$, and a bounded simply connected (i.e., “without holes”) region $D \subset \mathbb{R}^2$. If $\text{tr} \left(\frac{\partial f(x)}{\partial x} \right) > 0 \forall x \in D$ or $\text{tr} \left(\frac{\partial f(x)}{\partial x} \right) < 0 \forall x \in D$, then D cannot contain periodic orbits for the system.

As a consequence, we have that the only periodic orbits that a linear system can have are the marginally stable trajectories of a center. In fact, for a linear system $\dot{x} = Ax$, $\frac{\partial f(x)}{\partial x} = A$, and $\text{tr}(A) = a_{11} + a_{22} = \text{const} \forall x$, hence only when $\text{tr}(A) = 0$ the Bendixson criterion is not valid (the Bendixson criterion is a sufficient condition for non-existence of periodic orbits, hence if we want periodic orbits it must be violated). But $\text{tr}(A) = 0 \implies \lambda_{1,2} = \pm \sqrt{-\det(A)}$, which leads to periodic trajectories only when $\det(A) > 0$ (i.e., $\lambda_{1,2} = \pm i\beta$, or $x^* = 0$ is a center).

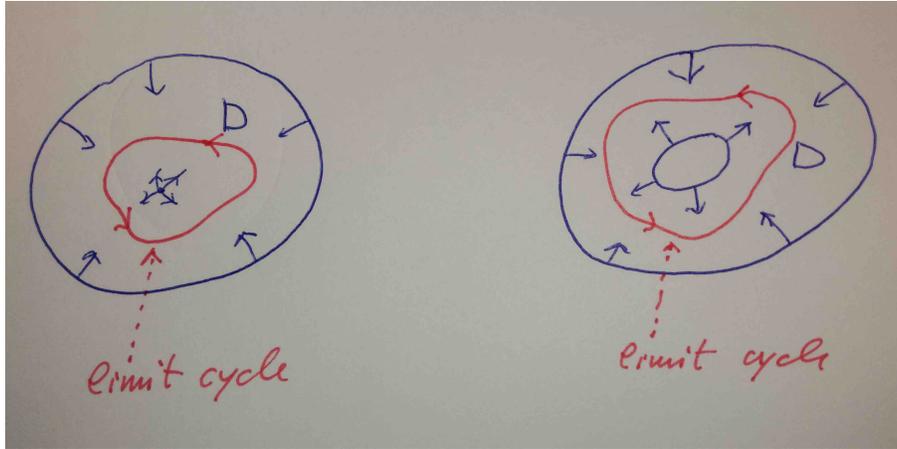


Figure 2: Poincaré-Bendixson theorem. Left: D has a single equilibrium which is a repeller. Right: D has no equilibria, and it has a “hole”.

3.2 Example: Glycolytic oscillator

Glycolysis is the metabolic pathway for the assimilation of sugar in the central metabolism of most living being (both prokaryotes and eukaryotes). The upstream part of this pathway is shown in Fig. 3.

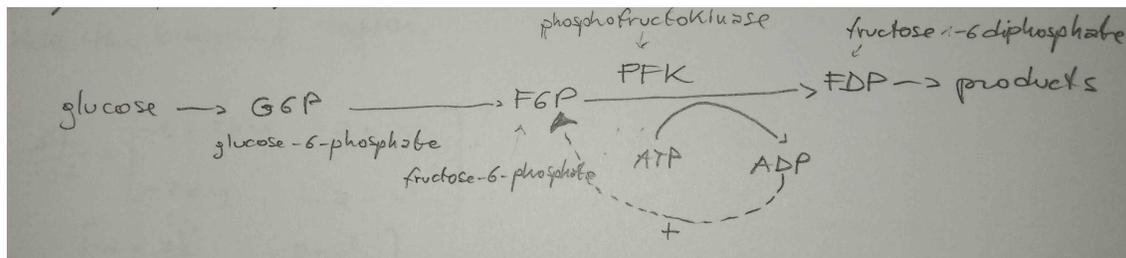


Figure 3: Scheme of the upper glycolysis pathway.

One of the reactions is catalyzed by the enzyme phosphofruktokinase (PFK). PFK converts fructose-6-phosphate (F6P) into fructose-1-6-diphosphate, using ATP as co-factor and producing ADP as by-product.



PFK has two activity states: a low activity state (basal) and a high activity state (stimulated by $\text{ADP} \implies$ allosteric effect). In Fig. 3, the dashed line represents this allosteric effect, but not on the enzyme, rather on the substrate fructose-6-phosphate (F6P) of the reaction. The argument is as follows: when PFK is in the high activity state more ADP is produced. The more ADP there is, the more F6P is consumed.

Let us consider a model of this feedback mechanism which takes as variables

- $x = [\text{ADP}]$

- $y = [\text{F6P}]$

and as ODEs:

$$\begin{aligned} \dot{x} &= -x + ay + x^2y \\ \dot{y} &= b - ay - x^2y \end{aligned} \quad (2)$$

In (2), ay represents the basal functioning of the PFK reaction, while x^2y represents the high activity mode ($-x$ represents a standard degradation/downstream utilization of ADP). The substrate of the reaction, y , is consumed accordingly. b is a constant production of F6P, depending on the upstream reactions, while $-ay$ and $-x^2y$ represent basal and high consumptions respectively. The equilibrium point for the system (2) is

$$\begin{bmatrix} x^* \\ y^* \end{bmatrix} = \begin{bmatrix} b \\ \frac{b}{a+b^2} \end{bmatrix}$$

and the nullclines are

$$\begin{aligned} x_{\text{null}} : y &= \frac{x}{a+x^2} \\ y_{\text{null}} : y &= \frac{b}{a+x^2} \end{aligned}$$

The nullclines, together with the qualitative picture of the phase flow in \mathbb{R}_+^2 are shown in Fig. 4. In order to compute the stability character of the equilibrium point, let us look at the Jacobian

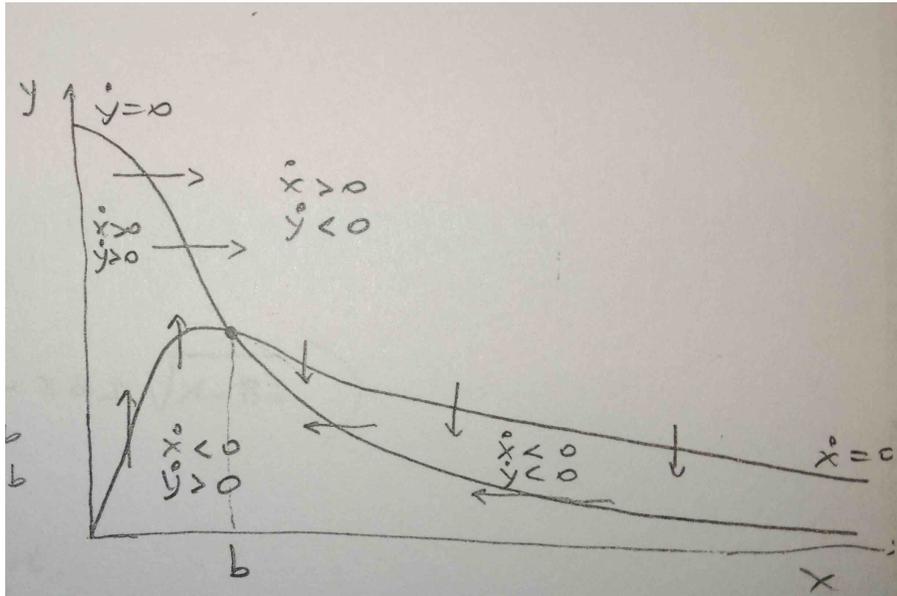


Figure 4: Phase portrait of the system (2).

linearization:

$$A = \begin{bmatrix} -1 + 2xy & a + x^2 \\ -2xy & -a - x^2 \end{bmatrix} \Big|_{(x^*, y^*)} = \begin{bmatrix} -1 + \frac{2b^2}{a+b^2} & a + b^2 \\ -\frac{2b^2}{a+b^2} & -a - b^2 \end{bmatrix}$$

for which

$$\det(A) = a + b^2 > 0$$

$$\operatorname{tr}(A) = -\frac{b^4 + (2a - 1)b^2 + a(a + 1)}{a + b^2}$$

$\operatorname{tr}(A)$ changes sign according to the values of the parameters (a, b) . For the values of the parameters for which $\operatorname{tr}(A) < 0$, the equilibrium point (x^*, y^*) is a repeller, hence the Poincaré-Bendixson theorem can in principle be applied. To do that, we need to find a bounded region $D \subset \mathbb{R}_+^2$ which is forward invariant for the system. Let us consider the region in Fig. 5. From the direction of the

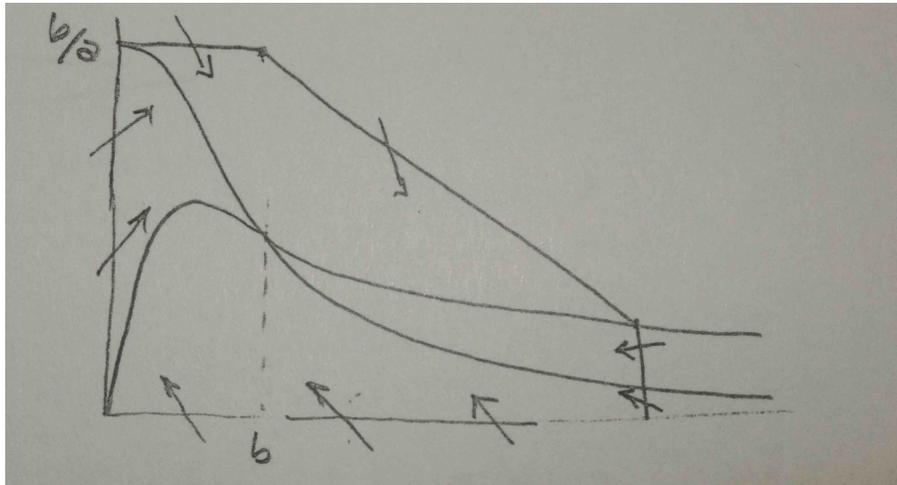


Figure 5: Forward-invariant region of the system (2).

flow, in 4 out of 5 pieces of the boundary of D we already know that the flow points inside. We only need to check it on the line segment of negative slope, whose equation is for example

$$y = -x + c$$

for some intercept $c > 0$. To do it let us check what happens to the solution of the system (2) once it is initialized on $x + y = c$. Differentiating:

$$\dot{x} + \dot{y} = -x + ay + x^2y + b - ax - x^2y = -x + b$$

For $x > b$ it is $\dot{x} + \dot{y} < 0 \implies$ the flow is pointing inwards also on this part of the boundary. Hence D is a forward-invariant region for the system (2) and indeed the Poincaré-Bendixson theorem can be applied.

The region in the (a, b) parameter space in which the equilibrium point (x^*, y^*) is a repeller is shown in red in Fig. 6. In the red region we can then conclude that D contains at least one periodic trajectory. A numerical simulation is shown in Fig. 7. Notice that from the Poincaré-Bendixson theorem we cannot conclude on the presence or less of a stable limit cycle. If we look at the trajectories in the phase plane, however, in this case it is plausible that indeed a stable limit cycle exists, see Fig. 8.

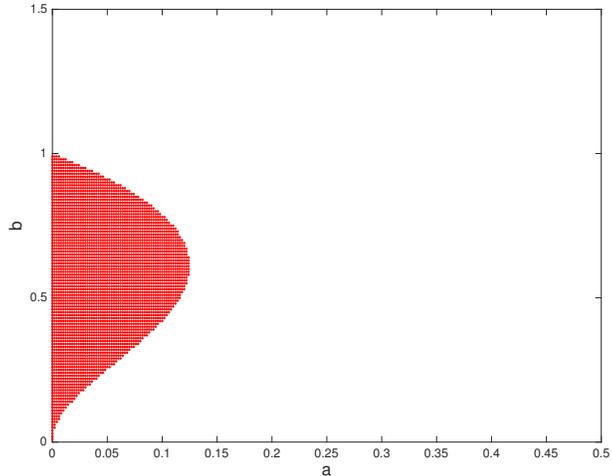


Figure 6: Region in parameter space in which the equilibrium point is unstable (in red).

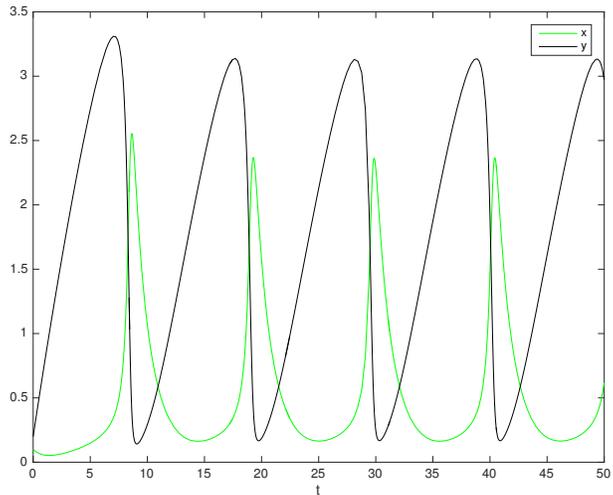


Figure 7: One trajectory of the system (2) for a choice of parameters in the red region of Fig. 6. After a transient the trajectory is periodic.

3.3 Hopf bifurcations

For the glycolytic example (2) let us consider what happens when we continuously vary one of the parameters. For example let us change a as in Fig. 9. Moving from right to left in the 3 plots, we pass from a region (in parameter space) in which the system (2) has an asymptotically stable equilibrium point to one in which the equilibrium is a repeller. Fig. 10 shows how the eigenvalues of the Jacobian linearization A move as we vary a . It can be observed that for the linearization the equilibrium passes from being a stable spiral (Fig. 10, right plot, $a > a^*$) to being an unstable spiral (Fig. 10, left plot, $a < a^*$). However, in the last case we know that the Poincaré-Bendixson theorem holds, hence trajectories stay confined in D in spite of the instability. What happens is

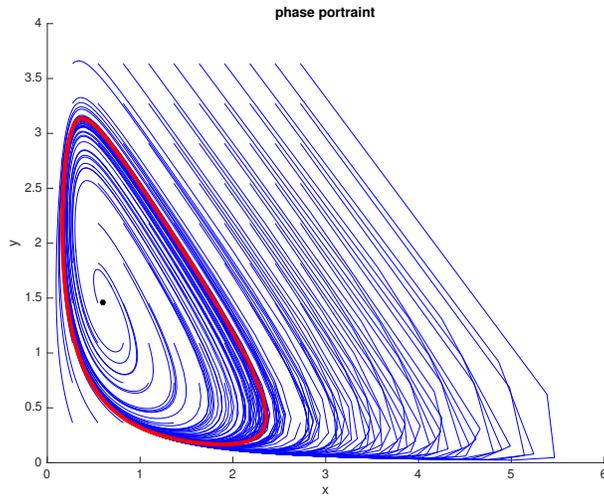


Figure 8: Phase plane trajectories of the system (2) for a choice of parameters in the red region of Fig. 6. The limit cycle is shown in red. In black the unstable equilibrium point is shown.

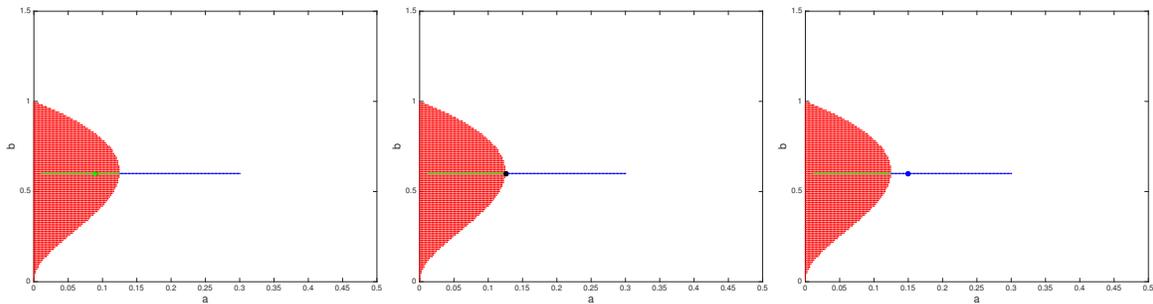


Figure 9: Bifurcation analysis: changing values of the parameter a . Left: $a < a^*$; Middle: $a = a^*$; Right: $a > a^*$.

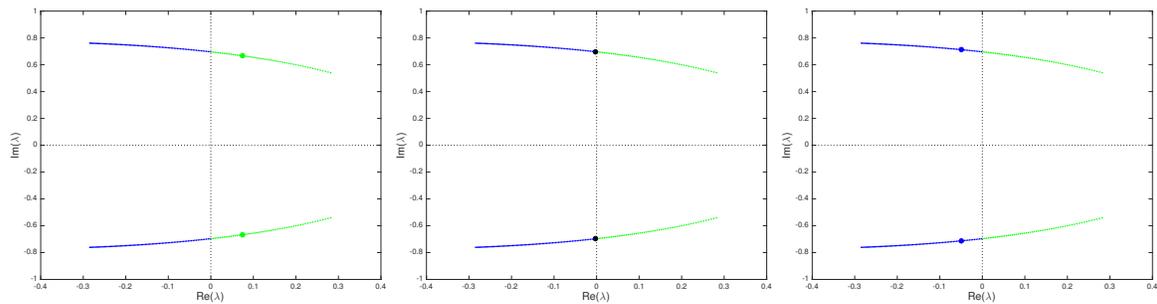


Figure 10: Bifurcation analysis: eigenvalues of the Jacobian linearization for the various values of a . Left: $a < a^*$; Middle: $a = a^*$; Right: $a > a^*$.

that the unstable equilibrium point becomes surrounded by a stable limit cycle (we do not have a formal proof, but this is what the simulations suggest). The phase portrait in the 3 cases, Fig. 12, confirms this picture.

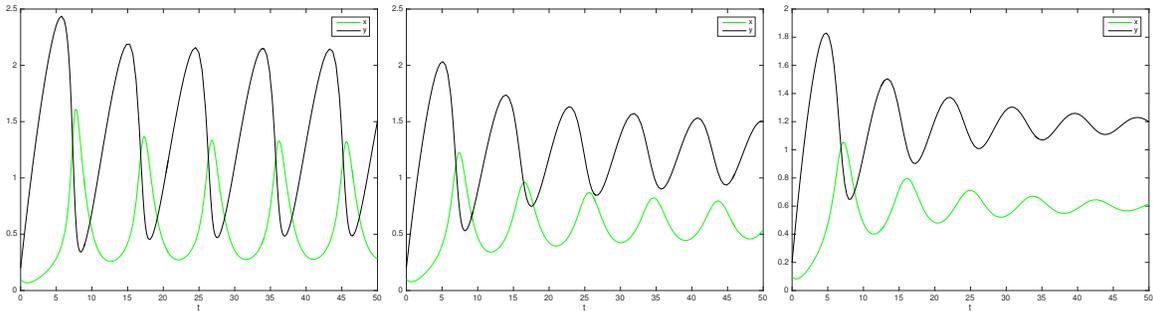


Figure 11: Bifurcation analysis: a sample trajectory for the various values of a . Left: $a < a^*$; Middle: $a = a^*$; Right: $a > a^*$.

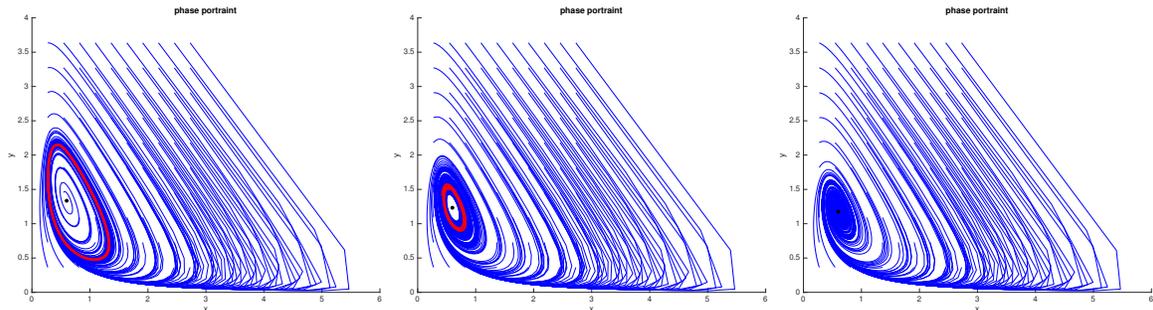


Figure 12: Bifurcation analysis: phase portrait for the various values of a . Left: $a < a^*$; Middle: $a = a^*$; Right: $a > a^*$.

The qualitative change just described is called a *supercritical Hopf bifurcation*. The peculiarity of a Hopf bifurcation is that, as we vary the parameter a , two complex conjugate eigenvalues of the linearization have real part that changes sign while the imaginary part never vanishes. The adjective “supercritical” refers to what happens at the bifurcation point, i.e., when $a = a^*$ (middle plot in Figs. 9-12). At $a = a^*$, $\text{Re}[\lambda_i] = 0$ hence the linearization cannot be used to describe the equilibrium of the original nonlinear system. When a stable limit cycle appears, then the Hopf bifurcation is said *supercritical*. This is the case shown in Fig. 13. At $a = a^*$ the equilibrium point becomes “surrounded” by a stable limit cycle, hence the effect of the instability of the equilibrium point (when $a < a^*$) is mitigated by the attractivity of the stable limit cycle around it. The amplitude of the oscillations at the bifurcation point is determined by the real part of the eigenvalues in Fig. 10, and typically grows slowly from 0 as we pass the critical point.

When instead an unstable limit cycle appears at $a = a^*$, then the Hopf bifurcation is said *subcritical*, see Fig. 14. In this case, it is the stable equilibrium point to be surrounded by an unstable limit cycle. This is a much more dramatic case, as big amplitude oscillations suddenly appear in this case when the critical point is passed. The simulations of Fig. 12 (middle plot) show

that our example has a supercritical Hopf bifurcation. Supercriticality/Subcriticality of a Hopf bifurcation is normally checked via simulations.

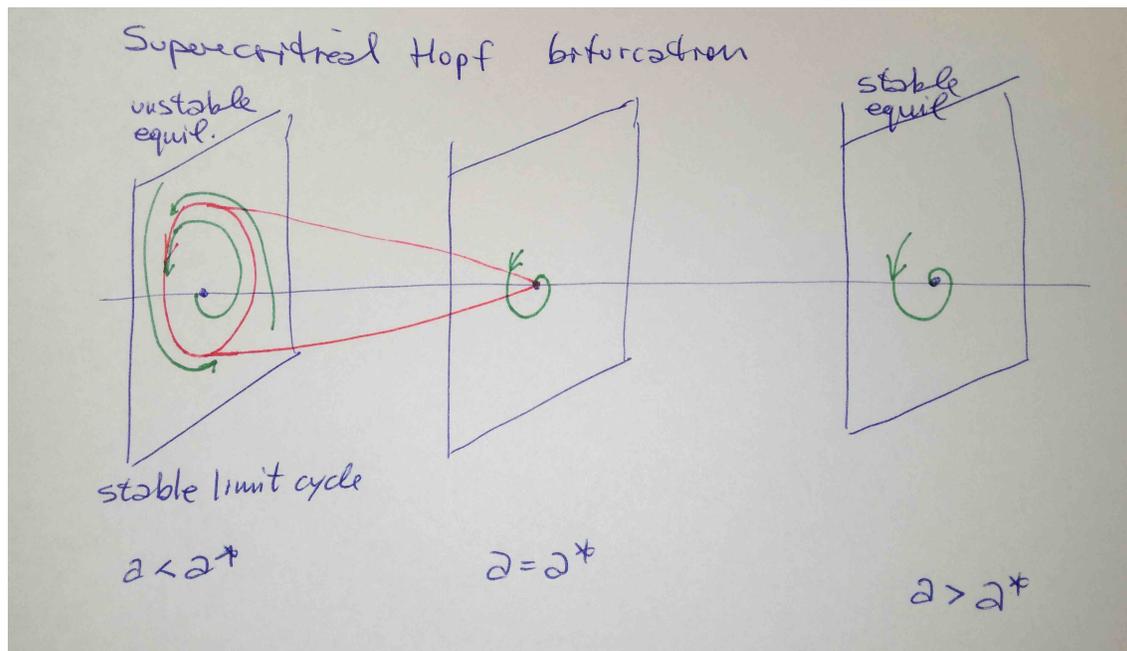


Figure 13: Supercritical Hopf bifurcation: a stable limit cycle appears at $a = a^*$.

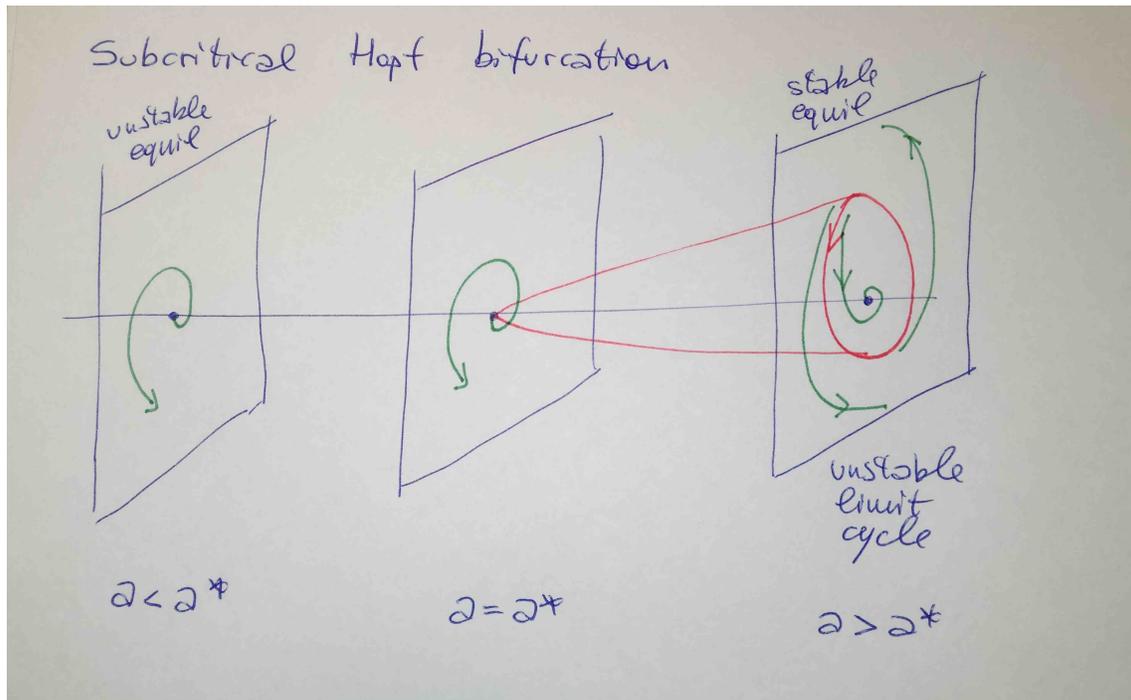


Figure 14: Subcritical Hopf bifurcation: an unstable limit cycle appears at $a = a^*$.