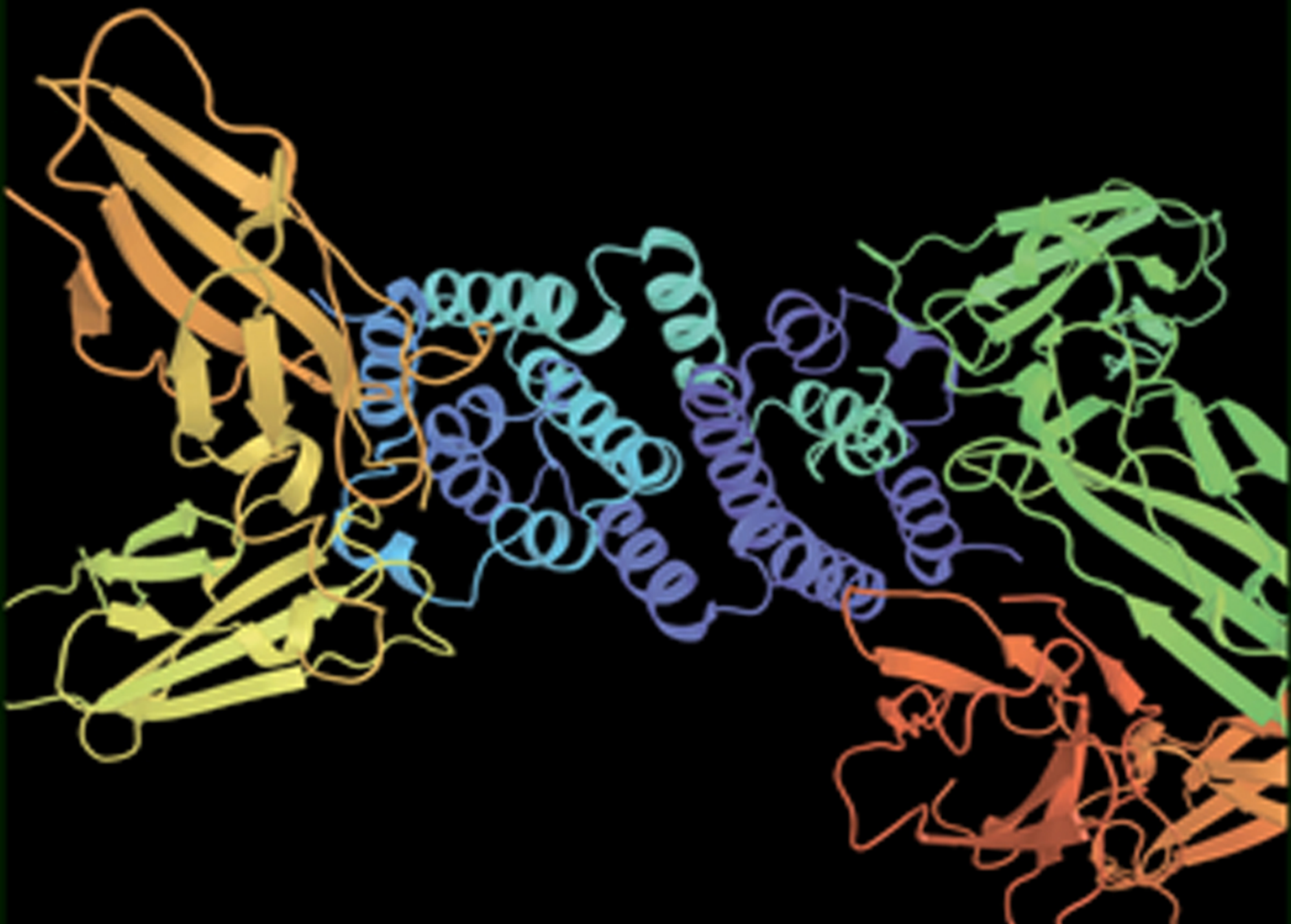
ANDREY B. RUBIN

COMPENDIUM OF Biophysics



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PART III BIOPHYSICS OF MEMBRANE PROCESSES

Andrey B. Rubin is a professor of biophysics at Lomonosov Moscow State University in the Department of Biophysics. Born in Russia, he is chair of the National Committee for Biophysics in the Russian Academy of Science. He has been head of the Department of Biophysics at MSU, Governor of the Task Force on Education in Biophysics, and a member of the RAS Council on Space Biology and Biological Membranes since 2005. He has received many awards for his contributions to the science of biophysics, and he holds many patents and inventions, as well as having been the author of numerous papers. He is also on the editorial board of the journal, Biophysics, in the Russian language.

The book does not forgive you for being lazy, And like a hoover, will refresh your brain. Its aim is not to make you go crazy But save your gyri from chondrosis pain.

Introduction

Biophysics is a science about physical and physicochemical interactions which lie in the basis of biological processes. Modern theoretical constructions and biophysical models are based on physical notions of energy, force, types of interactions, on general principles of physical and formal kinetics, thermodynamics and information theory. These notions reflect the nature of fundamental interactions and laws of motion of matter that is the subject of physics as a basic natural science. As a biological science, biophysics has biological processes and phenomena in the focal point of its interests. The key challenge for up-to-date biophysics is the insight into the deepest elemental levels, which comprise the molecular basis of the structural organization of living organisms.

The present stage of biophysics development is characterized by principal advances, associated first of all with the great progress in biophysics of complex systems and molecular biophysics. It is namely in these fields, studying the laws of dynamic behavior of biological systems and mechanisms of molecular interaction in biological structures, that general results were obtained and then used to form the general theoretical basis of biophysics. Main ideas developed in such parts of biophysics as kinetics, thermodynamics, the theory of regulation of biological systems, structures of biopolymers and their electronic and conformational properties, provide a deep insight intomechanisms of important biological processes.

At the same time, the specificity of biological systems is also displayed in the uniqueness of the physical mechanisms of their molecular processes. A principal distinction is that specific parameters of elementary interactions can vary depending on the conditions in organisms where they proceed. For example, parameters of individual elementary acts of electron transfer in photosynthetic reaction centers not only change specifically in a life cycle, but vary also in different types of plants distinguished by physiological and biochemical parameters and fertility. This means that molecular interaction mechanisms do depend on the local environment in biological systems and are themselves exposed to the direct physiological and biochemical regulation. This forms an indissoluble connection between molecular interactions and characteristics of biological phenomena that develop on their basis. That is why studies of deep biophysicalmechanisms, associatedwith physiological and biochemical peculiarities of biological objects, are a base for practical application of the results of biophysical research. Suffice it to mention the development of different methods of early diagnostics of the state of biological systems, based on the data of molecular mechanisms of biological processes, which are widely used in diverse ranges of medicine and agriculture.

In this book, the main ideas of modern biophysics are presented in the form accessible to wide circles of readers. Biophysics (biological physics) is a science about physical and physico-chemical mechanisms of interactions which lie in the basis of biological processes. Physical properties of biopolymers and kinetics of cell metabolic reactions are responsible for molecular characteristics of biological processes. A biomacromolecule as the main structure element in a cell is considered in biophysics as a peculiar molecular machine where energy is transformed and conversed from one type of energy into another. It is pertinent to recall what Bruce Alberts, a well-known American biologist, said about a cell. Hewrote that "the entire cell can be viewed as a factory that contains an elaborate network of interlocking assembly lines, each of which is composed of a set of large protein machines" (Cell, 1998, vol. 92, pp. 291–294).

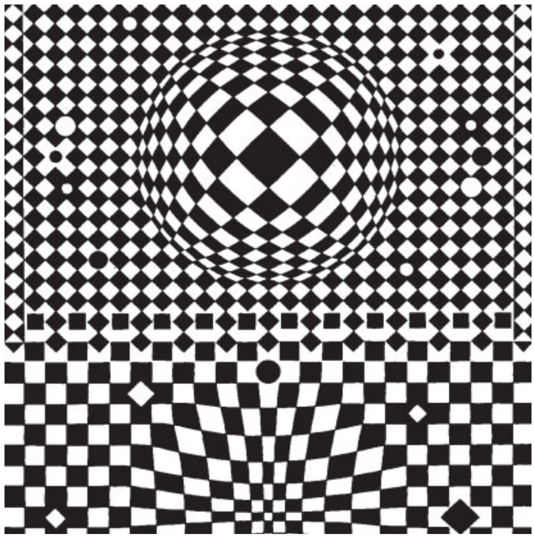
The real understanding of how these protein machines operate demands the knowledge of not only atomic equilibrium structure, but also our understanding of kinetic and energy characteristics of intermediate transformations. In the postgenome sequencing era, the first priority is given to the mechanisms of intramolecular mobility of macromolecular complexes as the base of their activity. Such an approach corresponds to the biophysical concept of directed electron-conformational interactions when energy transformation and reaction product generation become a result of internal interaction between separate parts within the whole macromolecular complex. In other words, this is the concept of a "physicalmachine" put forward in the 1970–1980s by D. S.Chernavsky, L.A. Blumenfeld, and M.V.Volkelshtein.

In theoretical biophysics, generalized kinetic and physical models of interactions allow us to describe different biological phenomena. However, the analysis of such models clearly demonstrates that different biological processes can very often be similar with respect to their molecular mechanisms. For example, mechanisms of primary photobiological processes (photosynthesis, visual reception), enzyme catalysis in the enzyme active center, and ion transfer through membrane channels are governed by similar physical principles. It follows that educational programs for biology at universities should necessarily include ideas of physics, mathematics and physical chemistry, thus illustrating their efficiency in solving biological problems. Biophysics bears the main responsibility of showing the important role of the regular application of ideas from exact sciences in studying biological processes.

PART I

BIOPHYSICS OF COMPLEX SYSTEMS

I
Kinetics of Biological Processes



1

Qualitative Methods
for Studying Dynamic Models
of Biological Processes

2

Types of Dynamic Behavior
of Biological Systems

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Kinetics of Enzyme Processes

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Self-organization Processes
in Distributed Biological Systems

1

Qualitative Methods for Studying Dynamic Models of Biological Processes

The functioning of the integrated biological system is a result of interactions of its components in time and space. Elucidation of the principles of regulation of such a system is a problem that can be solved only with the use of correctly chosen mathematical methods.

The kinetics of biological processes includes the time-dependent behavior of various processes proceeding at different levels of life organization: biochemical conversions, generation of electric potentials on biological membranes, cell cycles, accumulation of biomass or species reproduction, interactions of living populations in biocommunities.

1.1 General Principles of Description of Kinetic Behavior of Biological Systems

The kinetics of a system is characterized by a totality of variables and parameters expressed via measurable quantities, which at each instant of time have definite numerical values. □

In different biological systems, different measurable values can play the role of variables: those are concentrations of intermediate substances in biochemistry, the number of microorganisms or their overall biomass in microbiology, the species population number in ecology, membrane potentials in biophysics of membrane processes, etc. Parameters may be temperature, humidity, pH, electric conductance of membranes, etc.

This is sufficient to construct a general mathematical model representing a system of n differential equations:

$$\begin{aligned} dc_1/dt &= f_1(c_1, \ldots, c_n); \\ &\ldots\ldots\ldots\ldots\ldots\ldots \\ dc_n/dt &= f_n(c_1, \ldots, c_n), \end{aligned} \tag{1.1}$$

where $c_1(t), \ldots, c_n(t)$ are unknown functions of time describing the system variables (for example, substance concentrations); dc_i/dt are rates of changes of these variables; f_i are functions dependent on external and internal parameters of the system. A comprehensive model of type (1.1) may contain a large number of equations, including nonlinear ones.

Many essential questions concerning the qualitative character of the system behavior, in particular, stability of stationary states and transition between them, oscillation modes and others, can be solved using methods of the qualitative theory of differential equations. These methods permit revealing important general properties of the model without determining explicitly the unknown functions $c_1(t), \ldots, c_n(t)$. Such an approach gives good results when analyzing the models that consist of a small number of equations and reflect the most important dynamic features of the system.

The key approach in the qualitative theory of differential equations is to characterize the state of the system as a whole by variables $c_1, c_2, \ldots, c_n$, which they aquire at each instant of time upon changing in accord with (1.1). If the values of variables $c_1, c_2, \ldots, c_n$ are put on rectangular coordinate axes in the n-dimensional space, the system state will be described by some point M in this space with coordinates $M(c_1, c_2, \ldots, c_n)$. The point M is called a representation point.

The change in the system state is comparable to the displacement of the point M in the n-dimensional space. The space with coordinates $c_1, c_2, \ldots, c_n$ is a phase state; the curve, described in it by the point M, is a phase trajectory.

1.2 Qualitative Analysis of Elementary Models of Biological Processes

Let us consider qualitative methods of studying such systems represented as a system of two independent differential equations (the right-hand parts do not depend explicitly on time), that can be written as:

$$dx/dt = P(x, y), \quad dy/dt = Q(x, y). \qquad \square \tag{1.2}$$

Here $P(x, y)$ and $Q(x, y)$ are continuous functions, determined in some range G of the Euclidean plane (x and y are Cartesian coordinates) and having continuous derivatives not lower than the first order.

The range may be both unlimited and limited. When variables x and y have a certain biological meaning (substance concentrations, species population number), some restrictions are usually superimposed on them. First of all, biological variables cannot be negative.

Accept the coordinates of the representation point M_0 to be (x_0, y_0) at $t = t_0$. At every next instant of time t, the representation point will move in compliance with the system of equations (1.2) and have the position $M(x, y)$, corresponding to $x(t), y(t)$. The set of points on the phase plane x, y is a phase trajectory. □

The character of phase trajectories reflects general qualitative features of the system behavior in time. The phase plane, divided in trajectories, represents an easily visible "portrait" of the system. It allows grasping at once the whole set of possible motions (changes in variables x, y) corresponding to the initial conditions. The phase trajectory has tangents, the slopes of which in every point $M(x, y)$ equals the derivative value in this point dy/dx. Accordingly, to trace a phase trajectory through point $M_1(x_1, y_1)$ of the phase plane, it is enough to know the direction of the tangent in this point of the plane or the value of the derivative

$$\left.\frac{dy}{dx}\right|_{\substack{x=x_1\\y=y_1}}.$$

To this end, it is required to have an equation with variables x, y and without time t in an explicit form. For that, let us divide the second equation in system (1.2) by the first one. The following differential equation is obtained

$$\frac{dy}{dx} = \frac{Q(x,y)}{P(x,y)}, \tag{1.3}$$

which is frequently much more simple than the initial system (1.2). Solution of equation (1.3) $y = y(x, c)$ or in an explicit form $F(x, y) = C$, where C is the constant of integration, yields a family of integral curves — phase trajectories of system (1.2) on the plane x, y.

But generally, equation (1.3) may have no analytical solution, and then integral plotting should be done using qualitative methods.

Method of Isoclinic Lines. The method of isoclinic lines is typically used for qualitative plotting of a phase portrait of a system. In this case, lines, which intersect the integral lines at a certain angle, are plotted on the phase plane. The analysis of a number of isoclinic lines can show the probable course of the integral lines. □

The equation of isoclinic lines can be obtained from equation (1.3). Suppose $dy/dx = A$, where A is a definite constant value. The value of A is a slope of the tangent to the phase trajectory and, consequently, can have values from $-\infty$ to $+\infty$. Substituting the A value instead of dy/dx in (1.3), we get the equation of isoclinic lines:

$$A = \frac{Q(x,y)}{P(x,y)}. \tag{1.4}$$

By giving different definite numeric values to A, we obtain a family of curves. In any point of each of these curves, the tangent slope to the phase trajectory, passing through this point, is the same value, namely the value of A, which characterizes the given isoclinic line.

Note that in the case of linear systems, i.e. systems of the type

$$dx/dt = ax + by, \quad dy/dt = cx + dy, \tag{1.5}$$

isoclinic lines represent a bundle of straight lines, passing through the origin of coordinates:

$$\frac{cx + dy}{ax + by} = A \quad \text{or} \quad y = \frac{(Aa - c)x}{d - Ab}.$$

Singular Points. Equation (1.3) determines directly the singular tangent to the corresponding integral curve in each point of the plane. Exclusion is the point of intersection of all isoclinic lines ($\overline{x}$, $\overline{y}$), at which the tangent direction is indefinite, because in this case the value of the derivative is ambiguous:

$$\left.\frac{dy}{dx}\right|_{\substack{x=\overline{x}\\ y=\overline{y}}} = \frac{Q(\overline{x},\overline{y})}{P(\overline{x},\overline{y})} = \frac{0}{0}.$$

The points, in which time derivatives of variables x and y turn concurrently to zero

$$\left.\frac{dx}{dt}\right|_{\overline{x},\overline{y}} = P(\overline{x},\overline{y}) = 0, \quad \left.\frac{dy}{dt}\right|_{\overline{x},\overline{y}} = Q(\overline{x},\overline{y}) = 0 \tag{1.6}$$

and in which the direction of tangents to integral curves is indefinite, are singular points. The singular point in the equation of phase trajectories (1.3) complies with the stationary state of system (1.2), because the rates of changes of variables in this point are equal to zero, and its coordinates are stationary values of variables $\overline{x}, \overline{y}$.

For a qualitative study of a system, it is often possible not to go beyond plotting only some isoclinic lines on the phase plane. Of special interest are the so-called basic isoclinic lines: $dy/dx = 0$ is the isoclinic line of horizontal tangents to phase trajectories, the equation of which is $Q(x, y) = 0$, and the isoclinic of vertical tangents $dy/dx = \infty$, which is in line with equation $P(x, y) = 0$. □

The plotting of the basic isoclinic lines and the determination of their intersection point, the coordinates of which satisfy the following conditions

$$P(\overline{x},\overline{y}) = 0, \quad Q(\overline{x},\overline{y}) = 0, \tag{1.7}$$

gives the intersection point of all isoclinic lines on the phase plane. As mentioned above, this point is a singular point and corresponds to the stationary state of the system (Fig. 1.1).

Figure 1.1 demonstrates the case of one stationary point of intersection of basic isoclinic lines of the system. The figure shows directions of the tangents dy/dx to the trajectories on the phase plane.

The number of stationary states in system of equations (1.2) is equal to the number of intersection points of basic isoclinic lines on the phase plane.

Stability of Stationary States. Assume the considered system to be in the equilibrium state. Then the representation point on the phase plane is stationary in one of the singular points of the equation of integral curves (1.3), because, by definition, in these points $dx/dt = 0$, $dy/dt = 0$.

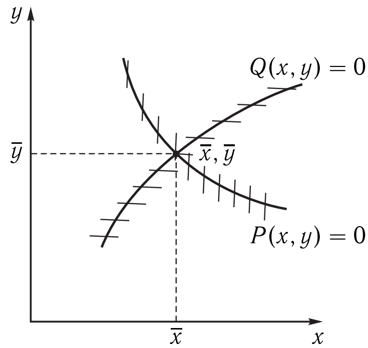

Figure 1.1. The stationary state is determined by the point of intersection of the basic isoclinic lines.

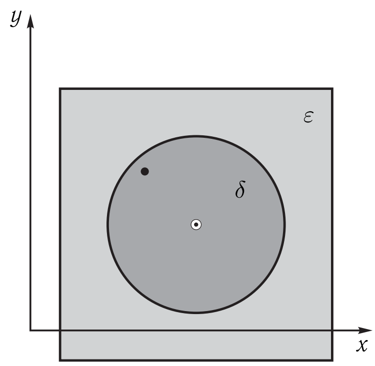

Figure 1.2. Illustration of determination of stability.

The state of equilibrium is stable (according to the Lyapunov theory) if for any given region of permissible deviations from the equilibrium state (region ε), region $\delta(\varepsilon)$, surrounding the equilibrium state and having such a property that neither of the representation point movements, beginning in δ, will never reach the boundary of region ε. On the contrary, the equilibrium state is unstable, if it is possible to indicate the region of deviations from the equilibrium state ε, for which there is no region δ surrounding the equilibrium state and having the property that neither of the motions, beginning inside region δ, will never reach the boundary of region ε.

Now if the system is displaced from the equilibrium state, the representation point will be displaced from the singular point and will move along the phase plane in compliance with equations of its motion (1.2). The question, if the analyzed point is stable, is determined correspondingly by whether the representation point is displaced from a given region, surrounding the singular point (this region can be larger of smaller depending on the statement of the problem) (Fig. 1.2).

Studies of stability of the equilibrium state (the point of intersection of basic isoclinic lines $P(x, y) = 0$, $Q(x, y) = 0$) are connected with the analysis of the character of displacements of the representation point upon deviation from the equilibrium state. To facilitate calculations, let us instead of variables x, y introduce new variables ξ, η determining them as displacements relative to the equilibrium position on the phase plane:

$$x = \overline{x} + \xi, \quad y = \overline{y} + \eta. \tag{1.8}$$

Substituting these expressions in (1.2), we get

$$d\overline{x}/dt + d\xi/dt = P(\overline{x} + \xi, \overline{y} + \eta),$$
$$d\overline{y}/dt + d\eta/dt = Q(\overline{x} + \xi, \overline{y} + \eta), \tag{1.9}$$

$d\overline{x}/dt = d\overline{y}/dt = 0$, because $\overline{x}, \overline{y}$ are the coordinates of the singular point.

Let us factorize the right-hand side of the above equations in Taylor series by variables ξ, η and cast out nonlinear members. The following system of linear equations will be obtained:

$$d\xi/dt = a\xi + b\eta, \quad d\eta/dt = c\xi + d\eta, \tag{1.10}$$

where coefficients a, b, c, and d are values of quotient derivatives in point $(\overline{x}, \overline{y})$:

$$a = P'_x(\overline{x}, \overline{y}), \quad b = P'_y(\overline{x}, \overline{y}), \quad c = Q'_x(\overline{x}, \overline{y}), \quad d = Q'_y(\overline{x}, \overline{y}).$$

System (1.10) is called a linearized system or the system of the first approximation. □

For a large class of systems, namely structurally stable, or "rough" systems, the character of phase trajectories near singular points is preserved at any sufficiently small changes in the right-hand side of equations (1.2) — functions P and Q, if the changes in the derivatives of these functions are also small. For such systems, studies of equations of the first approximation (1.10) give a correct answer to the question on the stability of the equilibrium state of system (1.2) and on the topological structure of the phase plane near this equilibrium state.

System (1.10) is a linear one, and therefore its analytical solution is possible. The general solution of the system is found as follows:

$$\xi = Ae^{\lambda t}, \quad \eta = Be^{\lambda t}. \tag{1.11}$$

By substitution of these expressions in (1.10) and reduction of the obtained expressions by $e^{\lambda t}$, the following expression is obtained:

$$\lambda A = aA + bB, \quad \lambda B = cA + dB. \tag{1.12}$$

Algebraic system of equations (1.12) with unknown members A and B has, as known, a nonzero solution only if its determinant, consisting of coefficients at the unknown members, is zero:

$$\begin{vmatrix} a - \lambda & b \\ c & d - \lambda \end{vmatrix} = 0.$$

Having uncovered this determinant, we get the so-called characteristic equation of the system:

$$\lambda^2 - (a + d)\lambda + (ad - bc) = 0. \quad \square \tag{1.13}$$

The solution of this equation yields indices $\lambda_{1,2}$ at which nonzero solutions for A and B of system (1.12) are possible:

$$\lambda_{1,2} = \frac{a + d}{2} \pm \sqrt{\frac{(a + d)^2}{4} + bc - ad}. \tag{1.14}$$

If the radicand is negative, $\lambda_{1,2}$ are complex conjugate values. Let us assume that both roots of equation (1.13) have real numbers varying from zero, and there are no multiple roots. Then the general solution of system (1.10) written as (1.11) may be represented as a linear combination of exponents with indices λ_1 and λ_2:

$$\xi = C_{11}e^{\lambda_1 t} + C_{12}e^{\lambda_2 t}, \quad \eta = C_{21}e^{\lambda_1 t} + C_{22}e^{\lambda_2 t}. \tag{1.15}$$

The behavior of variables ξ, η, in compliance with (1.15) and, consequently, the behavior of variables x and y near the singular point $(\overline{x}, \overline{y})$ depend on the type of indices of the exponents λ_1 and λ_2. When the indices λ_1 and λ_2 are real and have the same sign, the singular point is called a node (Fig. 1.3).

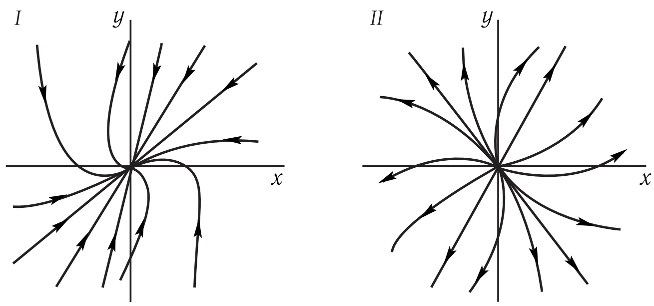

Figure 1.3. Stable (*I*) and unstable (*II*) nodes on phase plane.

If $\lambda_{1,2} < 0$, the values of variables ξ, η (deviations from the equilibrium position) decrease with time. In this case, singular point $(\overline{x}, \overline{y})$ is a stable node (*I*). If $\lambda_{1,2} > 0$, values ξ, η increase with time and the singular point is an unstable node (*II*).

Many biological systems are characterized by a "non-oscillatory" transition from an arbitrary initial state to the stationary one, which corresponds to a stationary solution of the stable node type in the model.

When roots of $\lambda_{1,2}$ are real, but have opposite signs, the behavior of variables is represented by hyperbolic-type curves on the phase plane (Fig. 1.4). Such a singular point is unstable and is called a singular point of the "saddle" type. It can be seen that independent of the position of the representation point at the initial time (with the exception of the singular point and the separatrix), in the long run it will always move away from the equilibrium.

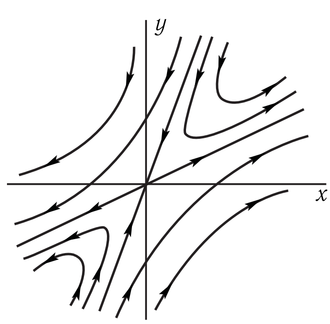

Figure 1.4. Singular point of a "saddle" type on phase plane (xy).

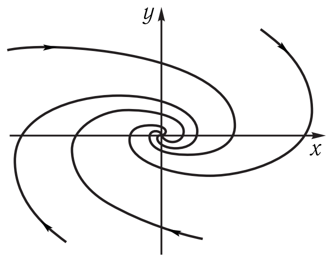

Figure 1.5. Singular point of a "focus" type on phase plane (xy).

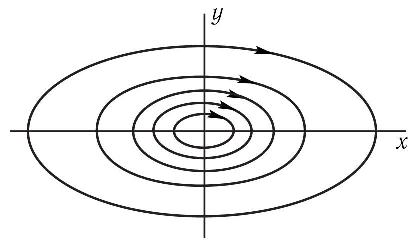

Figure 1.6. Singular point of a "center" type on phase plane (xy).

Singular points of the "saddle" type play an important role in the so-called "trigger" biological systems (see in detail in Section 1 of Chapter 2).

If λ_1 and λ_2 are complex conjugate, changes of variables x and y in time have an oscillation character, and the phase trajectories look like helices (Fig. 1.5). In this case, the singular point is called a focus. At the same time, if real numbers $\lambda_{1,2}$ are negative ($\mathrm{Re}\,\lambda_{1,2} < 0$), oscillations decay and the position of equilibrium is a stable focus. But if $\mathrm{Re}\,\lambda_{1,2} > 0$, the oscillation amplitude increases with time, and the singular point is an unstable focus.

When $\mathrm{Re}\,\lambda = 0$, phase trajectories near the singular point have the shape of ellipsoids (Fig. 1.6). In this case, no integrated curve passes through the singular point. Such an isolated singular point, near which integrated curves have the shape of closed curves, in particular ellipsoids, "mutually enclosed in each other" and including the singular point, is called a center.

Let us formulate the above classification of singular points of a linear system (1.10). If degeneration is absent ($ad - bc \neq 0$), six types of equilibrium states can exist depending on the character of the roots of characteristic equation (1.13) which are also called Lyapunov indices:

1) Stable node (λ_1 and λ_2 are real and negative);
2) Unstable node (λ_1 and λ_2 are real and positive);
3) Saddle (λ_1 and λ_2 are real and have opposite signs);
4) Stable focus (λ_1 and λ_2 are complex and $\mathrm{Re}\,\lambda < 0$);
5) Unstable focus (λ_1 and λ_2 are complex and $\mathrm{Re}\,\lambda > 0$);
6) Center (λ_1 and λ_2 are imaginary). □

Equilibrium states (1–5) are rough: their character does not change at rather small changes in the right-hand sides of equations (1.2) and their derivatives of the first order.

Analysis of the "Predator–Prey" Model (1.17). Now let us consider the ecological Volterra model. Assume that in some closed region there live prey and predators, for example, hares and wolves. Hares feed on plant food that is always abundant. Wolves (the predators) can feed only on hares (the prey). Let us designate the number of hares as x and the number of wolves as y. Since the amount of food for hares is unlimited, we can suggest that hares reproduce at a rate proportional to their amount:

$$\dot{x}_{\mathrm{dimens}} = \varepsilon_1 x. \tag{1.16}$$

(Equation (1.16) is in compliance with the equation of an autocatalytic chemical reaction of the first order.)

Accept the loss in the number of hares to be proportional to the probability of their encounter with wolves, i.e. proportional to the product $x \times y$. The number of wolves also increases the faster, the more frequent their encounters with hares, i.e. proportional to $x \times y$. In chemical kinetics, this corresponds to a bimolecular reaction, when the probability of appearance of a new molecule is proportional to the probability of encounter of two molecules, i.e. the product of their concentrations. In addition, natural death of wolves takes place, the rate of decrease in the number of species being proportional to their number. This is in compliance with the process of a chemical outflow from the reaction sphere. As a result, the following system of equations is obtained for changes in the number of hares x and wolves y:

$$dx/dt = x(\varepsilon_1 - \gamma_1 y), \quad dy/dt = -y(\varepsilon_2 - \gamma_2 x). \tag{1.17}$$

Let us study the singular point in the Volterra predator-prey model (1.17). Its coordinates are found promptly if the right-hand sides of equations in system (1.17) are equal to zero. This yields stationary non-zero values: $\overline{x} = \varepsilon_2/\gamma_2$, $\overline{y} = \varepsilon_1/\gamma_1$. As parameters $\varepsilon_1, \varepsilon_2, \gamma_1, \gamma_2$ are positive, point $(\overline{x}, \overline{y})$ lies in the positive quadrant of the phase plane. Linearization of this point yields

$$\frac{d\xi}{dt} = -\gamma_1 \overline{x}\eta = -\frac{\gamma_1\varepsilon_2}{\gamma_2}\eta; \quad \frac{d\eta}{dt} = -\gamma_2 \overline{y}\xi = -\frac{\gamma_2\varepsilon_1}{\gamma_1}\xi.$$

Here $\xi(t)$, $\eta(t)$ are deviations from the singular point on the phase plane:

$$\xi(t) = x(t) - \overline{x}, \quad \eta(t) = y(t) - \overline{y}.$$

The characteristic equation of the system is as follows:

$$\begin{vmatrix} -\lambda & \dfrac{-\gamma_1\varepsilon_2}{\gamma_2} \\ \dfrac{\gamma_2\varepsilon_1}{\gamma_1} & -\lambda \end{vmatrix} = 0, \qquad \lambda^2 + \varepsilon_1\varepsilon_2 = 0.$$

The roots of this equation are purely imaginary: $\lambda_{1,2} = \pm i\sqrt{\varepsilon_1\varepsilon_2}$.

In this case, phase trajectories near the singular point look like concentric ellipsoids, and the singular point itself is the center (Fig. 1.7). Far from the singular point, phase trajectories are closed, though their shape varies from the ellipsoid one.

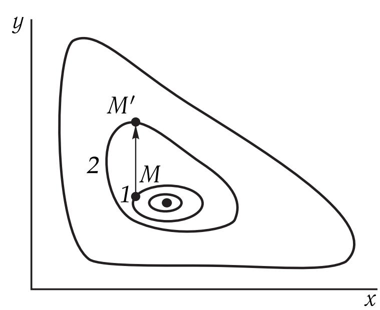

Figure 1.7. Phase portrait of the predator — prey system (the singular point of a "center" type).

On the whole, the singular point of the "center" type is unstable. Let oscillations $x(t)$ and $y(t)$ proceed so that the representation point moves along the phase trajectory *1* (Fig. 1.7). At the instant of time when the point is in position M, such a number of species Δy is added to the system from the outside that the representation point jumps from point M to point M'. After that, if the system is again left on its own, oscillations $x(t)$ and $y(t)$ will occur with larger amplitudes than previously, and the representation point will move along trajectory 2. So, upon external action the oscillations change their characteristics forever.

Figure 1.8 shows plots of functions $x(t)$ and $y(t)$. It is seen that $x(t)$ and $y(t)$ are periodic functions of time, the maximum of the prey number surpassing the maximum of the number of predators.

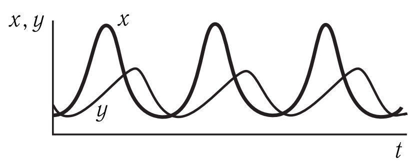

Figure 1.8. Dependence of the number of predators y and prey x on time.

Figure 1.9 shows curves of the number of North American hares and lynxes in Canada, plotted using the data on the number of harvested skins. The shape of real curves is much less correct than that of theoretical ones. But the model ensures the coincidence of the most essential characteristics of these curves — the values of amplitudes and the lagging of oscillations in the numbers of predators and prey.

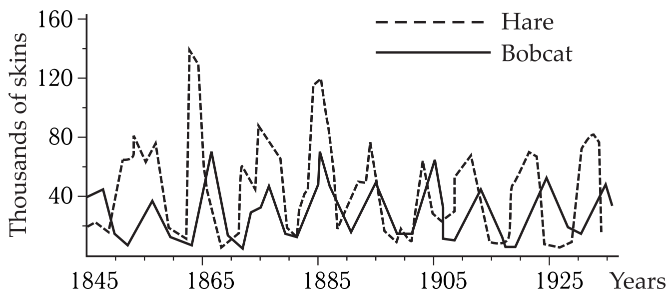

Figure 1.9. Curves of hare and lynx numbers in Canada (Villee, Dethier, 1971).

Periods of hare (prey) and bobcat (predators) population waves are approximately the same and make 9–10 years, the maximum of hare numbers surpasses that of boncts by a year.

A much more serious disadvantage of the Volterra model is instability of solutions of the system of equations, when any random change in the number of a species leads to a change in the oscillation amplitude of both types. Needless to say, in natural conditions, animals are affected by a huge number of such random actions. But as seen from Fig. 1.9, the oscillation amplitude of the number of species changes insignificantly from year to year.

Because of the "unrough" character of the Volterra system, an arbitrarily small change in the form of the right-hand parts of equations in system (1.17) leads to changes in the type of the singular point and, as a result, the character of phase trajectories of the system.