M1 BBS - EM8BBSEM

Simulation de Systèmes Biologiques

(#4)

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Eléments de la théorie qualitative de jeux des équations différentielles

A natural assumption about the growth of a population is that ***the number of offspring at any given time is proportional to the number of adults at that time***. Let $y(t)$ denote the number of adults at time t. In any given small interval of time Δt, the number of offspring in that time represents the change in the population Δy. The ratio $\Delta y/\Delta t$ is the average rate of growth of the population over the time period Δt. The derivative ***dy/dt*** is the instantaneous rate of growth at time ***t***. Thus, (with the assumption that new offspring are immediately adults) we obtain the following mathematical expression of the statement above:

$$\frac{dy}{dt} = ky$$

In other words, the rate of growth is proportional to the number present. The solution of this equation is given by an exponential curve:

$$y(t) = y_0 e^{kt}$$

This situation is typical and can be encountered nearly everywhere (populations, biomass, etc.).

Mathematical models of biological and biochemical processes are usually represented as ***systems of differential equations*** of the form:

$$\frac{dx_1}{dt} = F_1(x_1, x_2, ..., x_n)$$

....

$$\frac{dx_n}{dt} = F_n(x_1, x_2, ..., x_n)$$

where functions $\boldsymbol{F_i}$ are in general nonlinear and do not depend explicitly on time $\boldsymbol{t}$, while $\boldsymbol{x_i}$ are unknown functions of time which may be constrained (e.g. concentrations cannot have negative values).

Systems of this kind are often encountered in classical description of motion (dynamics). Look at the second Newton's law (***F* = *ma***):

$$m\frac{d^2x}{dt^2} = F\left(x, \frac{dx}{dt}\right)$$

Upon substitution of a new variable ***y* = *dx/dt*** it becomes a system of two equations of the fist order:

$$\frac{dx}{dt} = y$$

$$\frac{dy}{dt} = \frac{1}{m}F(x, y)$$

One of the two independent variables is coordinate ***x***, the other is velocity ***y***. Coordinates and velocities fully describe a state (phase) of a system, therefore the plane in which we plot them is called a ***phase plane***. This term is used even if the functions $\boldsymbol{x_i}$ are of the same type (e.g. concentrations).

If $\boldsymbol{x_i}$ are ***linear*** functions of their arguments, one can solve the system ***analytically***. In case of ***nonlinear*** equations, only ***numerical*** solutions are readily available. Their major drawback is that they do not permit to extrapolate the results to other regions of the phase plane (results of ***N*** consecutive calculations permit to determine the state, i.e. phase, of the system in ***N*** points of the phase plane, but do not give any basis to predict the result of calculation ***N+1***).

In most cases we are not interested in quantitative results. Sometimes it is even impossible to know the exact conditions of a given biological process (affinity values, initial conditions, etc.). Much more important is to be able to characterize the system qualitatively, to determine the existence of its ***stationary states***, the character of their ***stability***, and the changes in stability induced by modifications of model parameters.

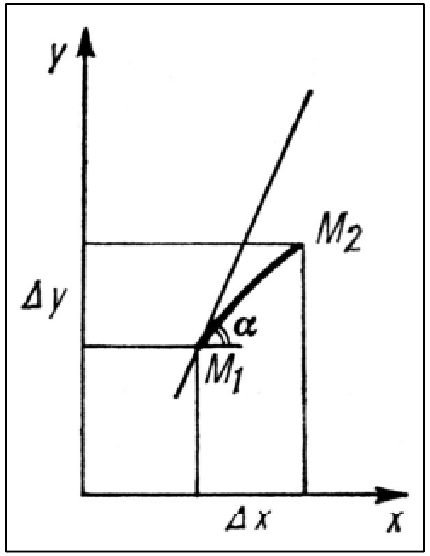
The above problems constitute the essence of the ***qualitative theory of differential equations*** which, instead of finding the exact analysis of the solutions (i.e. no explicit form of functions x_i is sought), focuses on ***general behavior of studied systems***, as deduced from the form of functions $F_i(x_1,\ldots,x_n)$.

The type of information provided by the theory:

- **existence of stationary states (equilibrium)**
- **character of equilibrium (stable, unstable)**
- **phase trajectories (isoclines, asymptotic cycles)**

Elements of analysis: phase portrait

Many interesting mathematical models can be represented by a limited number of differential equations of the first order. We will consider the following example:



$$\frac{dx}{dt} = P(x, y)$$

$$\frac{dy}{dt} = Q(x, y)$$

At a given moment t_1 the system is in state M_1, characterized by $x(t_1)$ and $y(t_1)$. This state can be represented as a point in a two-dimensional phase plane (phase space in three dimensions, etc.). After time Δt the coordinate x will be incremented by Δx and y by Δy, as a result of which the system will be found in the state M_2. Analysis of infinitesimally small time increments permits to construct the ***trajectory*** of the system (see the figure below). Needless to say, tan(α) (inclination of the straight, adjacent to the phase trajectory at a given point) is equal to the derivative dy/dx at that point.

By eliminating time from the previous system of equations we arrive at the following single differential equation:

$$\frac{dy}{dx} = \frac{Q(x, y)}{P(x, y)}$$

The solution of this equation is a ***family of phase trajectories*** ***y=y(x,C)***, where the unknown parameter ***C*** can be determined from the initial conditions. Thus, we arrive at the ***phase portrait*** of the studied system.

***Note**: finding a solution of the above equation allows monitoring the relation between x and y, but their explicit time variations x(t) and y(t) still remain unknown. The role of the qualitative theory of dynamic systems is to understand the properties of the functions x(t) and y(t) from the analysis of the studied system's phase portrait.*

According to the Cauchy theorem, each point of the phase plane can be traversed by only ***one*** trajectory. The only exceptions are ***singular points***, at which the inclination of the adjacent straight, tan(α), is not defined:

$$\frac{dy}{dx} = \frac{0}{0}$$

$$\Downarrow$$

$$P(x, y) = 0 \quad \text{AND} \quad Q(x, y) = 0$$

Multiple trajectories may traverse the singular points of the phase plane.

The conditions ***P(x,y)=0*** and ***Q(x,y)=0*** are equivalent to setting the rates of time variation of ***x*** and ***y*** to 0: ***dx/dt = 0*** and ***dy/dt = 0***. Hence, the singular points of the phase plane correspond to ***stationary states*** of the studied dynamic system.

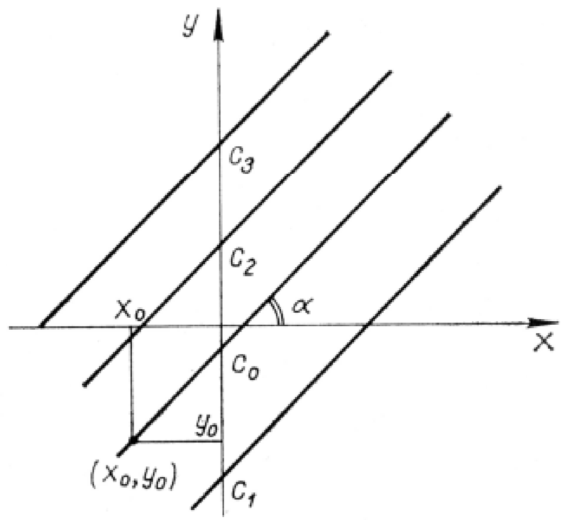
Example:

$$\frac{dx}{dt} = A = const \qquad \frac{dy}{dt} = B = const$$

There are no singular points in the phase plane. Elimination of time gives the following equation:

$$\boxed{\frac{dy}{dx} = \frac{B}{A}} \quad \text{whose solution is given by:} \quad \boxed{y = \frac{B}{A}x + C}$$

which defines a family of straight lines (see figure below), with ***tan(α)=B/A***. ***C*** depends on the initial conditions [e.g. $\boldsymbol{C_0 = y_0 - (B/A)x_0}$].



The direction of the movement along the lines can only be determined from the analysis of the original equations ({A, B} > 0 => upwards, {A, B} < 0 => downwards).

Example : $\dfrac{dx}{dt} = -x \qquad \dfrac{dy}{dt} = -y$

There is one singular point here, given by the coordinates: ***x*** = ***y*** = 0.
The family of trajectories is given by the equation (see figure below):

$$dx = -xdt \qquad \mathrm{dy} = -\,ydt$$

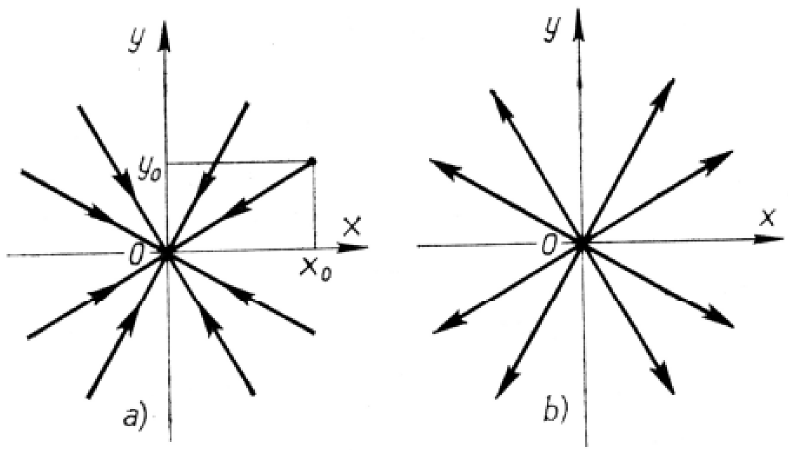
$$\frac{dy}{dx} = \frac{y}{x}$$

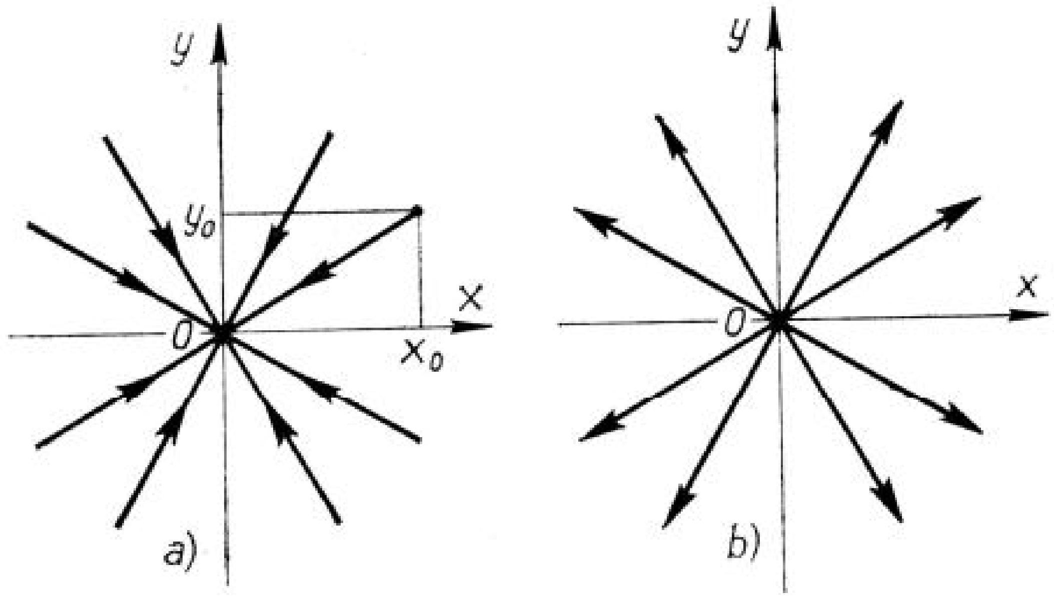
$$dx = -xdt \qquad \mathrm{dy} = -\,ydt$$

$$\frac{dy}{dx} = \frac{y}{x} \qquad \frac{dy}{y} = \frac{dx}{x}$$

$$\int \frac{dy}{y} = \int \frac{dx}{x} \qquad \ln(y) = \ln(x) + const = \ln(Cx)$$

$$y = Cx \qquad \left(C = \frac{y_0}{x_0} \right)$$





Vectors in ***(a)*** show the system's time evolution, which depends on the signs in the rhs of the above equation. Since they are negative, all trajectories converge to the singular point (0,0) representing a ***stable node***.

If the signs were both positive, the trajectories would diverge to infinity, as in ***(b)***. If the system would initially be at (0,0), any random fluctuation would drive it away from it and the system would drift away along one of the trajectories. In this case the singular point (0,0) is an ***unstable node***.

Elements of analysis: singular points

Q: ***How to determine in a general way the type of stability of a singular point in the phase plane?***

A: Apply a ***small perturbation*** to check if the system returns to the initial point.

Let's begin with the original set of equations:

$$\frac{dx}{dt} = P(x, y)$$

$$\frac{dy}{dt} = Q(x, y)$$

Let ***(x_s, y_s)*** denote the coordinates of a singular point in the phase plane of the system. Application of a small perturbation will drive the system away from the stationary point (equilibrium). The coordinates become:

$$x = x_s + \xi, \qquad y = y_s + \eta \qquad \left(\left| \frac{\xi}{x_s} \right| << 1, \quad \left| \frac{\eta}{y_s} \right| << 1 \right)$$

We substitute the latter into the former, expanding the functions ***P(x,y)*** and ***Q(x,y)*** into a Taylor series about the singular point ***(x_s, y_s)***. Since the perturbation is small, we may limit the expansion to first order terms only.

The Taylor expansion yields:

$$P(x,y) = P(x_s, y_s) + a_{11}\xi + a_{12}\eta + \dots$$
$$Q(x,y) = Q(x_s, y_s) + a_{21}\xi + a_{22}\eta + \dots$$

The coefficients $\boldsymbol{a_{ij}}$ are partial derivatives of functions ***P*** and ***Q*** calculated at the singular point $\boldsymbol{(x_s, y_s)}$:

$$a_{11} = \left.\frac{\partial P}{\partial x}\right|_{x_s, y_s} \qquad a_{12} = \left.\frac{\partial P}{\partial y}\right|_{x_s, y_s}$$

$$a_{21} = \left.\frac{\partial Q}{\partial x}\right|_{x_s, y_s} \qquad a_{22} = \left.\frac{\partial Q}{\partial y}\right|_{x_s, y_s}$$

On the other hand, we know that at the singular point ***(x_s, y_s)***:

$$P(x_s, y_s) \equiv 0, \qquad Q(x_s, y_s) \equiv 0.$$

Hence, in the first-order approximation, we get the following relations for the small perturbations about the singular point:

$$\frac{dx}{dt} = P \quad \Rightarrow \quad \frac{d}{dt}(x_s + \xi) = P \quad \Rightarrow \quad \boxed{\frac{d\xi}{dt} = a_{11}\xi + a_{12}\eta}$$

$$\frac{dy}{dt} = Q \quad \Rightarrow \quad \frac{d}{dt}(y_s + \eta) = Q \quad \Rightarrow \quad \boxed{\frac{d\eta}{dt} = a_{21}\xi + a_{22}\eta}$$

The above ***linearized*** equations describe the system's behavior near the singular point. This method of analysis is called ***perturbation theory***.

In ***matrix notation*** the equations can be written in a compact way:

$$\left.\begin{aligned}\frac{d\xi}{dt} &= a_{11}\xi + a_{12}\eta \\ \frac{d\eta}{dt} &= a_{21}\xi + a_{22}\eta\end{aligned}\right\} \quad \Rightarrow \quad \frac{d\mathbf{v}}{dt} = \mathbf{A}\mathbf{v}, \qquad \mathbf{v} = \begin{pmatrix}\xi \\ \eta\end{pmatrix} \quad \mathbf{A} = \begin{pmatrix}a_{11} & a_{12} \\ a_{21} & a_{22}\end{pmatrix}$$

A solution is sought as a function of the form:

$$\xi = Ae^{\lambda t}, \qquad \eta = Be^{\lambda t}$$

Substituting these expressions into the above equations and dropping the exponential term yields:

$$\lambda A = a_{11}A + a_{12}B$$

$$\lambda B = a_{21}A + a_{22}B$$

Solving the second equation for ***A*** [$\boldsymbol{A = B(\lambda - a_{22})/a_{21}}$] and substituting it into the first one gives:

$$\left[(a_{11} - \lambda)\cdot(a_{22} - \lambda) - a_{12}\cdot a_{21}\right]\cdot B = 0$$

Since only non-zero amplitudes are interesting ($\boldsymbol{B \neq 0}$), we get:

$$\lambda^2 - (a_{11} + a_{22})\lambda - a_{12}\cdot a_{21} + a_{11}a_{22} = 0$$

$$\left.\begin{aligned} 2\delta &= -(a_{11} + a_{22}) \\ \omega_0^2 &= a_{11}a_{22} - a_{12}a_{21} \end{aligned}\right\} \quad \Rightarrow \quad \lambda^2 + 2\delta\lambda + \omega_0^2 = 0$$

<u>Note</u>: ***identical expression can be obtained from matrix A by calculating:***

$$\det\left|\mathbf{A} - \lambda\mathbf{I}\right| = 0$$

Another way to obtain the characteristic equation is to convert two equations of the first order into one equation of the second order:

$$\left.\begin{aligned} &(a) \quad \frac{d\xi}{dt} = a_{11}\xi + a_{12}\eta \\ &(b) \quad \frac{d\eta}{dt} = a_{21}\xi + a_{22}\eta \end{aligned}\right\} \Rightarrow \left\{\begin{aligned} &\frac{d^2\xi}{dt^2} = a_{11}\frac{d\xi}{dt} + a_{12}\frac{d\eta}{dt}, \quad \text{from (b)}: \\ &\frac{d^2\xi}{dt^2} = \left(a_{11}{}^2 + a_{12}a_{21}\right)\xi + \left(a_{11}a_{12} + a_{12}a_{22}\right)\eta, \quad \text{from (a)}: \\ &\frac{d^2\xi}{dt^2} - \left(a_{11} + a_{22}\right)\frac{d\xi}{dt} + \left(a_{11}a_{22} - a_{12}a_{21}\right)\xi = 0 \end{aligned}\right.$$

The last equation can be written as:

$$\left.\begin{aligned} 2\delta &= -\left(a_{11} + a_{22}\right) \\ \omega_0^2 &= a_{11}a_{22} - a_{12}a_{21} \end{aligned}\right\} \Rightarrow \frac{d^2\xi}{dt^2} + 2\delta\frac{d\xi}{dt} + \omega_0^2\xi = 0$$

The solution is sought as a function of the form:

$$\xi(t) = Ae^{\lambda t}$$

The derivatives of this function are given by:

$$\frac{d\xi(t)}{dt} = A\lambda e^{\lambda t} = \lambda \xi(t)$$

$$\frac{d^2\xi(t)}{dt^2} = \lambda \frac{d\xi(t)}{dt} = \lambda^2 \xi(t)$$

Substitution of the above relations into the equation for $\boldsymbol{\xi(t)}$ yields:

$$\left(\lambda^2 + 2\delta\lambda + \omega_0^2\right)\xi(t) = 0$$

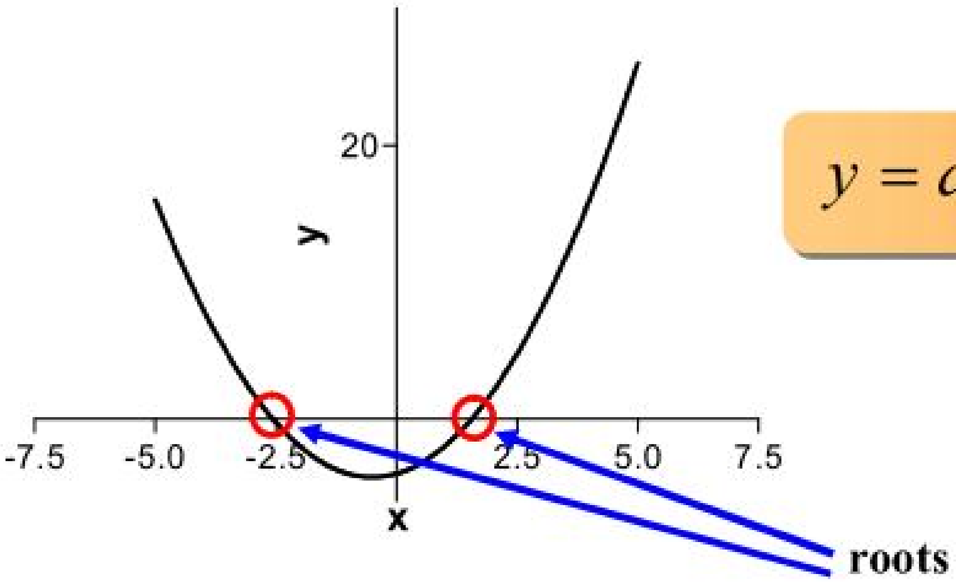
which, for non-zero $\boldsymbol{\xi(t)}$, gives the characteristic equation for $\boldsymbol{\lambda}$:

$$\lambda^2 + 2\delta\lambda + \omega_0^2 = 0$$

Math Reminder: properties of a parabole

Definition of the curve

A parabole is a curve, given by the equation:



$$y = ax^2 + bx + c$$

By replacing ***x*** by a new variable ***x = Az + B*** we obtain:

$$\begin{aligned} y &= a(Az+B)^2 + b(Az+B) + c \\ &= aA^2z^2 + (2aAB + bA)z + \left(aB^2 + bB + c\right) \end{aligned}$$

We choose the constants ***A*** & ***B*** in such a way as to simplify the above expression:

$$\left.\begin{aligned} aA^2 &= 1 \\ 2aAB + bA &= 0 \end{aligned}\right\} \Rightarrow \left\{\begin{aligned} A &= a^{-\frac{1}{2}} \\ B &= -\frac{b}{2a} \end{aligned}\right\} \Rightarrow \quad x = \frac{z}{\sqrt{a}} - \frac{b}{2a}$$

As a result, we get the following equivalent equation:

$$y = z^2 - \frac{\Delta}{4a}, \qquad \Delta = b^2 - 4ac$$

How to find roots of a quadratic equation?

To find roots of the equation:

$$y = z^2 - \alpha^2, \qquad \alpha = \frac{b^2 - 4ac}{4a}$$

we search for ***z*** such that:

$$0 = z^2 - \alpha^2$$

Since the following relation holds:

$$(a+b)\cdot(a-b) = a^2 - ab + ab + b^2 = a^2 - b^2$$

we may write:

$$0 = (z-\alpha)\cdot(z+\alpha)$$

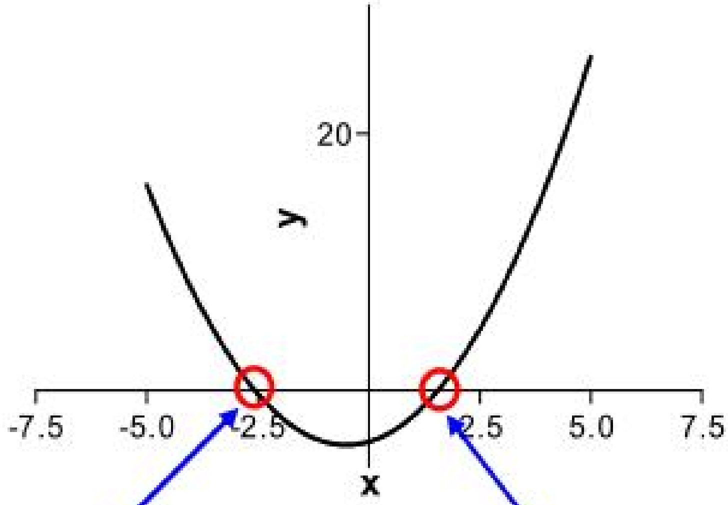
$$0 = (z - \alpha) \cdot (z + \alpha)$$

which has two obvious roots: ***z* = +α** and ***z* = -α**. Hence, the solution is:

$$z = \mp\alpha = \pm\sqrt{\frac{\Delta}{4a}}$$

Finally, we return to the variable ***x***:

$$x = \frac{z}{\sqrt{a}} - \frac{b}{2a} = \frac{-b \mp \sqrt{\Delta}}{2a}$$



$$x = \frac{-b - \sqrt{\Delta}}{2a} \qquad x = \frac{-b + \sqrt{\Delta}}{2a}$$

Analysis of roots

Obviously, the values of ***x*** depend on parameters ***a***, ***b*** and ***c***:

$$x = \frac{-b \mp \sqrt{\Delta}}{2a} = \frac{-b \mp \sqrt{b^2 - 4ac}}{2a}$$

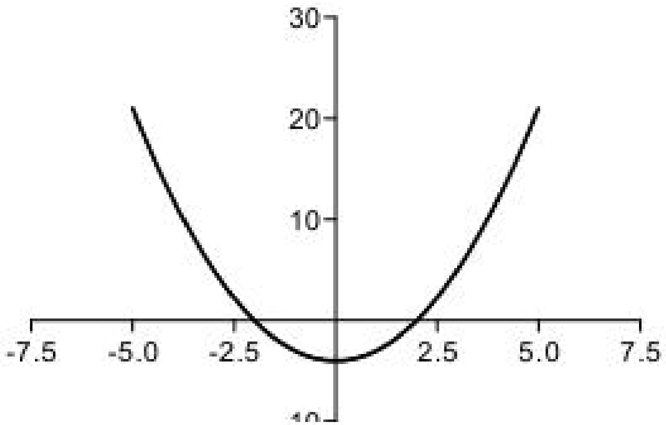
There are three possibilities:

1. Δ > 0

There are two different real roots.

$$x_1 = \frac{-b - \sqrt{\Delta}}{2a}$$

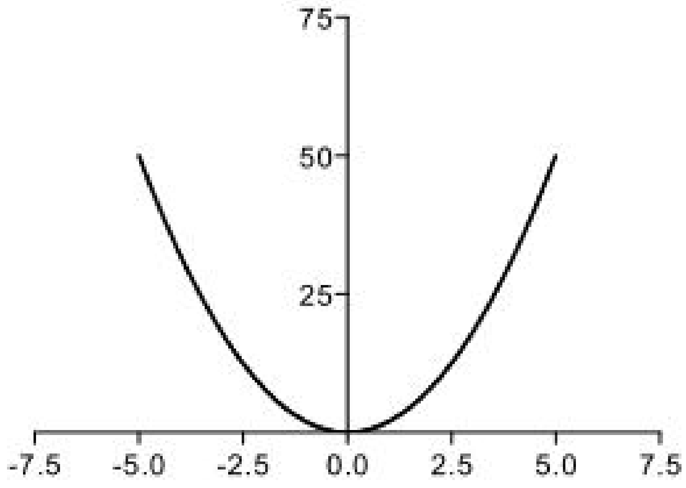
$$x_2 = \frac{-b + \sqrt{\Delta}}{2a}$$



2. Δ = 0

There is one double real root.

$$x_1 = x_2 = \frac{-b}{2a}$$

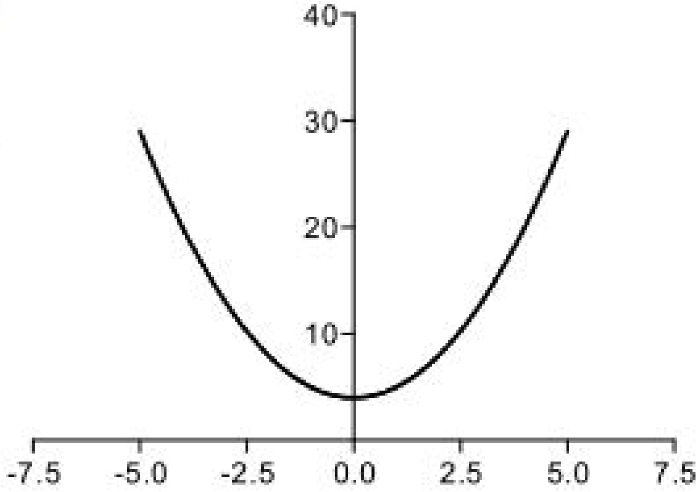


3. Δ < 0

There are two complex conjugate roots.

$$x_1 = \frac{-b - i\sqrt{|\Delta|}}{2a}$$

$$x_2 = \frac{-b + i\sqrt{|\Delta|}}{2a}$$



$$\boxed{\lambda^2 + 2\delta\lambda + \omega_0^2 = 0}$$

The characteristic equation has two roots, given by λ_1 and λ_2:

$$\lambda_{1,2} = -\delta \mp \omega$$

$$\omega^2 = \delta^2 - \omega_0^2$$

In the case of multiple roots, the general solution of the equations for ξ and η is a linear superposition of specific solutions, corresponding to each of the roots:

$$\xi = C_{11}e^{\lambda_1 t} + C_{12}e^{\lambda_2 t}$$

$$\eta = C_{21}e^{\lambda_1 t} + C_{22}e^{\lambda_2 t}$$

Amplitudes C_{ij} depend on initial conditions (only two of the four are independent).

Values of λ_1 and λ_2 determine the system behavior about the singular point and thus characterize the nature of the singularity.

Analysis of the nature of the stationary point allows drawing conclusions concerning the stability of the system near this particular point.

In order to further the analysis, various combinations of λ_1 and λ_2 values have to be considered in detail. Their character and values depend on the sign of the determinant ***D***:

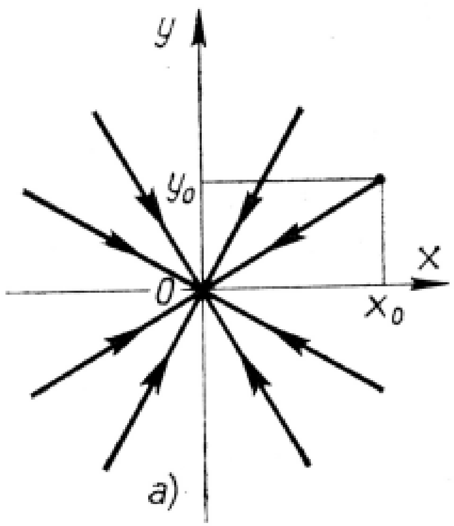
$$\begin{aligned} D &= \left(a_{11} + a_{22}\right)^2 + 4\left(a_{12}a_{21} - a_{11}a_{22}\right) \\ &= \left(a_{11} - a_{22}\right)^2 + 4a_{12}a_{21} \\ &= 4\left(\delta^2 - \omega_0^2\right) \\ &= 4\omega^2 \end{aligned}$$

First case: $D \geq 0$

In this case both λ_1 and λ_2 are real. There are three possibilities here:

1. Both λ_1 and λ_2 are negative.

Solutions for ξ and η (i.e. evolutions of perturbations about the stationary point (x_s, y_s)) are combinations of exponentially decaying functions. Hence, the singular point describes a ***stable equilibrium*** (see figure ***a)*** below).

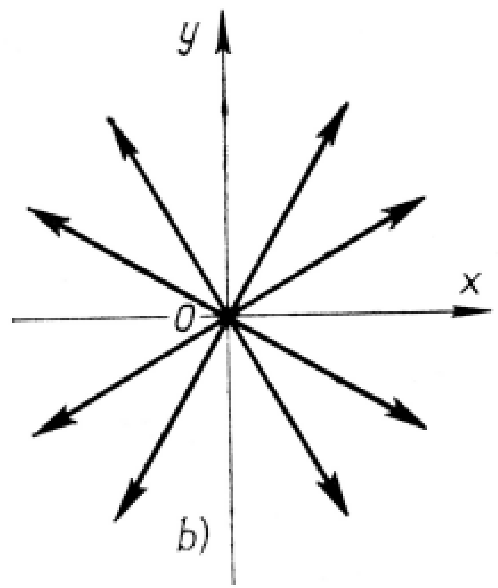


stable node

First case: $D \geq 0$

2. Both λ_1 and λ_2 are positive.

Both solutions (perturbations) exponentially increase, driving the system away from the stationary point. This is an ***unstable equilibrium*** (see ***b)*** below).



unstable node

First case: D ≥ 0

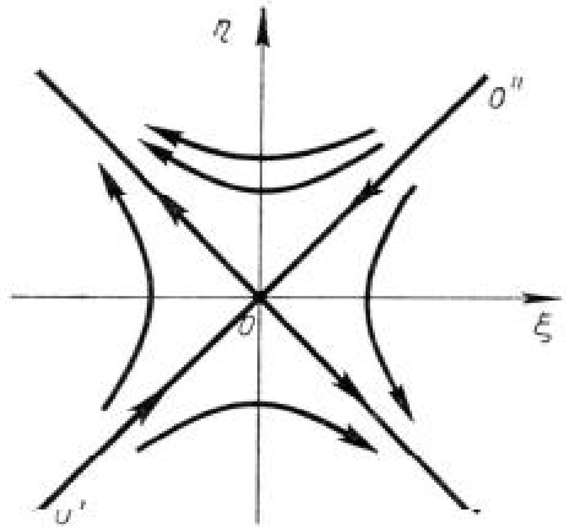
3. λ_1 and λ_2 have opposite signs.

If the roots have mixed signs (e.g. $\lambda_1 > 0$ and $\lambda_2 < 0$), the singular point is ***unstable***, because the term with the positive exponent will dominate after a sufficiently long time.

An ***exception*** may occur only when the initial conditions are such that the coefficients C_{ij} for terms with positive exponents are zero, so that only decreasing terms are left, e.g.:

$$\xi = C_{12} e^{-|\lambda_2| t}, \qquad \eta = C_{22} e^{-|\lambda_2| t}$$

As a consequence, we observe a straight line in the phase plane (***O'-O"*** in the figure below), given by $\xi = (C_{12}/C_{22})\eta$, along which the system converges to the stationary point (***O***). The other straight line passing through the singular point is the trajectory that diverges to infinity. The two straight lines are called ***separators*** and divide the phase plane into regions in which trajectories have common features.



Other trajectories feature an interesting property: initially they approach the singular point, but later on they go away from it. Such a point is called ***saddle*** and is analogous to what is known in geography as ***pass***: it's the lowest point between two peaks.

Second case: D < 0

$$D = 4\left(\delta^2 - \omega_0^2\right) = 4\omega^2 < 0 \quad \Rightarrow \quad \delta^2 < \omega_0^2$$

In this case the roots of the characteristic equation are complex conjugate numbers:

$$\lambda_{1,2} = -\delta \pm i\omega, \qquad \omega^2 = \omega_0^2 - \delta^2$$

The exponential term in the solution takes the form:

$$e^{\lambda t} = e^{-\delta\, t \pm i\omega\, t} = e^{-\delta\, t} \cdot e^{\pm i\omega\, t} = e^{-\delta\, t}\left(\cos\omega t \pm i \sin\omega t\right)$$

The general solution of the equations is now given by the expression:

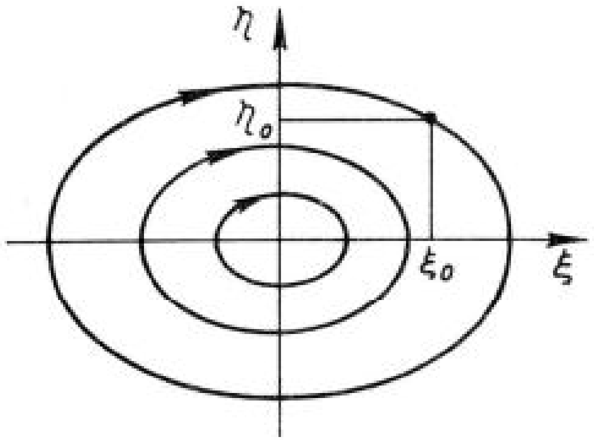
$$\xi(t) = e^{-\delta\, t}\left(C_1 \cos\omega t \pm C_2 \sin\omega t\right)$$

In view of the periodicity of the term on the right (containing ω) it can be seen that the character of the singular point is determined exclusively by the value and the sign of δ. There are three cases possible:

<u>Second case</u>: D < 0

1. $\delta = 0$.

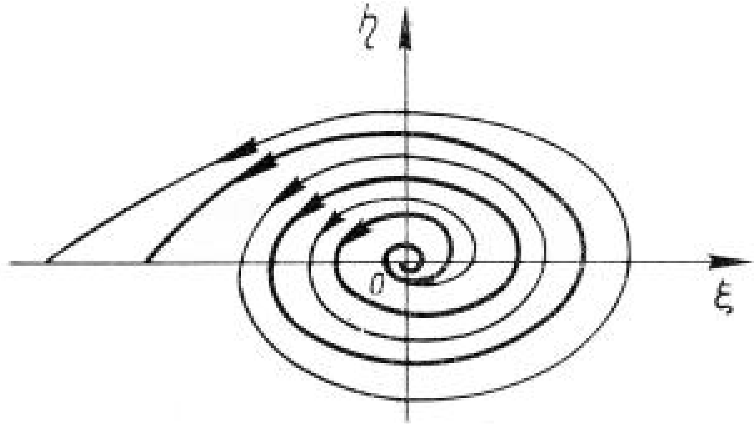
$\xi(t)$ is a periodic function of time, i.e. a perturbation causes non-decaying oscillations of the system with frequency ω. The trajectories in the phase plane are concentric ellipses whose shape depends on the initial conditions. Singularity of this type is called a ***center***. The stationary point is ***neutrally stable***.



<u>Second case</u>: D < 0

2. $\delta < 0$.

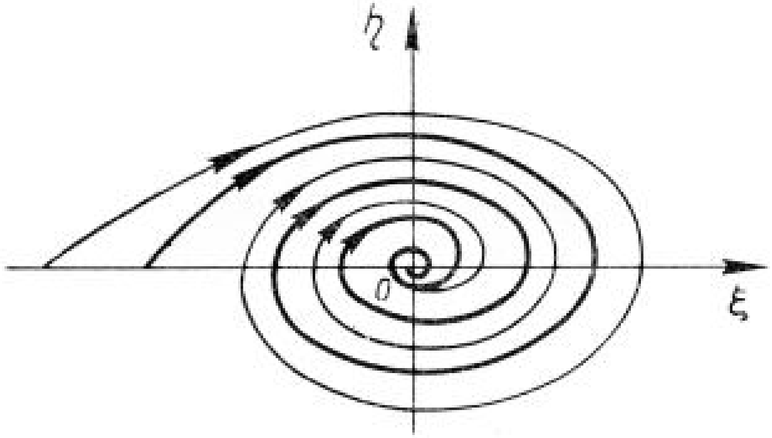
The exponential factor $\mathbf{e}^{|\delta|t}$ drives the system away from the stationary point to infinity. The trajectories represent a family of unwinding spirals (see figure below). The stationary point is an ***unstable manifold***.



Second case: D < 0

3. $\delta > 0$.

The perturbation causes decaying oscillations and return to the stationary point, called a ***stable manifold***.



***Note 1**: the density of the spiral coils depends on the ratio of δ and ω.*

***Note 2**: **Center** ($\delta = 0$) is **unstable**, because a fluctuation leading to a small modification of δ leads to its transformation into a **stable** ($\delta > 0$) or **unstable** ($\delta < 0$) **manifold**. Hence, center is on the border between these two different physical states of the system. Such a radical change of the state caused by a small perturbation is called **bifurcation**.*

Elements of analysis: asymptotic limits

Q: ***What happens ultimately to the trajectories, which diverge from the unstable stationary points?***

A: ***Learn to construct a phase portrait of the system far from equilibrium.***

The theory of perturbations allows studying the behavior of a system in the proximity of the stationary points. When the system leaves an unstable equilibrium, its trajectories lead to points located so far from the initial stationary point that the linearized equations no longer apply. Further analysis can be done by ***qualitative geometric construction of integration curves***.

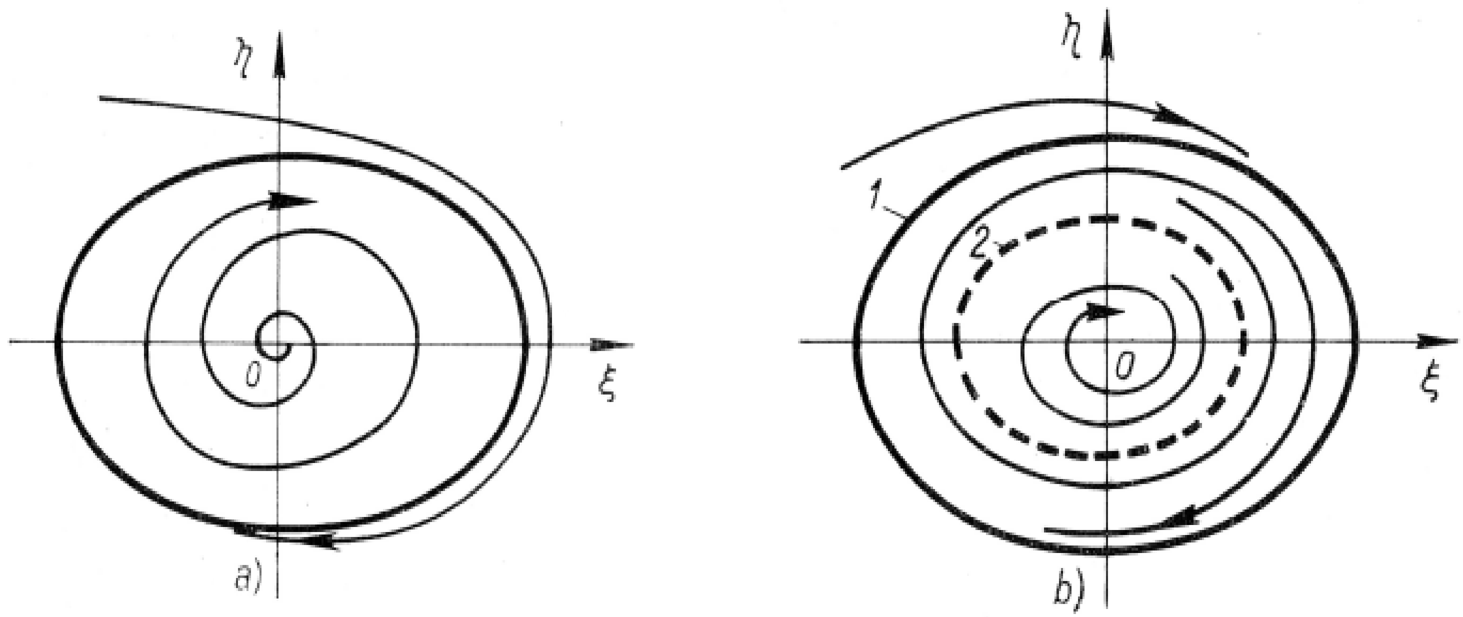
Note: ***In reality, trajectories should not diverge to infinity, because in the physical world parameter values (concentrations, velocities, etc.) cannot be infinite. If an analysis of a system of differential equations indicates existence of a stable stationary point in infinity, it usually means that the model portraying that system is imperfect, e.g. some limiting factor has been left out.***

Trajectories drifting away from unstable stationary points tend to attain their ***basins of attraction***. There are two possibilities:

1. *Somewhere near the unstable stationary point there exists a* ***stable equilibrium****, to which the trajectories converge.*

2. *There are no stable equilibria nearby, but trajectories do not diverge to infinity. Instead, they gradually approach a* ***closed curve****, which represents an* ***asymptotic cycle****.*

Example: a system featuring one ***(a)*** and two ***(b)*** ***asymptotic cycles***. The singular point is at the origin ***O*** of the coordinate system.

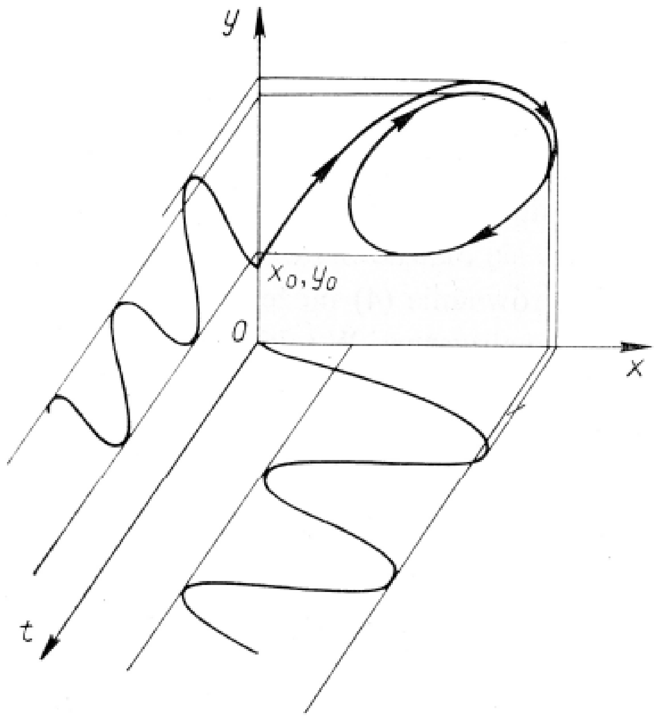


In ***(a)*** the trajectories leave an unstable stationary point ***O*** to reach the stable asymptotic cycle (thick line).

In ***(b)*** the trajectories diverge from the unstable asymptotic cycle ***2*** (dotted line) either to the stable stationary point ***O*** or to the stable asymptotic cycle ***1***.

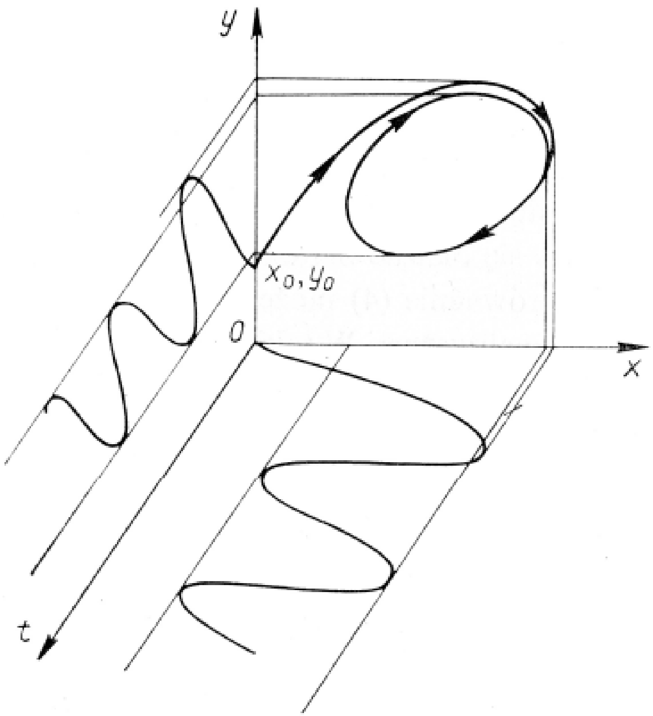
Q: ***What physical state corresponds to an asymptotic cycle?***

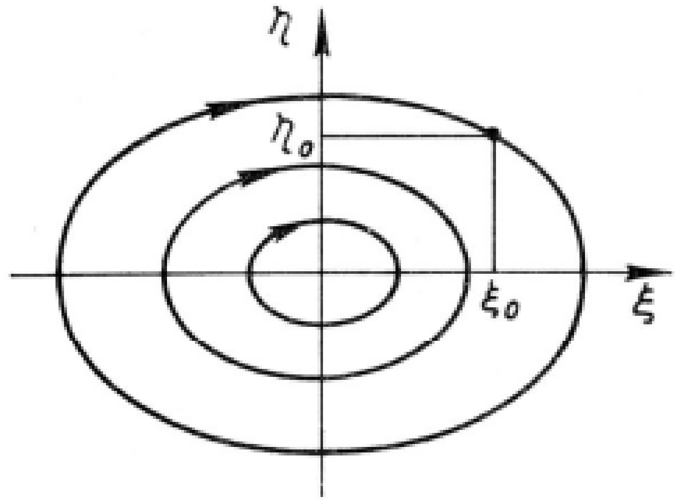
A: Looking at a system's 3D phase portrait (where time ***t*** has been added to the 'regular' coordinates ***x*** and ***y***) facilitates the analysis of a closed cycle (see figure below). Since an asymptotic cycle is a closed curve, periodic movement will be observed. Thus, an asymptotic trajectory corresponds to ***oscillations with constant amplitude***. It is a self-regulating system in the sense that oscillations occur spontaneously, without any external periodic factors, and because the system is stabilized in that state.



<u>Q</u>: *What is the difference between an asymptotic cycle and a center?*

<u>A</u>: *In both cases the system moves along elliptical trajectories. However, in the case of center the amplitude depends on initial conditions and is very sensitive to small perturbations.*





Elements of analysis: isoclines

Definition: ***isoclines*** are such curves in the phase plane, which intersect all integration curves (solution trajectories) always at the same angle. Hence, they satisfy the condition ***dy/dx = const***. Particularly important are ***principal isoclines***, which satisfy the conditions:

$$\frac{dy}{dx} = 0, \qquad \frac{dy}{dx} = \infty$$

The equation we're trying to solve is given by the relation:

$$\frac{dy}{dx} = \frac{Q(x, y)}{P(x, y)}$$

Hence, the principal isoclines are determined by the expressions:

$$Q(x, y) = 0$$
$$P(x, y) = 0$$

Singular points are located at the intersection of these curves.

The figure below illustrates the fact that by plotting principal isoclines and keeping track of the signs of derivatives we can sketch trajectories, which approach the stationary point ***0***.