Ecole Polytechnique – UPSay 2015-16

Master de Mécanique M2 Biomécanique

Qualitative Analysis of Dynamical Systems and Models in Life Science

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Dernière modification : February 5, 2016

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Chapter 1

Dynamical systems and models in Life Science

In this first part, we focus on dynamical systems, which is a term embedding in particular the systems of ordinary differential equations (ODE or differential systems) and discrete dynamics. Differential systems write :

$$\dot{x} = \frac{dx}{dt} = f(x, t), \quad x \in U, \quad t \in I,$$

where U is an open subset of \mathbb{R}^n , I an interval of \mathbb{R} and $f: U \times I \to \mathbb{R}^n$ is smooth in a sense to be specified according to the context. Discrete dynamics are systems of the form :

$$x^{(k+1)} = \psi(x^{(k)}, k), \quad x \in U, \quad k \in \mathbb{Z},$$

where $U \subset \mathbb{R}^n$ and $\psi : U \to U$. A link exists between these two types of dynamical systems that we will explain and use in this course.

The universality of the dynamical phenomenons emerging in Physics, Biology, Ecology, Economics, and many other application domains underlies the power of such formalism for aggregating the knowledge, analyzing the dynamical behaviors of the systems, predicting these behaviors according to the parameters. In this course, we introduce the classical results of qualitative analysis of dynamical systems and illustrate their application to models in Life Science.

1.1 Fundamental Theorems

This section is a reminder of known results on existence and unicity of the solution of differential equations, boundedness of positive solutions (Gronwall Lemma), smooth dependency of the solution on the initial conditions and the parameters.

Theorem 1. (Cauchy-Lipschitz)

We consider the following differential system

$$\dot{x} = f(x, t) \tag{1.1}$$

where f is continuous on the open set $\Omega = U \times I$, I interval of \mathbb{R} , $U \subset \mathbb{R}^n$. Consider $x_0 \in U$ and $t_0 \in I$. **Local result :** If f is locally Lipschitz with respect to x, there exists a unique maximal solution x(t) of (1.1) such that $x(t_0) = x_0$. Its definition interval is open.

Global result : If f is K-Lipschitz with respect to x uniformly with t on $[t_0 - a, t_0 + a] \subset I$, there exists a unique solution x(t) of (1.1) such that $x(t_0) = x_0$ defined on $[t_0 - c, t_0 + c]$ with $c < \min(a, 1/K)$.

Remark 1. For sake of simplicity, in this course, we assume that the function f defining the differential systems of type (1.1) satisfies a Lipschitz condition with respect to the space variable globally on an open domain U that we do not specify. Hence, we consider the context of the global Cauchy-Lipschitz theorem, which ensures the existence of a unique solution of the Cauchy problem:

$$\dot{x} = f(x, t),\tag{1.2}$$

$$x(t_0) = x_0, (1.3)$$

Lemma 1. (Gronwall)

Let φ denote a continuous non negative function defined on $[t_0, t_0 + T]$. We assume that there exist real constants a, b, c with a > 0 such that, for any $t \in [t_0, t_0 + T]$,

$$\varphi(t) \le a \int_{t_0}^t \varphi(s) ds + b(t - t_0) + c.$$

then for any $t \in [t_0, t_0 + T]$,

$$\varphi(t) \le \left(\frac{b}{a} + c\right) e^{a(t-t_0)} - \frac{b}{a}.$$

In the context of modeling, we often consider a dynamics depending on one or several parameters. One of the main aims of the qualitative analysis is to explain the dependency of the dynamics structure (in particular, the solutions of (1.1)) according to the parameter values. The following theorem concern the regularity of a solution according to the initial condition and the system parameters.

Theorem 2. Consider the following dynamical system depending of parameters

$$\dot{x} = f(x, t, \lambda), \tag{1.4}$$

where f is K-Lipschitz on U w.r.t x uniformly according to $\lambda \in \mathbb{R}^p$ and $t \in [t_0 - T, t_0 + T]$. Then, for any $x_0 \in U$, there exists a unique maximal solution $\phi_{(t_0,x_0)}(t)$ de (1.4) such that $\phi_{(t_0,x_0)}(t_0) = x_0$, defined on the maximal interval $I_{(t_0,x_0)} = (\alpha(t_0,x_0,\lambda),\beta(t_0,x_0,\lambda))$. Moreover,

$$\forall t \in I_{(t_0, x_0)} \cap I_{(t_0, y_0)}, \quad |\phi_{(t_0, x_0)}(t) - \phi_{(t_0, y_0)}(t)| \le e^{K|t - t_0|} |x_0 - y_0|.$$

This theorem states that the solution depends continuously on the initial condition. By applying this result to the system

$$\dot{x} = f(x, t, \lambda), \tag{1.5}$$

$$\dot{\lambda} = 0, \tag{1.6}$$

we immediately obtain that the solution depends continuously on the parameter λ as well.

Remark 2. The continuous dependency with respect to t_0 results directly from the formal (implicit) integral satisfied by the solution. More generally, if we assume that the function f is differentiable, then the solution depends on (t_0, x_0) in a differentiable way.

1.2 Flow, phase portrait, orbit

Definition 1. Let U denote an open subset of \mathbb{R}^n . A \mathcal{C}^k vector field on U is a \mathcal{C}^k map

$$X: x = (x_1, \dots, x_n) \mapsto (f_1(x), \dots, f_n(x))$$
(1.7)

defined on U. With such a vector field is associated the differential system

$$\{\dot{x}_i = f_i(x_1, ..., x_n) | i \in \{1, ..., n\}\} \quad \Longleftrightarrow \quad \dot{x} = X(x).$$
(1.8)

which is said "autonomous". It is a particular case of differential system (1.1) where f does not depend on time.

The open set U is called the phase space of the vector field (and of the associated differential system).

Generally, we call differentiable vector field any \mathcal{C}^k vector field with $k \geq 1$.

From theorem 1, for any $x_0 \in U$, there exists a unique maximal solution x(t) of the Cauchy problem

$$\begin{cases} \dot{x} = X(x), \\ x(0) = x_0. \end{cases}$$
(1.9)

Note that, in this context, any initial condition $x(t_0) = x_0$ can be turned into $x(0) = x_0$ by a trivial translation of the time variable.

Definition 2. Given a value t, the flow at time t of the vector field X is the map $\phi_t : x_0 \mapsto x(t)$ associating with an initial condition x_0 the value at the time t of the maximal solution x(t) du problème de Cauchy (1.9).

The flow of the vector field X is the map ϕ associating with (t, x_0) the value at the time t of the maximal solution x(t) du problème de Cauchy (1.9):

$$(t, x_0) \mapsto \phi(t, x_0) = \phi_t(x_0) = x(t).$$

If ϕ is defined for any $t \in \mathbb{R}$ and any $x_0 \in U$, then the flow is said "complete".

Definition 3. The orbit (or integral curve) Γ of the vector field X containing x_0 is the differentiable curve constituted by the points $x(t) \in U$ given by the solution of (1.8) with initial condition x_0 . This curve is oriented by the time t. At each point x(t), its tangent is the straight line passing through x(t) directed by the vector X(x(t)). Sometimes, we distinguish the positive orbit $\Gamma_+ = \{x(t), t \geq 0\}$ from the negative orbit $\Gamma_- = \{x(t), t \leq 0\}$.

Corollary 1. The orbit of the vector field X form a partition of the phase space U called the phase portrait.

This corollary is a direct consequence of the unicity of the solution of a well-posed Cauchy problem and, therefore, of the Cauchy-Lipschitz theorem.

The qualitative analysis aims at studying the geometric structure (essentially the dynamical invariant) of the phase portrait and deducing the properties of the solutions from this underlying organization. **Definition 4.** A singular point (or equilibrium) of the vector field $X = (f_i)_{i=1}^n$ is a point $p \in U$ where all the components of the vector field vanish:

$$\forall i \in [\![1,n]\!], \quad f_i(p) = 0 \quad \Longleftrightarrow \quad X(p) = 0_{\mathbb{R}^n}.$$

A regular point is a non singular point.

Definition 5. Let X denote a differentiable vector field defined on an open subset U of \mathbb{R}^n . Let A denote an open subset of \mathbb{R}^{n-1} . A local transverse section of X is a differentiable map $g: A \to U$ such that, at any point $a \in A$, $Dg(a)(\mathbb{R}^{n-1}) \bigoplus X(g(a)) = \mathbb{R}^n$. The image $\Sigma = g(A)$ benefits from the induced topology. By abuse of language, if $g: A \to \Sigma$ is an homeomorphism, we will refer to Σ as a transverse section of X.

Definition 6. Two vector fields X and Y are topologically equivalent if there exists an homeomorphism h mapping the orbits of X onto the orbits of Y and preserving their orientation by the time variable. Hence, if X is defined on U and if we note $\phi(t, x)$ and $\psi(t, x)$ the flows of X and Y respectively, then

 $\forall x \in U, \quad \forall \delta > 0, \quad \exists \varepsilon > 0, \quad \forall t \in]0, \delta[, \quad \exists t' \in]0, \varepsilon[, \quad h(\phi(t, x)) = \psi(t', h(x)))$

Definition 7. Two vector fields X and Y are conjugated by a diffeomorphism (resp. topologically conjugated) if there exists a diffeomorphism h (resp. homeomorphism) mapping the X orbits onto the Y orbits and preserving their orientation by the time variable. Hence :

$$h(\phi(t,x)) = \psi(t,h(x)).$$

Remark 3. If the diffeomorphism h is defined on the same open domain U as X, the conjugacy by h corresponds to a global change of variable. Note that this result remains true for a chosen local domain, corresponding to a local change of variable.

Theorem 3. (Rectification of the flow)

Let X denote a \mathcal{C}^k vector field defined on the open subset U of \mathbb{R}^n , p a regular point of X, $g: A \to \Sigma$ a local transverse section of X such as g(0) = p. There exists a neighborhood V of p and a \mathcal{C}^k diffeomorphism $h: V \to (-\varepsilon, +\varepsilon) \times B$ where B is an open ball of \mathbb{R}^{n-1} centered at the origin, such that

- i) $h(\Sigma \cap V) = \{0\} \times B$
- ii) h conjugates $X_{|V}$ and the constant vector field

$$Y: (-\varepsilon, +\varepsilon) \times B \to \mathbb{R}^n, \quad Y = (1, 0, 0, ..., 0) \in \mathbb{R}^n.$$

Corollary 2. Let Σ denote a local transverse section of a \mathcal{C}^k vector field X and $p \in \Sigma$. There exists $\varepsilon_p > 0$, a neighborhood V of p and a map $\tau \in \mathcal{C}^k(V, \mathbb{R})$ such that

- i) $\tau(V \cap \Sigma) = 0$,
- ii) For any $q \in V$, the integral curve $\phi(t,q)$ of $X_{|V}$ exists for any value $t \in (-\varepsilon_p + \tau(q), \varepsilon_p + \tau(q))$,
- iii) $q \in \Sigma$ if and only if $\tau(q) = 0$.

Definition 8. Let X denote a vector field defined on the open subset U of \mathbb{R}^n . Let Γ denote the orbit of X containing x_0 . It is parameterized by a maximal solution x(t) of the associated Cauchy problem: $\Gamma = \{x(t) | t \in (\alpha, \beta)\}.$

• If $\beta = +\infty$, the ω -limit set of Γ (or equivalently of x_0) is defined by

$$\omega(x_0) = \{ q \in U \,|\, \exists (t_n) \in \mathbb{R}^{\mathbb{N}}, (t_n) \to +\infty \text{ et } (x(t_n)) \to q \}.$$

• If $\alpha = -\infty$, the α -limit set of Γ (or equivalently of x_0) is defined by

$$\alpha(x_0) = \{ q \in U \mid \exists (t_n) \in \mathbb{R}^{\mathbb{N}}, (t_n) \to -\infty \text{ et } (x(t_n)) \to q \}.$$

All the points of an orbit have the same α -limit and ω -limit.

In the following theorem, one can replace ω -limit by α -limit with obvious changes.

Theorem 4. Let X denote a \mathcal{C}^k vector field defined on an open subset U and $p \in U$. We assume that the positive half-orbit $\Gamma^+(p) = \{\phi(t,p) | t \ge 0\}$ is included in a compact set $K \subset U$. Then $\omega(p)$ is non empty, compact connected, and invariant under the flow.

Definition 9. A periodic orbit of a vector field X is an orbit $\{x(t) | t \in \mathbb{R}\}$ that contains no singular point of X and such as there exists T > 0, called period, satisfying

$$\forall t \in \mathbb{R}, \quad x(t+T) = x(t). \tag{1.10}$$

Such an orbit Γ containing a point x_0 is therefore entirely defined by

$$\Gamma = \phi_{[0,T[}(x_0) = \{\phi_t(x_0) | t \in [0,T[\} = \{x(t) | t \in [0,T[\}\})\}$$

A limit cycle is an isolated periodic periodic.

The minimal period of a periodic orbit is the smallest positive real number T satisfying condition (1.10). Without any further specification, the period of an orbit will refer to its minimal period and "a T-periodic orbit" will refer to an orbit of minimal period T.

Theorem 5. Let $\Gamma = \phi_{[0,T]}(x_0)$ denote a *T*-periodic orbit of a \mathcal{C}^k vector field *X*. Consider $\varepsilon > 0$ and let Σ_{ε} denote the part of the hyperplane Σ orthogonal to Γ at x_0 defined by:

$$\Sigma_{\varepsilon} = \{ x | (x - x_0) \cdot f(x_0) = 0 \text{ et } |x - x_0| < \varepsilon \}.$$

We assume ε small enough such that $\Sigma_{\varepsilon} \cap \Gamma = \{x_0\}$. Then, there exists $\delta > 0$ and a unique map $x \mapsto \tau(x)$ of class \mathcal{C}^k defined on the part of Σ defined by

$$\Sigma_{\delta} = \{x | (x - x_0) \cdot f(x_0) = 0 \text{ et } |x - x_0| < \delta\}$$

such as

$$\phi_{\tau(x)}(x) \in \Sigma_{\varepsilon}.$$

Map τ is called the "map of first return time" of X on Σ .

Definition 10. The C^k map

$$\Pi: x \mapsto \Pi(x) = \phi_{\tau(x)}(x),$$

is called "first return map" or Poincaré application associated with the periodic orbit Γ .

Using the first return map Π , we reduce the study of a *n* dimensional differential system in the neighborhood of a periodic orbit to the study of the discrete system $x^{(k+1)} = \Pi(x^{(k)})$ defined from Σ of dimension n-1 into itself. More generally, a first return map defined on a transverse section to a flow can be defined in certain cases even if no periodic orbit exists and the same reduction to a discrete system can be performed.

Definition 11. A fixed point of the map F is a point x such that F(x) = x. It corresponds to a T-periodic orbit of the flow of X. More generally, a periodic point of period n is a fixed point of the iterate F^n :

$$F^n(x) = x_i$$

that is not a fixed point of F^m for m < n.

1.3 ODE Models in Life Science

The universality of the dynamical system formalism allows us to develop models in a vast panel of applicative contexts. In particular, when the time variations of variables under identified dynamical laws carry the essential properties of a system, the development of models becomes a powerful tool for representing these underlying mechanisms. In the following, we introduce some historical models, still used nowadays, in population dynamics, neuroscience, climatology. In particular, we focus on the paradigms leading to the building of these models, the illustration of the complexity of the behaviors they can reproduce despite their compact writing, the interpretation of the model behaviors using the notions reminded in the preceding section.

1.3.1 Population dynamics (Lotka-Volterra, May-Kolmogorov, response functions)

Modèle de Lotka-Volterra

In 1925-26, Alfred Lotka and Vito Volterra have independently proposed a simple system for studying population dynamics. The Lotka-Volterra model describe the interactions between a population of preys and a population of predators: the state variable are x, the representation of number of preys, and y, the representation of the number of predators. We assume that, without any predator, the prey population grows exponentially with an exponent a > 0 and, without any prey, the predator population decreases exponentially with an exponent -c < 0. When the two populations coexist, we assume that the prey population decreases and the predator population increases linearly according to xy with constant factors -b < 0 et d > 0respectively. Hence, one obtains the following system:

$$\dot{x} = x(a - by), \tag{1.11}$$

$$\dot{y} = y(-c+dx).$$
 (1.12)



Figure 1.1: Example of a phase portrait (left panel) and x and y signals generated along the orbits (right panels) of the Lotka-Volterra model. All the orbits of the positive quadrant $\mathbb{R}^*_+ \times \mathbb{R}^*_+$ are periodic.

Kolmogorov system and May model

Andrei Kolmogorov has generalized the formalism introduced by Lotka and Volterra by introducing the following class of systems:

$$\dot{x} = xf(x,y), \tag{1.13}$$

$$\dot{y} = yg(x,y), \tag{1.14}$$

with the following conditions on f and g functions assumed to be at least C^1 :

$$\frac{\partial f}{\partial y} < 0, \quad \frac{\partial g}{\partial y} < 0, \quad \frac{\partial f}{\partial x} < 0 \text{ pour } x \text{ grand }, \quad \frac{\partial g}{\partial x} > 0.$$
 (1.15)

These conditions appear when one include natural conditions on the dynamical interactions between populations. Indeed, the two first conditions result from the hypothesis that the growth rates of each populations decreases when the predator population increases. The two last conditions are sufficient to ensure the existence and unicity of an equilibrium corresponding to a coexistence of both populations, i.e. a singular point of the dynamics lying in $\{x > 0, y > 0\}$ (the verification of this property is left as an exercise).

One of the most classical example of a Kolmogoroff type model has been introduced by Robert May in 1972. It is obtained from the Lotka-Volterra model by replacing the exponential growth of the prey without predator by a logistic growth (involving an asymptotic saturation) and by introducing a saturation effect in the predation efficiency. This model writes

$$\dot{x} = ax(1-x) - b\frac{xy}{A+y},$$
 (1.16)

$$\dot{y} = -cy + d\frac{xy}{A+y}.$$
(1.17)

Response functions of Holling type and trophic chains

The type of coupling between the dynamics of x (prey) and y (predator) embeds intrinsic properties of the trophic links between the populations (functional response). Crawford S. Holling (1959) has performed a general classification of the functional response types, i.e. the variations of the number of preys consumed by the predator population according to the prey density :



Density of prey population

- Type I response: linear function of the prey density up to a saturation value above which the number of preys consumed remains constant.
- Type II response: consumption rate regularly decreasing according to the density of preys (Arthropodes).
- Type III response: sigmoidal variation of the consumption rate (vertebrates, parasites).

Note that the functional response is also associated to a numerical response (variation of the predator density according to the density of preys). The whole predation phenomenon is therefore a combination of the functional and numerical responses

One can use the same approach for generalizing the models to trophic chains by considering

- a complex trophic tree, i.e. various populations of preys, consumed by different populations of predators, that can also be predated by other species (super-predators), etc.;
- different types of growth, functional and numerical responses for coupling the dynamics of the variables representing the populations.

Complex dynamical behaviors already emerge for a limited number of populations. In the following section, we introduce an example of prey-predator-superpredator model ("tritrophic") and the generated behaviors for various values of one parameter.

Tritrophic model

We consider a generalization of May's model by introducing a super-predator. Note X, Y, Z the representation of the preys, predators and super-predators respectively. We consider a logistic growth of the prey population resulting from the following equation

$$\dot{r} = \alpha r (K - r). \tag{1.18}$$

The non negative solution of this equation asymptotically converge to K when $t \to +\infty$. We consider response function of Holling type II between prey and predator population on one hand, and between super-predators and predators on the other hand. One obtains the following dynamics

$$\dot{X} = X \left(R \left(1 - \frac{X}{K} \right) - \frac{P_1 Y}{S_1 + X} \right)$$
(1.19)

$$\dot{Y} = Y \left(E_1 \frac{P_1 X}{S_1 + X} - D_1 - \frac{P_2 Z}{S_2 + Y} \right)$$
(1.20)

$$\dot{Z} = Z \left(E_2 \frac{P_2 Y}{S_2 + Y} - D_2 \right)$$
 (1.21)

where the positive parameters represent :

 P_i : the maximal predation rates,

 S_j : the half saturation constant of the response functions,

 D_i : the death rates,

 E_i : the predation efficiencies.

1.3.2 A few models in Neuroscience : Integrate-and-Fire, Hodgkin-Huxley, Fitzhugh-Nagumo

Several modeling approaches have been introduced and used since the beginning of the XXth century for tackling the tremendously complex, yet very exciting, problem of neuronal communication. We only introduce here a few physiological notions, deliberately simplified for sake of clarity. Moreover, we only describe a few models among the most revolutionary and best fitting the formalism studied in this course. Numerous other approaches and theories have been and are still currently developed. We invite the students interested in this thematics to enlarge their knowledge by reading the references given at the end of this course.

A very short introduction to neuronal electrophysiology

Neurons are cells characterized by two essential physiological properties : excitability, i.e. the ability to respond to stimuli and to convert them into neuronal impulses, and the conductivity, i.e. the ability to convey and transmit the impulses. At rest, there exists a negative difference in electric potentials (polarization) between the intracellular and extracellular faces of the neuron membrane, which envelops the cell body (soma), the axon and the dendrites. This resting membrane potential results from a difference in the ionic concentrations due to a selective permeability of the membrane according to the ion type.

The neuronal information is conveyed through instantaneous and localized changes in the membrane permeability, resulting in short-lasting events, called action potentials (see Figure below), in the electrical membrane potential which rapidly rises and falls, following a consistent trajectory. Action potentials are generated by special types of voltage-gated ion channels embedded in a cell's plasma membrane.

These channels are shut when the membrane potential is near the resting potential of the cell, but they rapidly begin to open if the membrane potential increases to a precisely defined threshold value. When the channels open (in response to depolarization in transmembrane voltage), they allow an inward flow of sodium ions, which changes the electrochemical gradient,

which in turn produces a further rise in the membrane potential. This then causes more channels to open, producing a greater electric current across the cell membrane, and so on.



The process proceeds explosively until all of the available ion channels are open, resulting in a large upswing in the membrane potential. The rapid influx of sodium ions causes the polarity of the plasma membrane to reverse, and the ion channels then rapidly inactivate. As the sodium channels close, sodium ions can no longer enter the neuron, and then they are actively transported back out of the plasma membrane. Potassium channels are then activated, and there is an outward current of potassium ions, returning the electrochemical gradient to the resting state. After an action potential has occurred, there is a transient negative shift, called the afterhyperpolarization or refractory period, due to additional potassium currents. This mechanism prevents an action potential from traveling back the way it just came. (voir Figure ci-contre).

Records of the instantaneous potential difference of a neuron has been since 1930s using microelectrodes. The modeling of the action potential generation, already undergone at the beginning of the XXth century with the Integrate-and-Fire models, has been based on experiences for including a biophysical interpretation of the model parameters. Hence, quantitative knowledge from experiences have been used for deriving the dynamics : this approach was introduced by Hodgkin and Huxley.

Integrate-and-Fire model

Historically, the first attempt for modeling the action potential has been performed by Louis Lapicque who built the Integrate-and-Fire model. It is inspired by a simple electric circuit formed by a capacity C and a resistance R in series, with an additional leak term and a reset mechanism when the potential V reaches a threshold V_{th} . Under an input current I(t), the potential V is driven by the following differential equation :

$$C\dot{V} = I(t) - \frac{1}{R}V.$$

If the input current is too weak, i.e.

$$I(t) < I_{\rm th} = V_{\rm th}/R,$$

the solution remains under the threshold V_{th} . Otherwise, there exists a time t^* such that $v(t^*) = V_{\text{th}}$, and one applies the reset mechanism $v(t^*) = V_0$. For a constant input I(t)(autonomous system) strong enough, one obtains a burst of action potentials.



This approach is essentially phenomenological : the dynamics is not based on mechanistic lows underlying the living system and none of the parameters can be interpreted as a biophysical entity. Yet, extensions of this approach have been intensively used for building versatile models that can generate the entire panel of behaviors expected from the Physiology. In particular, the bi-dimensional non linear IF model introduced by Eugene Izhikevic has been proven able to reproduce regular spiking, fast spiking, bursting, Mixed-Mode Oscillations, Mixed-Mode Bursting Oscillations, etc.

L'approche de Hodgkin et Huxley

In 1952, Hodgkin and Huxley have founded the mechanistic approach called "conductancebased" approach, by introducing the currents through the neural membrane induced by the ionic dynamics, sodium Na^+ (responsible for the depolarization) and potassium K^+ (responsible for the repolarization). We introduce this approach, that has been intensively used afterwards for perfecting the models.

Note I the total membrane current, C_m the capacity of the membrane by surface unit, V the difference between the membrane potential and its equilibrium value, I_{Na} the sodium current and I_K the potassium current. As for the Integrate-and-Fire model, the Hodgkin-Huxley model involves a leak current I_f . One obtains

$$C_m V = I - I_{Na} - I_K - I_f, (1.22)$$

with

$$I_{Na} = g_{Na}(V - V_{Na}), (1.23)$$

$$I_K = g_K(V - V_K),$$
 (1.24)

$$I_f = \overline{g}_f (V - V_f), \qquad (1.25)$$

and V_{Na}, V_K, V_f are the resting potentials (or inverse potentials) and $g_{Na}, g_K, \overline{g}_f$, are the conductances of the membrane for each ion type. This mechanistic approach is completed by experimental observations based on patch-clamp technics: $V_{Na}, V_K, V_f, \overline{g}_f$ are assumed to be constant, g_{Na} and g_K vary with time and V:

$$g_{Na} = \overline{g}_{Na} m^3 h, \qquad (1.26)$$

$$g_K = \overline{g}_K n^4, \tag{1.27}$$

where n(t) is called the potassium activation function, m(t) the activation function and h(t) measures the sodium current inactivation. These functions are solutions of :

$$\dot{m} = \alpha_m(V)(1-m) - \beta_m(V)m,$$
 (1.28)

$$\dot{n} = \alpha_n(V)(1-n) - \beta_n(V)n,$$
 (1.29)

$$h = \alpha_h(V)(1-h) - \beta_h(V)h.$$
 (1.30)

The mechanistic approach (and therefore the biophysical interpretation of the parameters) are limited to this level since Hodgkin and Huxley fit the functions α and β with experimental results and introduce phenomenologically:

$$\begin{aligned} \alpha_m(V) &= 0.1 \frac{25 - V}{\exp(\frac{25 - V}{10}) - 1}, \quad \alpha_n(V) = 0.01 \frac{10 - V}{\exp(\frac{10 - V}{10}) - 1}, \quad \alpha_h(V) = 0.07 \exp(\frac{-V}{20}), \\ \beta_m(V) &= 4 \exp(\frac{-V}{18}), \qquad \beta_n(V) = 0.125 \exp(\frac{-V}{80}), \qquad \beta_h(V) = \frac{1}{\exp(\frac{30 - V}{10}) + 1}. \end{aligned}$$

with $\overline{g}_{Na} = 120, \overline{g}_K = 36, \overline{g}_L = 0.3$ and the equilibrium potentials $V_{Na} = 115, V_K = -12, V_f = 10.6$.

A first success of this approach is to predict the shape of the action potential from experimental data and propose a mechanism for its generation. If the potential V is slightly higher than the equilibrium value under the influence of a current applied to the axon, it comes back to the equilibrium. If the external stimulus is stronger than a certain threshold, the sodium activation m contributes to raise the potential up to a maximum, then both potassium activation h and sodium deactivation n are turned on and participate in bringing the potential under its equilibrium state. Below this value, n decreases and the potential comes back to the resting state value, allowing the process to repeat.

FitzHugh-Nagumo model

The FitzHugh-Nagumo model is a simplification of the Hodgkin-Huxley system and can be considered as a paragon of excitable systems. It writes

$$\varepsilon \dot{x} = -y + 4x - x^3 + I, \qquad (1.31)$$

$$\dot{y} = a_0 x + a_1 y + a_2. \tag{1.32}$$

where $a_0 > 0$, $\varepsilon > 0$ and $a_1 > 0$ are assumed to be small. From the qualitative analysis viewpoint, the cubic curve $y = -x^3 + 4x$ can be replaced by any other S-shaped curve, i.e. admitting a local minimum x_- and a local maximum x_+ respectively. This curve can thus be split into three branches : left branch $(x < x_-)$, middle branch $(x \in [x_-, x_+])$ and left branch $(x > x_+)$.

Assume that the parameter values are chosen such that three singular points exist (intersection points of the cubic $y = -x^3 + 4x + I$ with $a_0x + a_1y + a_2 = 0$): for a_1 small, one lies high on the left branch, the other one lies low on the right branch, the third one can belong to any of the three branches. For I below a certain threshold $I_{\rm th}$, all orbits converge asymptotically towards this latter point. For values of I larger than $I_{\rm th}$, all the orbits admit the same periodic orbit (limit cycle) as ω -limit.

1.3.3 Climatology (Lorenz and deterministic chaos)

2

Mathematically, the coupling of the atmosphere with the ocean is described by a system of partial derivative equations of Navier-Stokes type. This system was too complex to solve numerically for the first computers. Edward Lorenz built then a very simplified model from these equations for studying a particular physical situation : the Rayleigh-Bénard convection phenomenon. He designed a differential system with only three degrees of freedom, much simpler to simulate numerically than the original equations:

$$\dot{x} = \sigma(y - x), \tag{1.33}$$

$$\dot{y} = \rho x - y - xz, \tag{1.34}$$

$$\dot{z} = xy - \beta z. \tag{1.35}$$

where σ, ρ, β are positive parameters. Variable x represents the intensity of the convection motion, y the temperature difference between ascending and descending air currents, et z the gap between the vertical temperature function and a linear function. Parameter σ , called Prandtl number, is the ratio between the cinematic viscosity and the thermal diffusivity. Parameter ρ characterizes the heat transfer inside the fluid.

Using numerical simulation, Lorenz discovered the chaotic property (in a deterministic sense) of the meteorological systems. Moreover, he highlighted the existence of ω - and α -limits with complex structure, known as strange attractors : one obtains in the phase space the well-known Lorenz "butterfly" illustrated on the right.



Chapter 2

Theory of stability

In this chapter, we focus on the different notions of stability emerging from the qualitative analysis of dynamical systems.

2.1 Structural stability of a vector field

Let M denote a compact submanifold of \mathbb{R}^n . Given a norm ||.|| on \mathbb{R}^n , we define the following norm of a \mathcal{C}^1 vector field on M

$$||X||_{CV} = \sup_{x \in M} ||X(x)|| + \sup_{x \in M} |DX(x)|.$$

Definition 12. A vector field $X \in \mathcal{C}^1(M)$ is structurally stable if there exists ε such that any $Y \in \mathcal{C}^1(M)$ satisfying

$$||X - Y||_1 < \varepsilon,$$

is topologically conjugated to X.

The structural stability means that the topological properties of a vector field are preserved under small deformations of the vector field.

2.2 Asymptotic stability of linear systems

We consider the linear differential system $\dot{x} = A.x$, for $x \in \mathbb{R}^n$ defined by the matrix $A \in \mathcal{M}_n(\mathbb{R})$.

Note $\lambda_j = a_j + ib_j$, $j \in \{1, ..., n\}$ the eigenvalues of A and $w_j = u_j + iv_j$ associated eigenvectors. We can sort the eigenvalues such that the k first are real (and consequently the k first eigenvectors are real) and that the vectors $(u_1, ..., u_k, u_{k+1}, v_{k+1}, ..., u_m, v_m)$ form a basis of \mathbb{R}^n with n = 2m - k.

We note E^s, E^u, E^c the stable, unstable and center subspaces defined as follows :

- E^s , the stable space generated by the vectors u_j, v_j such that $a_j < 0$,
- E^{u} , the unstable space generated by the vectors u_{i}, v_{i} such that $a_{i} > 0$,
- E^c , the center space generated by the vectors u_j, v_j such that $a_j = 0$.

Theorem 6. The space \mathbb{R}^n is decomposed as a direct sum

$$\mathbb{R}^n = E^s \bigoplus E^u \bigoplus E^c$$

of subspaces invariant under the flow $t \mapsto \exp(tA)$ of the linear system.

For the stable and unstable spaces, the following theorem applies.

Theorem 7. The following properties are equivalent:

- i) all the eigenvalues of A have strictly negative real parts,
- ii) $\exists M > 0, \exists c > 0, \forall x_0 \in \mathbb{R}^n, \forall t \in \mathbb{R}, \quad |\exp(tA).x_0| \le M|x_0|\exp(-ct).$
- iii) $\forall x_0 \in \mathbb{R}^n$, $\lim_{t \to +\infty} \exp(tA) \cdot x_0 = 0.$

Hence, we notice that, if all the eigenvalues of A have strictly negative real parts, the ω -limit of any orbit of the linear system is 0 (i.e. the unique singular point of the linear vector field). In the following section, we generalize this notion of stability for singular points of non linear systems as well as for their orbits.

2.3 Stability of a solution, Poincaré-Lyapunov theorem

Definition 13. A solution x(t) of a differential system $\dot{x} = f(x,t)$ is said stable if, for any $\varepsilon > 0$, there exists $\delta > 0$ such that, for any solution y(t)

$$||(x-y)(t_0)|| \le \delta \Longrightarrow \forall t \ge t_0, ||(x-y)(t)|| \le \varepsilon$$

If, moreover, $||y - x|| \to 0$ when $t \to +\infty$, the solution is said asymptotically stable.

Remark 4. Warning : the notion of instability often refers to the non-stability, i.e. if the properties of the above definition are not satisfied. We will refer to the notions obtained by changing $t \ge t_0$ and $t \to +\infty$ by $t \le t_0$ and $t \to -\infty$ respectively as "stability (resp. asymptotic stability) for the inverse flow", i.e. by changing the time orientation.

Remark 5. Since a singular point of a vector field is a particular orbit of an autonomous differential system, the notions of stability and asymptotic stability can be applied.

Theorem 8. (Poincaré-Lyapunov)

We consider the differential system $\dot{x} = Ax + h(x,t)$ where $A \in \mathcal{M}_n(\mathbb{R})$, h is continuous in the domain $D = \{(x,t)|||x|| \le \rho, t \ge 0\}$ where $\rho > 0$ and satisfies

$$\frac{||h(x,t)||}{||x||} \to 0 \text{ when } ||x|| \to 0 \text{ uniformly w.r.t. } t \ge 0.$$

If all the eigenvalues of A have strictly negative real parts, then the solution x = 0 is asymptotically stable.

Note : The proof (in french) can be found in Appendix A.1.

Remark 6. Reciprocally, if the matrix A has at least one eigenvalue with a positive real part, then x = 0 is an unstable solution of the system.

Definition 14. A linear system with coefficients depending on time, i.e.

$$\dot{y} = A(t)y$$

is said reducible (or A(t) is said reducible) in the sense of Lyapunov if there exists a change of function y = Q(t)x where Q(t) is a differentiable and invertible matrix such that

$$\sup_{t} ||Q(t)|| < +\infty, \qquad \sup_{t} ||Q^{-1}(t)|| < +\infty.$$

which transforms the system into

 $\dot{x} = Bx,$

where B is a constant matrix

We can obviously generalize the Poincaré-Lyapunov theorem to reducible systems.

2.4 Lyapunov function

Theorem 9. Let $f = (f_i)_{i=1}^n$ denote a differentiable vector field on an open subset U of \mathbb{R}^n associated with the autonomous system

$$\dot{x} = f(x)$$

Let $\phi(t, x)$ denote the associated flow and $x_0 \in U$ a singular point of f. We assume that there exists a function $G \in \mathcal{C}^1(V, \mathbb{R})$ where V is a neighborhood of x_0 , such that

$$G(x_0) = 0, (2.1)$$

$$\forall x \neq x_0, \quad G(x) > 0, \tag{2.2}$$

$$\forall x \in V, \quad \frac{d(G \circ \phi)}{dt}_{|t=0}(x) = DG(x).f(x) = \sum_{i=1}^{n} f_i(x) \frac{\partial G}{\partial x_i}(x) \le 0.$$
(2.3)

Then the singular point x_0 is stable. If, moreover,

$$\forall x \in V \setminus \{x_0\}, \quad \frac{d(G \circ \phi)}{dt}_{|t=0}(x) < 0.$$

then the singular point x_0 is asymptotically stable.

Remark 7. The function defined in the above theorem

$$\frac{d(G \circ \phi)}{dt}_{|t=0}(x) = DG(x).f(x)$$

is the derivative of the function G along the flow of the vector fiel or, equivalently, the derivative along the orbits of the system.

Definition 15. A function G satisfying the hypotheses (2.1)-(2.2)-(2.3) is called a Lyapunov function of the vector field.

We now focus on the specific case of planar dynamics. We consider a C^2 planar vector field associated with a differential system

$$\dot{x} = f(x, y), \tag{2.4}$$

$$\dot{y} = g(x, y). \tag{2.5}$$

where f and g are \mathcal{C}^2 on an open subset $U \subset \mathbb{R}^2$.

Definition 16. A first integral of the differential system (2.4)-(2.5) is a differentiable function $(x, y) \mapsto H(x, y)$ such that:

$$f(x,y)\frac{\partial H}{\partial x} + g(x,y)\frac{\partial H}{\partial y} = 0.$$

If such a function exists, system (2.4)-(2.5) is said conservative. Otherwise, it is called dissipative.

Remark 8. Function H can be interpreted as an energy function of the system, as a Lyapunov function. The terminology "conservative system" is inspired by the property of energy conservation along each orbit of the system.

Proposition 1. A conservative planar system that is non trivial, i.e. H is non constant according to its first and second variable, admits a continuum of periodic orbits.

Definition 17. The system (2.4)-(2.5) is hamiltonian if there exists a function $(x, y) \mapsto H(x, y)$ such that, for any (x, y),

$$f(x,y) = \frac{\partial H}{\partial y}$$
 et $g(x,y) = -\frac{\partial H}{\partial x}$.

Function H is therefore a first integral and the system is conservative.

2.5 Classification of singular points and invariant manifolds

We consider a differentiable vector field $f = (f_i)_{i=1}^n$ defined on an open subset U of \mathbb{R}^n associated with an autonomous differential system

$$\dot{x} = f(x) = f(x_1, ..., x_n) \tag{2.6}$$

Let $\bar{x} \in U$ denote a singular point $(f(\bar{x}) = 0)$. We note $J_f(\bar{x})$ the jacobian matrix associated with f evaluated at the point \bar{x} :

$$J_f(\bar{x}) = \left(\frac{\partial f_i}{\partial x_j}(\bar{x})\right)_{(i,j) \in \{1,\dots,n\}^2}.$$

Using a Taylor development of f in the neighborhood of \bar{x} , we can write system (2.6), after the change of variable $x \leftrightarrow x - \bar{x}$, as follows:

$$\dot{x} = J_f(\bar{x}).x + h(x)$$

where h is a continuous function such as $h(x) = O(||x||^2)$. Hence, near the singular point \bar{x} , we associate with the vector field f a linear vector field $\dot{x} = J_f(\bar{x}).x$ called the linearized vector field. We classify the singular points of the non linear differentiable vector fields according to the properties of the linearized vector field.

Definition 18. A singular point \bar{x} of a vector field X is hyperbolic if all the eigenvalues of $J_X(\bar{x})$ have a non zero real part.

Remark 9. The translation of \bar{x} to the origin allows us to consider that the singular point is the origin, which we will do in the following without loss of generality.

As for the singular point 0 of a linear differential system, there exist stable, unstable and center invariant manifolds associated with each singular point of a non linear system. The following theorem state the existence and the properties of the stable and unstable manifolds associated with a hyperbolic singular point and their link with the stable and unstable subspaces of the linearized system.

Theorem 10. Consider a \mathcal{C}^1 vector field, $\phi(t, x)$ its flow, and the associated system $\dot{x} = f(x)$ defined on an open subset of \mathbb{R}^n containing 0. We assume that 0 is a hyperbolic singular point and, thus, that the jacobian matrix $J_f(0)$ admits

- k eigenvalues $(\lambda_i)_{i=1}^k$ with strictly negative real part,
- n-k eigenvalues $(\lambda_i)_{i=k+1}^n$ with strictly positive real part.

We note E^s and E^u the stable and unstable subspaces of the linearized system $\dot{x} = J_f(0).x$. There exists a differentiable manifold \mathcal{W}^s of dimension k, tangent to E^s at 0, invariant under the flot ϕ and such that

$$\forall x_0 \in \mathcal{W}^s, \quad \lim_{t \to +\infty} \phi(t, x_0) = 0.$$

Similarly, there exists a differentiable manifold \mathcal{W}^u of dimension n - k, tangent to E^u at 0, invariant under the flow ϕ and such that

$$\forall x_0 \in \mathcal{W}^u, \quad \lim_{t \to -\infty} \phi(t, x_0) = 0.$$

Note : The proof (in french) can be found in Appendix A.2.

Example : planar dynamics. If a vector field admits a singular point (\bar{x}, \bar{y}) and if the associated jacobian matrix at this point has real eigenvalues $\lambda < 0$ and $\mu > 0$, the stable and unstable manifold of this point are differentiable curves containing (\bar{x}, \bar{y}) . They are tangent to the stable and unstable subspaces of the linearized vector field respectively, that are generated by an eigenvector of the jacobian matrix associated with λ and μ respectively. In that case, the singular point is called a saddle and the stable and unstable manifolds are called the separatrices of the saddle. We will describe the exhaustive classification of the singular points of a planar vector field in a subsequent section.

Definition 19. Consider a saddle singular point of a given planar vector field. If the invariant manifolds intersect at other points than the saddle, the saddle is called an homoclinic point. In that case, the common part of the stable and unstable manifolds is called an homoclinic connection.

Theorem 11. Hartman-Grobman theorem

Consider a \mathcal{C}^1 vector field defined on a neighborhood U of 0 in \mathbb{R}^n associated with the differential system

$$\dot{x} = f(x).$$

We assume that 0 is a hyperbolic singular point and note $J_f(0)$ the jacobian matrix evaluated at 0. There exists a homeomorphism $h: U \to U$ such that h(0) = 0 and

$$h \circ \phi_t(x) = e^{tJ_f(0)} \circ h(x).$$

If the vector field is \mathcal{C}^2 , h can be chosen such that it is a \mathcal{C}^1 -diffeomorphism.

The vector field is thus topologically conjugated (resp. C^1 conjugated) in the neighborhood of 0 with the linearized vector field. The proof of this result can be found in [Hartman, 1982].

The conjugacy results near non hyperbolic singular points need other informations than the linear approximation. However the existence of the center manifold associated with the center subspace of the linear system is stated by the following result.

Theorem 12. Existence of a center manifold

Consider a \mathcal{C}^k vector field defined on the neighborhood of the origin $0 \in \mathbb{R}^n$ associated with

$$\dot{x} = C.x + F(x, y, z),$$
 (2.7)

$$\dot{y} = P.y + G(x, y, z),$$
 (2.8)

$$\dot{z} = Q.z + H(x, y, z),$$
 (2.9)

where $x \in \mathbb{R}^r$, $y \in \mathbb{R}^p$, $z \in \mathbb{R}^q$, p+q+r=n,

 $C \in \mathcal{M}_r(\mathbb{R})$ and its eigenvalues have 0 real parts,

- $P \in \mathcal{M}_p(\mathbb{R})$ and its eigenvalues have strictly negative real parts,
- $Q \in \mathcal{M}_q(\mathbb{R})$ and its eigenvalues have strictly positive real parts.

Then, there exists a C^{k-1} submanifold W^c of dimension r, invariant under the flot, tangent to the subspace y = z = 0. Such a manifold is called a center manifold.

Remark 10. On the contrary of the stable and unstable manifolds, a center manifold is not uniquely defined. If f is C^{∞} then, for any $r \in \mathbb{N}$, there exists a C^r center manifold.

Theorem 13. Restriction to a center manifold

Under the hypotheses of the above theorem, there exists a neighborhood of \mathcal{W}^c and a local \mathcal{C}^k conjugacy on this neighborhood between the vector field and its restriction to the center manifold.

Practically, we search for a center manifold as the solution of a system of two equations :

$$y = h_1(x), \quad z = h_2(x).$$

Differentiating these equations, the invariance of \mathcal{W}^c under the flow implies

$$\dot{y} = Dh_1(x).\dot{x}, \quad \dot{z} = Dh_2(x).\dot{x}.$$

Hence one obtains the two equations for (h_1, h_2) :

$$Dh_1(x)[C.x + F(x, h_1(x), h_2(x))] - P.h_1(x) - G(x, h_1(x), h_2(x)) = 0, \qquad (2.10)$$

$$Dh_2(x)[C.x + F(x, h_1(x), h_2(x))] - Q.h_2(x) - H(x, h_1(x), h_2(x)) = 0.$$
(2.11)

The solution is not unique in general, which is consistent with the above remark. Given a solution (h_1, h_2) of system (2.10)-(2.11), the qualitative local behavior of the vector field is therefore described by the following theorem.

Theorem 14. Under the hypotheses of the above theorems, we consider a solution (h_1, h_2) de (2.10)-(2.11). Then, in the neighborhood of the singular point, the vector field is topologically conjugated with

$$\dot{x} = C.x + F(x, h_1(x), h_2(x)),$$

 $\dot{y} = P.y,$
 $\dot{z} = Q.z.$

2.6 Planar dynamics and Poincaré-Bendixson theorem

In this section, we focus on any \mathcal{C}^2 planar vector field associated with a differential system

$$\dot{x} = f(x, y), \tag{2.12}$$

$$\dot{y} = g(x, y). \tag{2.13}$$

where f and g are \mathcal{C}^2 on an open subset $U \subset \mathbb{R}^2$.

We restrict the study to the classification of the singular point of a non linear system using the local C^1 conjugacy of the flow with a linear system. Concerning the hyperbolic points, this linear system is the linearized system (defined by the jacobian matrix evaluated at the singular point) if the vector field is smooth enough (at least C^2), which we assume in the following. Results under weaker hypotheses exist and can be found, for instance, in [Wiggins, 1990].

Definition 20. Consider a hyperbolic singular point of the differential system (2.12)-(2.13). Note λ and μ the (complex) eigenvalues of the jacobian matrix associated with the vector field evaluated at this point. Thus, $\Re(\lambda) \neq 0$ and $\Re(\mu) \neq 0$. The following table

- defines the terminology used for describing the nature of the singular point according to λ and μ (the column entries distinguish between the real and complex cases, the raw entries distinguish the cases according to the number of eigenvalues with strictly negative real parts),
- specifies the dimension of the stable and unstable manifolds of the singular point,
- illustrates the local phase portrait in the neighborhood of the singular point (purple point) : blue orbits belong to \mathcal{W}^s , red orbits belong to \mathcal{W}^u , black orbits complete the phase portrait, the arrows indicate the sense to the flow.

Hyperbolic points	$\lambda,\mu\in\mathbb{R}$	$\lambda=\overline{\mu}\in\mathbb{C}\backslash\mathbb{R}$
$\Re(\lambda) < 0, \Re(\mu) < 0$ stable $\dim(\mathcal{W}^s) = 2$ $\dim(\mathcal{W}^u) = 0$	Attractive node	Attractive focus
$\Re(\lambda) > 0, \Re(\mu) > 0$ unstable $\dim(\mathcal{W}^s) = 0$ $\dim(\mathcal{W}^u) = 2$	Repulsive node	Repulsive focus
$\Re(\lambda) < 0, \Re(\mu) > 0$ unstable $\dim(\mathcal{W}^s) = 1$ $\dim(\mathcal{W}^u) = 1$	Saddle	Impossible !

For non hyperbolic singular points, there is no general result of conjugacy with the linearized flow. Hence, the classification can not be based on the eigenvalues of the jacobian matrix since the local phase portrait depends on higher degree terms of functions f and gdevelopments. However, certain cases are known and defined as follows. For each type, we give an instance of vector field for which the origin is a non hyperbolic singular point of this type.

Definition 21. A sector in \mathbb{R}^2 is hyperbolic (resp. parabolic, elliptic) if it is topologically conjugated with the sector shown in panel (a) (resp. (b), (c)) of the figure below.



Definition 22. An isolated singular point p of (2.12)-(2.13) is called

- a center if there exists a pointed neighborhood of p such that any orbit in this neighborhood is periodic and surrounds p;
- a center-focus, if there exists a sequence of close orbits (Γ_n) such that:
 - 1. for any n, Γ_n surrounds Γ_{n+1} ,
 - 2. $(\Gamma_n)_n \to \{p\},\$

- 3. any orbit between Γ_n and Γ_{n+1} spirals and reaches asymptotically Γ_n and Γ_{n+1} for $t \to \pm \infty$ respectively;
- an elliptic point if, locally around p, the vector field admits an elliptic sector;
- a saddle-node if, locally around p, the phase portrait is split into a hyperbolic sector and a parabolic sector;
- a cusp if, locally around p, the phase portrait is split into two and only two hyperbolic sectors.

The following table gives simple examples of planar vector fields for which the origin is an isolated and non hyperbolic singular point of a particular type mentioned above. The example of a center-focus is written in polar coordinates for sake of compactness.

centre	centre-foyer	p.s. à secteur elliptique	col-noeud	cusp
$\dot{x} = y$	$\dot{\rho} = \prod_{i=1}^{\infty} (\rho - r_i)$	$\dot{x} = y$	$\dot{x} = x^2$	$\dot{x} = y$
$\dot{y} = -x$	$ \begin{array}{l} \theta = 1 \\ (r_i) \text{ strictly} \\ \text{decreasing towards } 0 \end{array} $	$\dot{y} = -x^3 + 4xy$	$\dot{y} = y$	$\dot{y} = x^2$

Theorem 15. (Poincaré-Bendixson)

Let X denote a \mathcal{C}^1 vector field in an open subset $U \in \mathbb{R}^2$ associated with

$$\dot{x} = f(x, y), \tag{2.14}$$

$$\dot{y} = g(x, y). \tag{2.15}$$

Let K denote a compact set included in U and $\gamma_m = \{\phi(t,m) | t \in \mathbb{R}\}$ an orbit of X such that the positive half-orbit $\gamma_m^+ = (\phi(t,m) | t \ge 0) \subset K$. Assume that $\omega(m)$ contains a finite number of singular points of X.

- i) If $\omega(m)$ contains no singular point, then $\omega(m)$ is a periodic orbit.
- ii) If $\omega(m)$ contains both regular and singular points, then $\omega(m)$ is formed by singular points and orbits connecting them. In that case, $\omega(m)$ is called a graphic.
- iii) If $\omega(m)$ contains no regular point, then $\omega(m)$ is a singular point.

Note : The proof (in french) can be found in Appendix A.3.

Poincaré-Bendixson Theorem and the classification of the singular points of planar vector fields are powerful tools for the qualitative analysis of bidimensional models. In the particular case of hyperbolic structure, the phase portrait can be identified if we can restrict the flow to an invariant compact set such that the flow points towards its interior on the boundary and if the singular points are known.

CHAPTER 2. THEORY OF STABILITY

Chapter 3

Introduction to bifurcation and singular perturbation theories

3.1 Introduction to bifurcation theory

3.1.1 Bifurcation, unfolding and codimension

The bifurcation theory aims at describing the changes in the phase portrait of a vector field

$$\dot{x} = f(x, \lambda) \tag{3.1}$$

where f is assumed to be at least C^2 w.r.t. x and $\lambda \in \mathbb{R}^k$, when the values of parameter λ varies.

Definition 23. A value λ_0 of λ is called a bifurcation value for system (3.1) if the vector field $f(x, \lambda_0)$ is not topologically equivalent to $f(x, \lambda)$ for any λ in the neighborhood of λ_0 . In this case, system (3.1) undergoes a bifurcation for $\lambda = \lambda_0$.

A bifurcation of a vector field is thus a change in the structure of its phase portrait when the value of parameter λ (that may be multi-dimensional) passes by the value λ_0 . This involves the appearance, the disappearance or the change in the nature of certain dynamical invariants, in particular singular points or periodic orbits or more complex invariant manifolds. The bifurcation theory allows us to classify certain changes in the structure. Completing this theory is still nowadays an open problem since the theory of structural stability itself is not complete, even for planar dynamics. A large panel of problems linked with this theory are intensively studied.

Among the general tools developed for understanding the bifurcations, the notions of unfolding and codimension of a bifurcation are essential.

Definition 24. Let $f_0(x)$ denote a \mathcal{C}^1 vector field. An unfolding of this vector field is a family of \mathcal{C}^1 vector fields $f(x, \lambda)$ (indexed by λ) such that there exists λ_0 verifying $f(x, \lambda_0) = f_0(x)$. Such unfolding $f(x, \lambda)$ is said universal if any unfolding of $f_0(x)$ is topologically equivalent to an unfolding induced by a restriction of $f(x, \lambda)$.

Definition 25. Assume that (3.1) undergoes a bifurcation for $\lambda = \lambda_0$. The codimension of this bifurcation is the minimal number of parameter involved in a universal unfolding of the

vector field $f(x, \lambda_0)$, i.e. the smallest integer m such that there exists a universal unfolding $g(x, \mu), \mu \in \mathbb{R}^m$, of $f(x, \lambda_0)$.

In the following, we only present a few classical (and simple) bifurcations and the structure of the vector fields that undergo such bifurcation.

3.1.2 A few examples of codimension 1 bifurcations

In this section, we describe local codimension 1 bifurcations, "local" meaning that they only involves a change in a singular point of the bifurcating vector field (number, nature) and, hence, only affects the structure of the phase portrait locally near a singular point. The table below illustrates a few bifurcations of such type, a universal unfolding in dimension 1 (resp. 2 in polar coordinate for the Hopf bifurcation) and a scheme of the varying phase portrait w.r.t. the bifurcation parameter λ near the bifurcation value $\lambda = 0$.

The saddle-node and Hopf bifurcations are "generic" (the notion of genericity will be specified in the following). However, other non generic bifurcations, in particular the transcritical and pitchfork bifurcations, are also crucial for understanding the phase portrait of models in Life Science. Therefore, we present them as well.

Saddle-node	Transcritical	Pitchfork	Hopf					
$\dot{x} = \lambda - x^2$	$\dot{x} = \lambda x - x^2$	$\dot{x} = \lambda x - x^3$	$\dot{\rho} = \rho(\lambda - \rho^2)$ $\dot{\theta} = 1$					
	x x x		y C A C					
 Blue lines : locus of the stable singular points ; Dashed blue lines : locus of the unstable singular points ; Black lines and arrows : orbits and orientation of the flow ; Red surface : family of limit cycles. 								

Saddle-node bifurcation Assume that the vector field (3.1) admits for $\lambda = \lambda_0$ a singular point x_0 at which the linearized system admits a single eigenvalue 0. The center manifold theorem allows us to reduce this type of bifurcation to a dimension 1 problem (i.e. $x \in \mathbb{R}$. More precisely, there exists a two-dimensional center manifold $\mathcal{W}^c \in \mathbb{R}^n \times \mathbb{R}$ associated with the flow of

$$\dot{x} = f(x,\lambda), \tag{3.2}$$

$$\dot{\lambda} = 0 \tag{3.3}$$

passing through (x_0, λ_0) and such that

- the tangent space to \mathcal{W}^c at (x_0, λ_0) is generated by an eigenvector of $D_x f(x_0, \lambda_0)$ associated with the eigenvalue 0 and a vector that is parallel to the λ axis;
- the manifold \mathcal{W}^c is \mathcal{C}^1 in the neighborhood of (x_0, λ_0) ;
- the flow associated with (3.2) is tangent to \mathcal{W}^c ;
- there exists a neighborhood U of (x_0, λ_0) such that all trajectories contained in U for all time belong to \mathcal{W}^c .

By restricting the vector field (3.2)-(3.3) to \mathcal{W}^c , one obtains a one-parameter family (indexed by λ) of equations on the curves \mathcal{W}^c_{λ} of \mathcal{W}^c obtained when fixing the value of λ . We can therefore formulate the transversality conditions of the problem (3.2) in one dimension for obtaining the saddle-node bifurcation. By hypothesis

$$\mathbf{D}_x f(x_0, \lambda_0) = 0$$

and we add the transversality condition

$$D_{\lambda}f(x_0,\lambda_0) \neq 0.$$

By the implicit function theorem, the locus of singular points of (3.1) when λ varies around λ_0 is a curve tangent to $\lambda = \lambda_0$. The additional transversality condition

$$D_r^2 f(x_0, \lambda_0) \neq 0$$

implies that the curve of singular points has a quadratic tangency with $\lambda = \lambda_0$ and, locally, lies on a single side of this straight line. Such a bifurcation can be interpreted as the disappearance (or appearance depending on the sense of variation of parameter λ) of two hyperbolic singular points. The dimension of their stable manifold is p and (p+1) respectively and the dimension of their unstable manifold is (n-p) and (n-p-1) respectively. At the bifurcation value, locally, there is only one singular point, non hyperbolic, at which the linearized system admits a unique eigenvalue with 0 real part (which is thus real and exactly 0).

The two conditions are sufficient to ensure the topological equivalency between the family of vector fields (3.2) and $\dot{x} = \lambda - x^2$. However, the transversality conditions can be expressed for a *n*-dimensional system without using the restriction to the center manifold.

Theorem 16. (Sotomayor)

Assume that (3.1) admits a singular point x_0 for $\lambda = \lambda_0$ $(f(x_0, \lambda_0) = 0)$ such that :

(SN1) $D_x f(x_0, \lambda_0)$ admits

• 0 as single eigenvalue with an associated eigenvector v,

- k eigenvalues with strictly negative real parts,
- n k 1 eigenvalues with strictly negative real parts.

Note w an eigenvector of the transpose matrix ${}^{t}D_{x}f(x_{0},\lambda_{0})$ for the eigenvalue 0.

(SN2) ${}^{t}wD_{\lambda}f(x_0,\lambda_0) \neq 0,$

(SN3) ${}^{t}w(D_{x}^{2}f(x_{0},\lambda_{0})(v,v)) \neq 0.$

Then, there exists a differentiable curve of singular points of (3.1) in $\mathbb{R}^n \times \mathbb{R}$ passing through (x_0, λ_0) and tangent to the hyperplane $\mathbb{R}^n \times \{\lambda_0\}$. According to the sign of the expressions in (SN1) and (SN2), in the neighborhood of x_0 , there is no singular point if $\lambda < \lambda_0$ and there are two singular points if $\lambda > \lambda_0$. The two singular points are hyperbolic and admits stable manifolds of dimension k and k+1 respectively.

Hence, the vector fields satisfying (SN2)-(SN3) are structures locally as the family $\dot{x} = \lambda - x^2$. This bifurcation is generic in the following sense : any one parameter vector field admitting, for a bifurcation value, a singular point with a single eigenvalue 0 can be perturbed into a one parameter vector field undergoing a saddle-node bifurcation. It is the case for the following transcritical and pitchfork bifurcations (non generic) described below.

Transcritical Bifurcation A transcritical bifurcation corresponds to the crossing phenomenon of two hyperbolic points involving the exchange of their nature. Hence, locally near (x_0, λ_0) , there exist two differentiable curves C_1 et C_2 of singular points of (3.1) in $\mathbb{R}^n \times \mathbb{R}$ such that :

- $C_1 \cap C_2 = \{(x_0, \lambda_0)\}.$
- C_1 and C_2 are graphs above λ . We note C_1^- and C_2^- (resp. C_1^+ et C_2^+) the parts of C_1 and C_2 above $\lambda < 0$ (resp. $\lambda > 0$).
- C_1^- and C_2^+ (resp. C_1^+ et C_2^-) are formed by points (x, λ) where x is a hyperbolic singular point for (3.1) with k (resp. k + 1) eigenvalues with negative real parts.

This type of bifurcation occurs for instance when, by construction, a system admits a trivial solution for any parameter value and from which a bifurcation arises. Hence, the universal unfolding given in the table at the beginning of the section $\dot{x} = \lambda x - x^2$ admits the trivial solution x = 0 corresponding to a singular point for any λ . This locus of singular points constitutes the curve C_1 or the curve C_2 . For any value of $\lambda \neq 0$, there exists another singular point $x = \lambda$. Obviously

- for $\lambda < 0$, x = 0 is stable and $x = \lambda$ is unstable,
- for $\lambda > 0$, x = 0 is unstable et $x = \lambda$ is stable,

More generally, in multidimensional cases, the transcritical bifurcation consists of the crossing at the bifurcation value $\lambda = \lambda_0$ of two hyperbolic singular points (for which the locus w.r.t. λ near λ_0 are differentiable curves) that exchange their nature: the stable manifold of one singular point wins an additional dimension while the stable manifold of the other one looses a dimension. **Application to May's Model** We illustrate two cases of transcritical bifurcation on the same model. First, we describe the bifurcation in dimension 1 when focusing on the prey dynamics and considering the density of predators as a parameter. Second, we consider the whole system in dimension 2 and show that a transcritical bifurcation occurs as well.

The first equation of May's model drives the dynamics of the prey when the predator y is considered as a constant parameter. We replace y by a fixed parameter \bar{y} in (1.16):

$$\dot{x} = x \left(a(1-x) - b \frac{\bar{y}}{A+\bar{y}} \right), \tag{3.4}$$

where a, b, A > 0.

For any value of $\bar{y} > 0$, this equation admits two singular points x = 0 and

$$x_{\bar{y}}^s = 1 - \frac{b\bar{y}}{a(A+\bar{y})}.$$

Hence, if b > a, for $\bar{y} = y_{\text{trans}} = aA/(b-a) > 0$ those two singular points collide (see Figure 3.1.2) and the (one-dimensional) jacobian matrix

$$J = a(1-2x) - \frac{by}{A+y}$$

evaluated for $\bar{y} = y_{\text{trans}}$ at $x = x_{y_{\text{trans}}}^s = 0$ is 0.



One can easily prove that:

- for $\bar{y} > y_{\text{trans}}$, 0 is attractive and $x_{\bar{y}}^s$ is repulsive,
- for $\bar{y} < y_{\text{trans}}$, 0 is repulsive et $x_{\bar{y}}^s$ is attractive.

Such uncoupling of the state variable can bring useful information on the complete structure of the flow. But, of course, one can also consider the whole model and vary a chosen parameter. We already proved that (1,0) is a singular point and, if b > a and d > cA, there is non trivial singular point in the quarter plane $\{x > 0, y > 0\}$. It is thus easy to show that, for d greater than (but close to) cA, the non trivial singular point is an attractive node, and for d = cA, the system undergoes a transcritical bifurcation : the non trivial and (1,0) collide. For d < cA, the non trivial point belongs to y < 0 and is a saddle while (1, 0) is an attractive node.

This change in the phase portrait is interpreted as a loss of viability of the trophic system: if the death rate c of the predator is too large (or if its predation efficiency is too weak), then the predator population tends towards extinction and the prey population reaches its maximal representation. We can then quantify this natural idea with the line of transcritical bifurcation in the parameter space (c, d) (the other parameters assumed to be constant) : crossing transversally this line in the parameter space corresponds to a transcritical bifurcation of the system. The figure below illustrates the passage through the transcritical bifurcation.



Pitchfork Bifurcation A pitchfork bifurcation occurs for system (3.1) if, from a hyperbolic singular point $x_0(\lambda)$ existing for any λ value near λ_0 , arise two other singular points of the same nature for $\lambda > \lambda_0$. More precisely, locally near $(x_0(\lambda_0), \lambda_0)$, there exist two differentiable curves $C_1 = \{(x_0(\lambda), \lambda) | \lambda \text{ in a neighborhood of } \lambda_0\}$ and C_2 of singular points in $\mathbb{R}^n \times \mathbb{R}$ such that:

- $C_1 \cap C_2 = \{(x_0, \lambda_0)\}.$
- C_1 is a graph above λ and C_2 lies in $\lambda \geq \lambda_0$.
- Except $x_0(\lambda_0)$ for $\lambda = \lambda_0$, for any point (x, λ) of C_1 or C_2 , x is an hyperbolic singular point for (3.1).
- Depending on the third derivative of the flow w.r.t. x at x_0 with $\lambda = \lambda_0$,
 - for $\lambda < \lambda_0$ there exists a unique singular point, which admits k + 1 (resp. k) eigenvalues with negative real parts and lies on C_1 ,
 - for $\lambda > \lambda_0$, there exists a singular point lying on C_1 admitting k (resp. k + 1) eigenvalues with negative real parts and two singular points lying on C_2 and admitting k + 1 (resp. k) eigenvalues with negative real parts.

The pitchfork bifurcation is then called supercritical (resp. subcritical).

Hopf Bifurcation

Theorem 17. Consider a one-parameter family of vector fields X_{λ} associated with the systems

$$\dot{x} = f(x, \lambda), \tag{3.5}$$

where f is \mathcal{C}^k . Assume that x_0 is a singular point of X_{λ_0} and satisfies the following properties:

(H1) $D_x f(x_0, \lambda_0)$ admits a single pair of conjugated purely imaginary eigenvalues $\mu(\lambda_0)$ and $\mu(\overline{\lambda}_0)$ and no other eigenvalues with null real part.

Then, in a neighborhood of λ_0 , there exists a differentiable curve (x_{λ}^s, λ) where every x_{λ}^s is a singular point of X_{λ} and passing through (x_0, λ_0) . In this neighborhood, the eigenvalues of $D_x f(x_{\lambda}^s, \lambda)$ vary in a differentiable way with respect to λ . If, moreover,

(H2)

$$\frac{d}{d\lambda} \left(\Re(\mu(\lambda)) \right)_{|\lambda=\lambda_0} = d \neq 0$$

the bifurcation is generic and called Hopf bifurcation. There exists a unique center manifold of dimension 3 of

$$\dot{x} = f(x,\lambda), \tag{3.6}$$

$$\dot{\lambda} = 0 \tag{3.7}$$

passing through (x_0, λ_0) and a C^3 change of variable preserving the hyperplanes $\lambda = cste$ for which the principal part of the Taylor development at order 3 on the center manifold is given by

$$\dot{x} = d\lambda x - (\omega + c\lambda)y + (ax + by)(x^2 + y^2), \qquad (3.8)$$

$$\dot{y} = (\omega + c\lambda)x + d\lambda y + (bx + ay)(x^2 + y^2).$$
(3.9)

In polar coordinates, it writes

$$\dot{\rho} = (d\lambda + a\rho^2)\rho, \qquad (3.10)$$

$$\dot{\theta} = \omega + c\lambda + b\rho^2. \tag{3.11}$$

If $a \neq 0$, there exists a one-parameter family, indexed by λ , of hyperbolic limit cycles of (3.5). This family of limit cycles defines a surface in the center manifold with a quadratic tangence with the two-dimensional eigenspace associated with $\mu(\lambda_0)$ and $\mu(\bar{\lambda}_0)$. The principal part of the development at order 2 of this surface coincide with the paraboloïd $\lambda = -a\rho^2/d$. Finally

- If a < 0, the limit cycles are attractive and the Hopf bifurcation is said supercritical;
- If a > 0, the limit cycles are repulsive and the Hopf bifurcation is said subcritical.

The supercritical Hopf bifurcation is then a destabilization of the "attractive focus part" of a hyperbolic singular point when the pair of complex conjugated eigenvalues associated with this part crosses the imaginary axis, turning this part into a "repulsive focus part". This destabilization gives birth to an attractive limit cycle which persists locally near the bifurcation

value $\lambda = \lambda_0$. Its radius grows as $\sqrt{\lambda - \lambda_0}$. When the bifurcation is subcritical, the limit cycle is repulsive with the same properties.

In application to models in Life Science, the Hopf bifurcation indicates, from the singular point analysis, the birth of a limit cycle and the emergence of oscillatory behaviors. In the general case, its is hard to characterize the interval of the parameter values for which the cycle persists, since, far away from the bifurcation value, it depends on the global dynamics. Nevertheless, it is a generic structure of a transition between a stationary behavior and an oscillatory behavior.

3.1.3 A few application to models in Life Science

Lorenz model We recall the equations of Lorenz model

$$\dot{x} = \sigma(y - x), \tag{3.12}$$

$$\dot{y} = \rho x - y - xz, \tag{3.13}$$

$$\dot{z} = xy - \beta z. \tag{3.14}$$

where the parameters ρ, σ, β are assumed positive. The origin is always a singular point and the jacobian matrix evaluated at the origin is

$$J(0) = \begin{pmatrix} -\sigma & \sigma & 0\\ \rho & -1 & 0\\ 0 & 0 & -\beta \end{pmatrix}$$
(3.15)

For $\rho < 1$, the origin is an attractive node. For $\rho = 1$, J(0) admits $0, -\beta < 0$ and $-1 - \sigma < 0$ as eigenvalues. For $\rho > 1$, the origin is a saddle with a one-dimensional unstable manifold and two non trivial singular points appear:

$$(x, y, z) = \left(\pm\sqrt{\beta(\rho-1)}, \pm\sqrt{\beta(\rho-1)}, \rho-1\right)$$

that are attractive nodes for

$$\rho \in]1, \rho_{\mathrm{H}}[$$
 with $\rho_{\mathrm{H}} = \sigma \frac{\sigma + \beta + 3}{\sigma - \beta - 1}.$

The origin undergoes a pitchfork bifurcation for $\rho = 1$.

For $\rho = \rho_{\rm H}$, two subcritical Hopf bifurcations occur simultaneously for the non trivial singular point. Indeed, the two eigenvalues are then

$$-(\sigma + \beta + a)$$
 et $\pm i\sqrt{(2\sigma(\sigma + 1)/(\sigma - \beta - 1))}$.

Note that a classical hypothesis on Lorenz model is $\sigma > 1 + \beta$.

This bifurcation study introduce the first elements for understanding the phase portrait of Lorenz model. A geometrical study of the stable and unstable manifolds of the non trivial singular points and their entertained structure allows describing the emergence of the strange attractor known as "Lorenz butterfly". **FitzHugh-Nagumo system** We describe the local bifurcations of the FitzHugh-Nagumo system when a whose parameter varies. The other parameter values need to be fixed in order to identify the codimension 1 bifurcations.

For fixing the ideas, we assume I = 0 in the Fitzhugh-Nagumo system which therefore writes

$$\varepsilon \dot{x} = -y + 4x - x^3, \tag{3.16}$$

$$\dot{y} = a_0 x + a_1 y + a_2. \tag{3.17}$$

We first focus on the case $a_0 > 0$ and a_1 small. One obtains the following sequence of bifurcation for increasing values of a_2 that can easily be calculated :

Bifurcation col-noeud \rightarrow Bifurcation de Hopf surcritique

\rightarrow Bifurcation de Hopf surcritique inverse \rightarrow Bifurcation col-noeud

We can visualize geometrically this sequence of bifurcations by translating the y-nullcline from the right to the left of the phase space, which corresponds to increasing a_2 . We detail this sequence in the following but leave to the reader the (explicit) calculation of the a_2 values for which the bifurcations occur.

For increasing values of a_2 from a large negative value, the first saddle-node bifurcation occurs when the y-nullcline of equation $a_0x + a_1y + a_2 = 0$ is tangent to the cubic x-nullcline $y = 4x - x^3$ for a value x > 0. It implies the birth of two singular points : a saddle and a stable node. When $a_2 < 0$ keeps increasing, the saddle node gets closer to the local maximum of the cubic (positive fold) and becomes an attractive focus. For a value of a_2 close to the one for which this focus coincide with the positive fold, a supercritical bifurcation occurs, implying the birth of an attractive limit cycle and the focus becomes an repulsive focus. The limit cycle persists until the focus approaches the local minimum of the cubic (negative fold). For a value of a_2 close to the one for which the focus coincide with this local minimum, another supercritical Hopf bifurcation (called inverse) occurs, the limit cycles disappears and the focus becomes stable. Finally, when a_2 keeps increasing, the focus becomes an attractive node and disappear afterwards by a saddle-node bifurcation when the y-nullcline is tangent to the cubic for a negative value of x.

Considering the other parameter values, other bifurcation may appear. For instance, the limit cycle may disappear through another bifurcation than a Hopf bifurcation. Hence, even a simple planar system may display a rich panel of behaviors that are structured by the bifurcation diagram involving the bifurcations listed above, but also non local ones (see examples in Appendix A.4 for periodic orbits) and bifurcations of codimension greater than 1 (see an example in Appendix A.5).

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Appendix A

A.1 Démonstration du théorème de Poincaré-Lyapunov

Theorem 18. (Poincaré-Lyapunov)

We consider the differential system

$$\dot{x} = Ax + h(x, t),\tag{A.1}$$

where $A \in \mathcal{M}_n(\mathbb{R})$, h is continuous in the domain $D = \{(x,t)|||x|| \leq \rho, t \geq 0\}$ where $\rho > 0$ and satisfies

$$\frac{||h(x,t)||}{||x||} \to 0 \text{ when } ||x|| \to 0 \text{ uniformly w.r.t. } t \ge 0.$$

If all the eigenvalues of A have strictly negative real parts, then the solution x = 0 is asymptotically stable.

Proof. Let $m = \sup_{D} ||h||, c \in \mathbb{R}^n$ such that $||c|| < \rho$ and d > 0 such that $||c|| + d \le \rho$. Then

$$\sup_{(x,t)\in D} ||A.x + h(x,t)|| \le ||A||\rho + m = m'.$$

From Cauchy-Lipschitz theorem, there exists a unique solution x(t) of (A.1) such that x(0) = c defined for $t \in [0,T]$ with $0 < T < \frac{d}{m'}$. Moreover, the trajectory x([0,T]) in included in the ball $||x|| \leq \rho$.

The solution Y(t) of the linear Cauchy problem

$$\dot{Y} = A.Y,$$

$$Y(0) = I_n,$$

converges to 0 when $t \to +\infty$ and

$$\int_0^{+\infty} ||Y(t)|| dt < +\infty.$$

The solution y(t) of

$$\dot{y} = A.y,$$

$$y(0) = c,$$

is precisely y = Y.c. Hence, there exists a depending on A only and that we can assume greater than 1, such that

$$||y|| \le ||Y|| . ||c|| \le a||c||.$$

The solution x(t) satisfies

$$x(t) = y(t) + \int_0^t Y(t-u)h(x(u), u)du.$$

Let us prove that, if c is small enough, then $\forall t \in [0, T], ||x(t)|| < 2a||c||$.

We choose

$$\varepsilon < \frac{1}{2} \left(\int_0^{+\infty} ||Y(u)|| du \right)^{-1}$$

and η such that

$$||x|| \le \eta \quad \Longrightarrow \quad \forall u \in [0,T], \quad ||h(x,u)|| \le \varepsilon ||x||$$

Then, for any $t \in [0, T]$,

$$||x(t)|| \le ||y(t)|| + \int_0^t ||Y(t-u)||\varepsilon||x(u)||du \le a||c|| + \frac{1}{2} \max_{t \in [0,T]} ||x(t)||$$

thus

$$\frac{1}{2}||x(t)|| \le a||c||.$$

By choosing the vector c such that

$$||c|| + d < \rho, \qquad ||c|| < \frac{\eta}{2a}, \qquad 2a||c|| + d < \rho,$$

then $||x(T)|| + d < \rho$. The solution x(t) can be prolonged for $t \in [T, 2T]$ and satisfies the same boundary by above. By iterating the process, we prove that x(t) exist for any t > 0 and satisfies $||x(t)|| + d < \rho$, which proves the stability.

Now, we prove the asymptotic stability. Consider $\lambda < 0$ greater than any the real part of any eigenvalue of A. We consider the change of function $x(t) = z(t)e^{\lambda t}$. From (A.1), z is solution of

$$\dot{z} = (A - \lambda I_n)z + e^{-\lambda t}h(ze^{\lambda t}, t)$$

If $||z|| \leq \eta$ alors $||e^{\lambda t}z|| \leq \eta$ and thus $||e^{-\lambda t}h(ze^{\lambda t},t)|| \leq e^{-\lambda t}\varepsilon||ze^{\lambda t}|| = \varepsilon||z||$. The above proof of the stability can be applied to z, since all the eigenvalues of $A - \lambda I$ have a strictly negative real part. Thus, if the norm of z(0) = x(0) is small enough, z remains bounded and $x(t) \to 0$ when $t \to +\infty$.

A.2 Démonstration de l'existence des variétés stables et instables

Theorem 19. Consider a \mathcal{C}^1 vector field, $\phi(t, x)$ its flow, and the associated system $\dot{x} = f(x)$ defined on an open subset of \mathbb{R}^n containing 0. We assume that 0 is a hyperbolic singular point and, thus, that the jacobian matrix $J_f(0)$ admits

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- k eigenvalues $(\lambda_i)_{i=1}^k$ with strictly negative real part,
- n-k eigenvalues $(\lambda_i)_{i=k+1}^n$ with strictly positive real part.

We note E^s and E^u the stable and unstable subspaces of the linearized system $\dot{x} = J_f(0).x$. There exists a differentiable manifold \mathcal{W}^s of dimension k, tangent to E^s at 0, invariant under the flot ϕ and such that

$$\forall x_0 \in \mathcal{W}^s, \quad \lim_{t \to +\infty} \phi(t, x_0) = 0.$$

Similarly, there exists a differentiable manifold \mathcal{W}^u of dimension n - k, tangent to E^u at 0, invariant under the flow ϕ and such that

$$\forall x_0 \in \mathcal{W}^u, \quad \lim_{t \to -\infty} \phi(t, x_0) = 0.$$

Proof. Après un changement linéaire de coordonnées, on peut considérer que $\dot{x} = f(x)$ s'écrit

$$\dot{x} = Ax + h(x), \quad h(x) = 0(||x||^2)$$
 (A.2)

où A est une matrice diagonale par blocs constituée:

- pour le bloc en haut à gauche de $P \in \mathcal{M}_k(\mathbb{R})$ de valeurs propres $(\lambda_i)_{i=1}^k$,
- pour le bloc en bas à droite de $Q \in \mathcal{M}_{n-k}(\mathbb{R})$ de valeurs propres $(\lambda_i)_{i=k+1}^n$.

Posons

$$U(t) = (\exp(tP), 0) \in \mathcal{M}_{n,1}(\mathbb{R}) \quad \text{et} \quad V(t) = (0, \exp(tQ)) \in \mathcal{M}_{n,1}(\mathbb{R}).$$

Soit α tel que $\forall j \in [\![1,k]\!], \Re(\lambda_j) < -\alpha$. Alors il existe des constantes K et σ telles que

$$\forall t \ge 0, \qquad ||U(t)|| < K \exp(-(\alpha + \sigma)t), \tag{A.3}$$

$$\forall t \le 0, \qquad ||V(t)|| < K \exp(\sigma t). \tag{A.4}$$

Considérons à présent l'équation (A.2) sous forme d'équation intégrale dépendant d'un paramètre $a \in \mathbb{R}^n$:

$$u(t,a) = U(t)a + \int_0^t U(t-s)h(u(s,a))ds - \int_t^\infty V(t-s)h(u(s,a))ds$$
(A.5)

et montrons que cette équation intégrale admet une solution à l'aide du théorème du point fixe. Toute solution continue de (A.5) est différentiable et solution du système différentiel (A.2). De plus,

$$\forall \varepsilon > 0, \exists \delta > 0, (||x|| \le \delta \text{ et } ||y|| \le \delta \Longrightarrow ||h(x) - h(y)|| \le \varepsilon ||x - y||.$$

Considérons la suite de fonction $t \mapsto u_i(t, a)$ définie par :

$$\begin{cases} u_0(t,a) = 0, \\ u_{j+1}(t,a) = U(t)a + \int_0^t U(t-s)h(u_j(s,a))ds - \int_t^\infty V(t-s)h(u_j(s,a))ds. \end{cases}$$

Montrons par récurrence que si $\frac{\varepsilon K}{\sigma} < \frac{1}{4}$, alors

$$|u_j(t,a) - u_{j+1}(t,a)| \le \frac{K|a|\exp(-\alpha t)}{2^{j-1}}.$$

APPENDIX A.

En supposant ce résultat pour $j \leq m$, on a

$$\begin{aligned} |u_{m+1}(t,a) - u_m(t,a)| &\leq \int_0^t ||U(t-s)||\varepsilon |u_m(s,a) - u_{m-1}(s,a)| ds \\ &+ \int_t^\infty ||V(t-s)\varepsilon |u_m(s,a) - u_{m-1}(s,a)| ds \\ &\leq \varepsilon \int_0^t K \exp(-(\alpha + \sigma)(t-s)) \frac{K|a| \exp(-\alpha s)}{2^{m-1}} ds \\ &+ \varepsilon \int_0^\infty K \exp(\sigma(t-s)) \frac{K|a| \exp(-\alpha s)}{2^{m-1}} ds \\ &\leq \frac{\varepsilon K^2 |a| \exp(-\alpha t)}{\sigma 2^{m-1}} + \frac{\varepsilon K^2 |a| \exp(-\alpha t)}{\sigma 2^{m-1}} \\ &\leq \left(\frac{1}{4} + \frac{1}{4}\right) \frac{K|a| \exp(-\alpha t)}{2^{m-1}} = \frac{K|a| \exp(-\alpha t)}{2^m}. \end{aligned}$$

Cette majoration montre que la suite de fonctions converge uniformément ainsi que ses dérivées successives et que la fonction limite u(t, a) vérifie

$$|u(t,a)| \le 2K|a|\exp(-\alpha t). \tag{A.6}$$

On peut donc choisir les n - k dernières composantes de a nulles puisqu'elles n'interviennent pas dans ce qui précède, et on a

$$\begin{cases} u_j(0,a) = a_j, & \text{pour } j \in [\![1,k]\!], \\ u_j(0,a) = -[\int_0^\infty V(-s)h(u(s,a_1,...,a_k,0))ds]_j, & \text{pour } j \in [\![k+1,n]\!]. \end{cases}$$

Pour j = [k + 1, n], on définit $\psi_j(a_1, ..., a_k) = u_j(0, a_1, ..., a_k)$. La variété \mathcal{W}^s définie par les équations

$$y_j = \psi_j(y_1, ..., y_k), \quad j \in [[k+1, n]].$$

vérifie alors les propriétés du théorème puisque si $y \in \mathcal{W}^s$, on peut poser y = u(0, a) et alors $y(t) = \phi_t(y) = u(t, a) \to 0$ quand $t \to +\infty$ d'après (A.6). L'estimée ci-dessus conduit à $\lim_{t\to\infty}(y(t)) = 0$.

L'existence de la variété instable \mathcal{W}^u et ses propriétés sont établies avec les mêmes arguments en changeant t en -t.

A.3 Démonstration du théorème de Poincaré-Bendixson

Theorem 20. (Poincaré-Bendixson)

Let X denote a \mathcal{C}^1 vector field in an open subset $U \in \mathbb{R}^2$ associated with

$$\dot{x} = f(x, y), \tag{A.7}$$

$$\dot{y} = g(x, y). \tag{A.8}$$

Let K denote a compact set included in U and $\gamma_m = \{\phi(t,m) | t \in \mathbb{R}\}$ an orbit of X such that the positive half-orbit $\gamma_m^+ = (\phi(t,m) | t \ge 0) \subset K$. Assume that $\omega(m)$ contains a finite number of singular points of X.

- i) If $\omega(m)$ contains no singular point, then $\omega(m)$ is a periodic orbit.
- ii) If $\omega(m)$ contains both regular and singular points, then $\omega(m)$ is formed by singular points and orbits connecting them. In that case, $\omega(m)$ is called a graphic.
- iii) If $\omega(m)$ contains no regular point, then $\omega(m)$ is a singular point.

Pour démontrer ce résultat, nous utilisons 4 lemmes.

Lemma 2. Soit Σ une section transverse au flot associé à $X, \gamma = \{\phi(t,q), t \in \mathbb{R}\}$ une orbite de X et $p \in \Sigma \cap \omega(\gamma)$. Il existe une suite $\phi(\tau_n, q)$ de points de Σ telle que

$$p = \lim_{n \to +\infty} \phi(\tau_n, q).$$

Proof. Soit V un voisinage ouvert de p pour lequel l'application de premier retour sur Σ associé à X soit bien définie sur $V \cap \Sigma$ et $\tau : V \to R$ l'application temps de premier retour. Comme $p \in \omega(\gamma)$, il existe une suite $(t_n) \to +\infty$ telle que $(\phi(t_n, q)) \to p$. A partir d'un certain rang, $\phi(t_n, q) \in V$. Posons

$$\tau_n = t_n + \tau(\phi(t_n, q)).$$

On a alors

$$\phi(\tau_n, q) = \phi(\tau(\phi(t_n, q)), \phi(t_n, q)) \in \Sigma_{+}$$

De plus, comme τ est continue,

$$\lim_{n \to +\infty} \phi(\tau_n, q) = \phi(\tau(\phi(t_n, q)), \phi(t_n, q)) = \phi(0, p) = p,$$

Toute section transverse à un champ de vecteurs du plan est, à l'évidence, difféomorphe à un intervalle. Il existe donc un ordre naturel sur les points les points de cette section.

Lemma 3. Soit Σ une section transverse à X. Une orbite positive $\gamma^+(p) = \{\phi(t, p), t \ge 0\}$ de X intersecte Σ en une suite monotone $(p_i)_{i \in \mathbb{N}}$.

Proof. Posons $D = \{t \ge 0, \phi(t, p) \in \Sigma\}$. La section Σ étant transverse au flot, D est un ensemble discret que l'on peut donc ordonner. Ainsi $D = \{t_i | i \in \mathbb{N}\}$ avec $t_0 = 0$ et $(t_i)_{i \in \mathbb{N}}$ une suite strictement croissante. On définit la suite $(p_i)_{i \in \mathbb{N}}$ par $p_{i+1} = \phi(t_i, p)$ pour tout $i \in \mathbb{N}$. Alors, si $p_1 = p_2$, l'orbite est périodique et $p_i = p$, pour tout i.

Supposons $p_1 < p_2$ sans perte de généralité. La section Σ étant connexe et transverse au flot associé à X différentiable, le champ est orienté dans le même sens tout le long de Σ , i.e. en tout point de la même face de Σ vers l'autre. On considère la courbe de Jordan formée de l'arc p_1p_2 de Σ (qui est orientée) et la trajectoire le long du flot reliant p_1 et p_2 , i.e. $\{\phi(t,p), 0 \leq t \leq t_1\}$. D'après le théorème de Jordan, cette courbe a un intérieur et un extérieur. L'orbite γ entre dans l'intérieur du domaine par le segment p_1p_2 et ne peut sortir du domaine par la suite. Il s'ensuit que $p_1 < p_2 < p_3$. On termine la démonstration par une récurrence évidente.

Lemma 4. Soit Σ une section transverse à X et $p \in U$. L'ensemble $\omega(p)$ contient au plus un point dans Σ .

Proof. D'après les résultats précédents, un point de $\Sigma \cap \omega(p)$ est la limite d'une suite de points de l'orbite appartenant à Σ et la suite des points d'intersection de Σ avec l'orbite positive est monotone. Elle est donc nécessairement convergente et toute sous-suite ne peut converger que vers un seul point qui est la limite de la suite.

Lemma 5. Soit $p \in U$ tel que la demi-orbite positive $\gamma^+(p)$ est contenue dans un compact K. Soit γ une orbite de X contenue dans $\omega(p)$. Si $\omega(\gamma)$ contient des points réguliers, alors γ est une orbite fermée et $\omega(p) = \gamma$.

Proof. Soit $q \in \omega(\gamma)$ un point régulier. Soit Σ une section transverse au flot qui contient q. Il existe une suite $t_n \to \infty$ telle que $\gamma(t_n) \in \Sigma$. Comme $\gamma(t_n) \in \omega(p)$, la suite se réduit à un point d'après le lemme précédent, ce qui montre que l'orbite γ est périodique.

Montrons à présent $\gamma = \omega(p)$. Comme $\omega(p)$ est connexe et γ est fermée, il suffit de montrer que γ est ouvert dans $\omega(p)$. Soit $\overline{p} \in \gamma$. Soient $V_{\overline{p}}$ le voisinage et $\Sigma_{\overline{p}}$ la section transverse pour lesquels l'applications de premier retour sur $\Sigma_{\overline{p}}$ est bien définie. On a bien sûr $(V_{\overline{p}} \cap \gamma) \subset (V_{\overline{p}} \cap \omega(p))$. Montrons l'inclusion inverse par l'absurde. Supposons qu'il existe un point $q' \in V_{\overline{p}} \cap \omega(p)$ qui n'appartient pas à γ . Puisque $\omega(p)$ est invariant par le flot, il existe $t \in \mathbb{R}$ tel que $\phi(t,q') \in \omega(p) \cap \Sigma_{\overline{p}}$ et $\phi(t,q') \neq \overline{p}$. Ainsi il existe deux points distincts de $\omega(p)$ dans $\Sigma_{\overline{p}}$ ce qui est en contradiction avec le lemme précédent. Ainsi $V_{\overline{p}} \cap \gamma = V_{\overline{p}} \cap \omega(p)$. Soit l'ouvert $U = \bigcup_{\overline{p} \in \gamma} V_{\overline{p}}$ qui vérifie $U \cap \omega(p) = U \cap \gamma = \gamma$. On a donc γ est ouvert dans $\omega(p)$.

Démonstration du théorème de Poincaré-Bendixson.

i) Supposons que tous les points de $\omega(p)$ sont réguliers et soit $q \in \omega(p)$. L'orbite γ_q est contenue dans $\omega(p)$. Comme $\omega(p)$ est compact, $\omega(\gamma_q)$ est non vide. Ainsi $\omega(p) = \gamma_q$ est une orbite périodique.

ii) Supposons que $\omega(p)$ contient des points réguliers et des points singuliers. Soit une orbite $\gamma \subset \omega(p)$ non réduite à un point singulier. D'après le lemme précédent, $\omega(\gamma)$ et $\alpha(\gamma)$ ne peuvent pas contenir de points réguliers, ils sont connexes et il existe un nombre fini de points singuliers dans $\omega(p)$. Il en résulte que ce sont des points singuliers.

iii) Supposons que tous les points de $\omega(p)$ sont singuliers. Le même raisonnement qu'au ii) montre que $\omega(p)$ est réduit à un point singulier.

A.4 Quelques exemples de bifurcations d'orbites périodiques

Nous donnons dans cette section deux exemples de bifurcations d'orbites périodiques d'un système dynamique. Les lecteurs intéressés pourront trouver une présentation plus détaillée dans les références données à la fin de ce cours, en particulier dans [Guckenheimer-Holmes, 1983].

La bifurcation pli de cycles limites Considérons le système écrit en coordonnées polaires et dépendant du paramètre λ :

$$\dot{\rho} = \lambda + (\rho - 1)^2 \tag{A.9}$$

$$\dot{\theta} = 1 \tag{A.10}$$

Pour $\lambda < 0$, ce système admet deux cycles limites $\rho = 1 \pm \sqrt{-\lambda}$, l'un étant attractif et l'autre répulsif, coïncidant quand $\lambda = 0$. Pour $\lambda > 0$, il n'y a pas de cycles limite. Cette bifurcation (globale puisqu'elle ne peut être caractérisée dans un voisinage d'un point) consistant en la coïncidence et la disparition de deux cycles limites est appelée une bifurcation pli de cycles limites. Elle peut être étudiée en considérant les points fixes de l'application de premier retour Π_0 bien définie pour $\lambda = 0$ sur un voisinage du cycle limite $\rho = 1$. Cette application peut alors être plongée dans une famille à un paramètre d'application de premier retour Π_{λ} au voisinage de $\lambda = 0$. Quand $\lambda < 0$, on voit apparaître deux points fixes de Π_{λ} correspondant aux cycles limites du système (A.9), l'un stable, l'autre instable, alors que pour $\lambda > 0$, Π_{λ} n'admet aucun point fixe.

A l'instar de la bifurcation pli de points singuliers, des conditions de transversalité sont nécessaires pour assurer la non-dégénérescence de cette bifurcation dans le cas général et assurer l'émergence des deux cycles limites d'un côté de la valeur de bifurcation.

La bifurcation homocline dans le plan Soit une famille de champs de vecteurs du plan indexée par un paramètre μ :

$$\dot{x} = f(x, y, \mu)$$

 $\dot{y} = g(x, y, \mu)$

Supposons que l'origine est un col pour μ voisin de 0 et que, pour $\mu = 0$, il existe une orbite homocline de l'origine. On désigne par $\lambda(\mu)$ et $\gamma(\mu)$, $\gamma(\mu) < 0 < \lambda(\mu)$, les valeurs propres de la jacobienne évaluée à l'origine. Le théorème de linéarisation permet d'obtenir un système de coordonnées de classe C^1 dans lequel le flot est linéaire :

$$\dot{x} = \lambda(\mu)x$$

 $\dot{y} = \gamma(\mu)y.$

Soit $\Sigma = \{(x, y) \in U | y = h\}$ et $\Sigma^1 = \{(x, y) \in U | x = h\}$ deux sections transverses du flot définies sur un voisinage de l'origine U suffisamment petit pour que le nouveau système de coordonnées soit défini sur U. Le flot induit une application $T_0: \Sigma \to \Sigma^1$:

$$T_0(x,h) = \begin{pmatrix} h \\ h\left(\frac{x}{h}\right)^{-\frac{\gamma(\mu)}{\lambda(\mu)}} \end{pmatrix}.$$

et une application $T_1: \Sigma^1 \to \Sigma$

$$T_1(h,y) = \begin{pmatrix} a(\mu)\mu + b(\mu)y + O(y^2) \\ h \end{pmatrix},$$

où a(0) > 0 et b(0) > 0.

En composant T_1 et T_0 , on obtient une application de premier retour $T : \Sigma \to \Sigma$, $T(x, h) = (T_1 \circ T_0)(x, h)$ bien définie pour μ assez petit et x > 0. Pour x < 0, la trajectoire s'échappe et ne revient pas sur Σ . On a ainsi :

$$T(x,h) = \begin{pmatrix} a(\mu)\mu + b(\mu)h\left(\frac{x}{h}\right)^{-\frac{\gamma(\mu)}{\lambda(\mu)}} + O\left(x^{-2\frac{\gamma}{\lambda}}\right) \\ h \end{pmatrix}$$

Le nombre $\delta = -\gamma(0)/\lambda(0)$ est appelé l'indice du col. Alors, si $\delta > 1$ et $\mu > 0$, l'application de premier retour présente un unique point fixe dans un voisinage de x = 0, dans x > 0, de la forme

$$x = a(0)\mu + O(\mu^{\delta}).$$

Ainsi quand μ varie et traverse 0, un unique cycle limite émerge de la connexion homocline. Cette bifurcation est appelée une bifurcation homocline.

A.5 Une bifurcation de codimension 2 : Bogdanov-Takens.

Une bifurcation de Bogdanov-Takens est une bifurcation de codimension 2 qui consiste en l'occurrence simultané pour un même point singulier d'une bifurcation pli et d'une bifurcation de Hopf. Considérons la famille de champ de vecteurs dépendant de deux paramètres a et b

$$\begin{aligned} \dot{x} &= y\\ \dot{y} &= a + by + x^2 + xy. \end{aligned}$$

Les points singuliers sont donnés par :

$$x = x^+ = \sqrt{-a}, \quad y = 0,$$

 et

$$x = x^- = -\sqrt{-a}, \quad y = 0.$$

Si a < 0, il y a donc deux points singuliers ; sur l'axe a = 0, il existe un unique point singulier; si a > 0, il n'y a aucun point singulier. La jacobienne au voisinage du point singulier $(\overline{x}, 0)$ est donné par

$$\begin{pmatrix} 0 & 1 \\ 2\overline{x} & b + \overline{x} \end{pmatrix}$$

Les valeurs propres λ_1^-, λ_2^- et λ_1^+, λ_2^+ correspondant aux deux points singuliers vérifient :

$$\lambda^2 - (b + \overline{x})\lambda - 2\overline{x} = 0.$$

Le point $(x^+, 0)$ est donc un col et le point $(x^-, 0)$, un noeud ou un foyer. Ce dernier point est stable si $b - \sqrt{-a} < 0$ et instable si $b - \sqrt{-a} > 0$. L'axe a = 0 correspond à une bifurcation

pli. On peut vérifier que le changement de stabilité du point $(x^-, 0)$ le long de la branche de parabole $b = \sqrt{-a}$ correspond à une bifurcation de Hopf sous-critique. Il apparaît donc en dessous de la parabole un cycle limite instable.

Nous décrivons par la suite la bifurcation responsable de la disparition de ce cycle limite qui nécessite un changement de variables dépendant d'un paramètre ε

$$t = \varepsilon \tau, \quad x = \varepsilon^2 u, \quad y = \varepsilon^3 v, \quad a = \varepsilon^4 \alpha, \quad b = \varepsilon^2 \beta.$$

On aboutit alors au système

$$\begin{aligned} \dot{u} &= v, \\ \dot{v} &= \alpha + u^2 + \varepsilon (\beta v + uv). \end{aligned}$$

Pour $\varepsilon = 0$, ce système est hamiltonien et admet la fonction d'énergie :

$$H = \frac{1}{2}v^2 - \alpha u - \frac{u^3}{3}.$$

Notons que ce système hamiltonien présente une connexion homocline γ_0 contenue dans la courbe H = 2/3. On fixe α et on cherche les valeurs de β pour lesquelles, lorsque ε est petit, la connexion homocline persiste. On doit donc considérer la fonction

$$M(\beta) = \int_{\gamma_0} (\beta v + uv) dv.$$

Le calcul de cette fonction se ramène à des intégrales elliptiques (voir [Guckenheimer-Holmes, 1983]) et conduit au fait que $M(\beta)$ s'annule pour $\beta = 5/7$. En revenant aux paramètres initiaux (a, b), on peut achever l'analyse de la bifurcation en ajoutant l'arc de parabole $a = -\frac{49}{25}b^2$ en dessous de l'arc de parabole de la bifurcation de Hopf et qui donne une approximation de la courbe le long de laquelle le cycle limite instable disparaît par bifurcation homocline. Cette bifurcation de Bogdanov-Takens est dite souscritique.



Une analyse analogue du système

$$\begin{aligned} \dot{x} &= y \\ \dot{y} &= a + bx + x^2 + xy. \end{aligned}$$

montre l'existence d'une courbe de bifurcations pli $(T_{-} \text{ et } T_{+} \text{ les deux branches de la courbe})$, un demi-axe le long duquel se produisent des bifurcations de Hopf surcritiques (H) et une courbe de bifurcations homoclines (P) faisant disparaître le cycle limite stable né de la bifurcation de Hopf. On obtient alors la partition de l'espace des paramètres représentée dans la figure suivante avec les notations introduites ci-dessus.