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Phenomenological theory of ontogenesis

ALEXEYI A. ZOTIN* and ALEXANDER I. ZOTIN

Kol'tsov Institute of Developmental Biology, Russian Academy of Sciences, Moscow, Russia

ABSTRACT In accordance to Prigogine-Wiame and phenomenological theories of ontogenesis, a continuous decreasing of specific entropy production measured by the intensity of heat production or respiration takes place during development, growth and aging. There are periods in the life of organisms when reverse processes occur: (initial stages of oogenesis, regeneration and malignant growth). The phenomenological theory of ontogenesis demonstrates that physical bases of individual development are characterized by two thermodynamic principles: minimum energy dissipation and fastest descent.

KEY WORDS: *Ontogenesis, principle minimum dissipation energy, principle fastest descent*

Introduction

All phenomena occurring in Nature may be subdivided into two classes: occurring on their own (that is spontaneous processes), and occurring as a result of some forces (action-compelling processes). It is evident that the development of an organism is a "spontaneous process", and we can hardly imagine this process to be the result of some forces outside an organism. We can not accept the vitalism views of special forces or laws inside organisms, which are not physical but may determine development.

The phenomenological theory of ontogenesis regards the processes of organism development, growth and aging as a spontaneous process of living system transition from a less probable state to a more probable one, which may be described in terms of thermodynamics. In this respect, it takes over after other thermodynamic theories of development (Bauer, 1935; Salzer, 1957) and especially the theory of Prigogine-Wiame (Prigogine and Wiame, 1946; Prigogine, 1967; Zotin,1972)

Prigogine-Wiame theory of development

According to the Prigogine-Wiame theory, development, growth and aging, are accompanied by incessant decrease of the dissipation function

(1)
$$\frac{d\psi}{dt} \leq 0,$$

where

(2)
$$\psi = \frac{T}{V}\frac{d_iS}{dt} = \sum_{j=1}^{n} J_j X_j,$$

Ψ represents *the specific dissipation function of the system; T-absolute temperature; V-volume or mass of the system;* d_iS/dt-*entropy production; J - specific thermodynamic flows; X-thermodynamic forces.*

As in living organisms $\Psi = q_{O_2} + q_{gl}$ (where q_{O_2} is oxygen consumption intensity; q_{gl} is glycolysis intensity from the point of view of the Prigogine-Wiame theory), during ontogenesis incessant decrease in oxygen consumption and glycolysis intensity occur.

A new organism starts its development from a rather high level of dissipation function. Consequently, in the life of each organism a period must exist, when dissipation function would be increased (Zotin, 1972). In thermodynamics of linear irreversible processes, which is the basis for the Prigogine-Wiame theory, it is improbable that a separately existing system, such as an embryo, growing or adult organism, should, deviate from a stationary trajectory of development under the same environmental parameters. A similar process, however, is possible in the period of oogenesis. During this period, the embryo is formed into maternal organism as a subsystem, and stable deviation of oocytes from the steady state may occur at the expense of coupled processes, proceeding in other parts of the maternal system:

(3)
$$\psi_c = \frac{T}{V}\frac{d_iS_c}{dt} = \sum_{k=1}^{m} J_k X_k \leq 0$$

and

(4)
$$\frac{d\psi_c}{dt} > 0,$$

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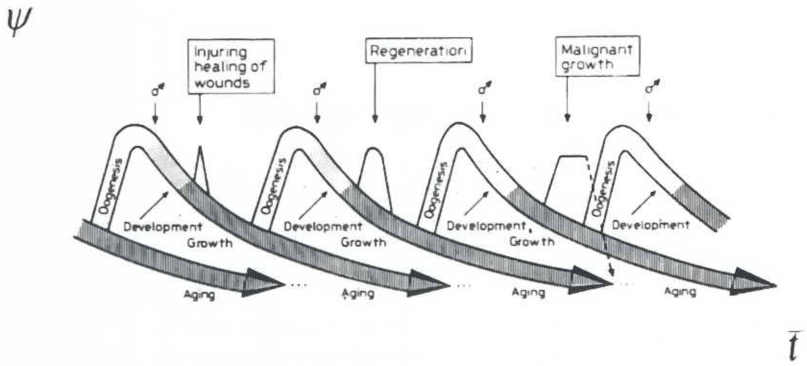

Fig. 1. Schematic representation of oogenesis, embryogenesis, growth, aging, wound healing, regeneration and malignant growth from the viewpoint of the Prigogine-Wiame theory of development. *(Zotin, 1972).*

where Ψ_c *is a dissipation function of the deviating part of maternal system.* Such a process does not contradict thermodynamics of irreversible processes. This is the first corollary of the Prigogine-Wiame theory (Fig. 1).

The second and the third corollaries concern the processes of regeneration and malignant growth (Fig. 1). For the regeneration process, living systems must be carried from a current steady state trajectory and reach the sufficient value of specific dissipation function. It is evident that such a deviation must happen at early stages of wound healing and regeneration. This conclusion does not contradict thermodynamics since the regenerating organ is a part of organism and its deviation from a steady state is possible at the expense of coupled processes (3) in another part of a whole system. On the other hand, due to the injury and especially shortly after it, external and internal parameters of the system can change, and a transition process to a new steady state could happen.

The third corollary of the Prigigine-Wiame thermodynamic theory of development concerns malignant growth. In this case, a living system also constitutively deviates from a steady state trajectory at early stages of carcinogenesis. This deviation is accompanied by increase of the system dissipation function at the expense of coupled processes in other parts of organisms (Fig. 1).

In terms of the thermodynamic theory of development, rejuvenation proceeds in oogenesis while at all other stages of organism's life aging is accompanied by decrease of the dissipation function. At the early stage of regeneration and malignant growth, a living system also involves constitutive deviation from the steady state trajectory (Fig. 1). This is the fourth corollary of the Prigogine-Wiame theory.

The dissipation function in a living system is equal to the intensity of respiration and glycolysis. Consequently, studying a mechanism decreasing in energy metabolism intensity, in the course of development and growth, is equal, in terms of this theory, to studying the mechanism of aging; while studying the mechanism of constitutive increase in respiration and glycolysis intensity is equal to studying the mechanism of rejuvenation (Zotin, 1972). We can go even further. On aerobic condition, glycolysis energy metabolism impact is neglected for the majority of animals. This reduces the field of study of constitutive process mechanisms, putting forward the most important of them (i.e., process of the change of oxygen consumption intensity). We may go further towards the main link in the chain of aging and rejuvenation mechanism if we consider the basic ways of regulation of cells respiration and especially at the expense of mitochondria concentration and change of its functioning (Zotin and Zotina, 1993). It is worth mentioning that other authors proceeding from thermodynamic consideration also come to similar conclusions concerning the problem of aging (Economos *et al.*, 1980; Miquel *et al.*, 1980, 1984).

The Prigogine-Wiame theory of development rested upon the thermodynamics of linear irreversible processes, i.e. the processes which should be realized in the systems close to equilibrium. However, living organisms are not systems close to equilibrium. In addition, they are referred to the category of organized systems, characterized by the presence of regulation and control processes. It is not surprising, therefore, that the Prigogine-Wiame theory caused much skepticism. At the same time, the theory of organism development covers all basic phenomena of developmental biology including oogenesis, embryonic development, growth and aging, organ regeneration and wound healing, malignant growth, ect. (Zotin, 1972; Nikolaev, 1976; Lamprecht and Zotin, 1978; Rubin, 1984; Brooks and Wiley, 1988; Leuschner, 1989). That is why we have undertaken the attempt to improve the theoretical basis of this theory (Zotin and Zotina, 1993). However, causes of living system deviations from basic trajectory of ontogenesis, as well as general causes of shape formation and differentiation were not shown. This is made in this article taking into account thermodynamic principle of fastest descent and principle of minimum energy dissipation.

Principle of minimum energy dissipation for organized systems

Some criteria of the system evolution to equilibrium or stationary state are accepted in thermodynamics of non-equilibrium processes. In the thermodynamics of linear irreversible processes this is the criterion of evolution (1) (Prigigine, 1967). The criterion of evolution for nonlinear systems is close to the linear ones and has a similar expression (Zotin, 1990):

$$\frac{d\psi_d}{dt} \le 0, \tag{5}$$

where Ψ_d is *the external dissipation function (psid-function)* from partition:

$$\psi = \psi_d + \psi_u, \tag{6}$$

where Ψ_u is *the bound dissipation function (psiufunction).*

Thus, the criterion of evolution for both, the systems close to equilibrium (1) and weakly nonlinear systems (5), suggests that during change of these systems the intensity of energy dissipation will decrease to a minimal value at the stationary state. We cannot yet prove inequalities of type (3) or (5) for strongly nonlinear systems, but such inequality can be introduced on the basis of the following postulate (Zotin, 1990): *in a stable state of any thermodynamic system, the rate of energy dissipation in it is minimal.*

This is the so-called *principle of minimum energy dissipation.* If we deal with strongly nonlinear systems, the psid-function in stationary state is not always constant, and criterion the of evolution (5) can be written as

(7) $$\frac{d\overline{\psi}_d}{dt} \le 0,$$

and the principle of minimum energy dissipation as

(8) $$\overline{\psi}_d = \min,$$

where $\overline{\psi}_d$ is the *average value of psid-function.* Moiseev (1987) proposed a somewhat different formulation of the principle of minimum energy dissipation.

The Partition (6) follows from the consideration of a physical sense of energy dissipation in the open system as well as from various thermodynamic considerations (Lamprecht and Zotin, 1978; Lurie and Wagensberg, 1979; Zotin, 1990). It follows from these considerations that the external dissipation function equals the intensity of heat production in the system,

$$\overline{\psi}_d = \overline{\dot{q}}$$

and since, for living system

$$\overline{\dot{q}} \approx \overline{\dot{q}}_{O_2}$$

the criterion of evolution (1), (5), (7) can be written as

(9) $$\frac{d\overline{\dot{q}}}{dt} \approx \frac{d\overline{\dot{q}}_{O_2}}{dt} \le 0.$$

According to criterion (9) and the principle of minimum energy dissipation, the specific heat production and respiration intensity of organisms should be decreased during ontogenesis. Approach to the equilibrium or stationary state means movement of the system toward a more probable state. The reverse process is a movement of the system from a more probable state to a less probable one. This follows from the fact that intensity of oxygen consumption of organisms is proportional to the external dissipation function and the latter is inversely proportional to the system state probability (Zotina and Zotin, 1983; Zotin, 1990):

(10) $$\psi_d = \frac{z}{p},$$

where *p* is the *system state probability* and *z* is *constant.*

Until now we have spoken about usual thermodynamic systems. Living organisms are not only open and nonlinear, but are also organized systems. Therefore, it is appropriate to characterize briefly (for more details see Poplavsky, 1981; Zotin, 1990) some problems of thermodynamics of information processes, organized systems, i.e. systems where the processes regulation and control take place.

Brillouin (1956) introduced the term "negentropy" and proposed the following scheme of negentropy, "transformation" into "information".

(11) *negentropy* → *information* → *negentropy.*

De Beauregard-Costa (1960) notes that the term "information" in formula (11) is used with two meanings: the transformation negentropy → information implies getting data, and the transformation of information → negentropy implies organization capability. Consequently, the notion of negentropy characterizes the system organization. According to Poplavsky (1981) the first member of formula (11) can be interpreted as an information price: to get, to store and to use information it is necessary to perform some physical actions, which are inevitably accompanied by entropy change in the system. He designated change of entropy in this case as ΔS_T (the entropy change in the thermostat containing the system). The second member in formula (11) corresponds to increasing of system organization, i.e., shows oneself ability to decrease entropy by ΔS_N. In this case, the negentropy principle of information (11) can be written (Poplavsky, 1981) as follows:

(12) $$|\Delta S_T| > |\Delta I| > |\Delta S_N|,$$

where ΔI is the *information change*, expressed in units compatible with energy. One can see from (12)

$$\Delta S_T - \Delta S_N \ge 0$$

or, dividing both parts by Δt, and passing over to the limit:

$$\frac{dS_T}{dt} - \frac{dS_N}{dt} \ge 0.$$

In the case of open systems, their organization is characterized not by the value of entropy diminishing ΔS_N, but by a change of specific external dissipation function (5). In living systems where irreversible processes characterized by psid-function $\overline{\psi}_d$, control and regulation process $\overline{\psi}_e$, negentropy effect $\overline{\psi}_n$ and coupled effect $\overline{\psi}_c$ emerge. External dissipation function for organized systems $\overline{\psi}_{or}$ is, therefore, equal to

(13) $$\overline{\psi}_{or} = \overline{\psi}_d + \overline{\psi}_k - (\overline{\psi}_n + \overline{\psi}_c) \ge 0.$$

The negentropy $\overline{\psi}_n$ and coupled $\overline{\psi}_c$ effects in the inequality (13) characterize the degree of system organization. It is related to the previous action of controlling systems which leads to specific organization of the given system. In living organisms, the question concerns genetic program realization, in artificial systems it is concerned with construction of apparatus or equipment. If we include that function Ψ_k is related to the realization of regulation and control, the principle of minimum energy dissipation for organized systems may be put down as follows (Zotin and Zotin, 1995)

(14) $$\overline{\psi}_d + \overline{\psi}_k - \overline{\psi}_n - \overline{\psi}_c = \min.$$

In this case, evolution criterion will take the form,

(15) $$\frac{d}{dt}(\overline{\psi}_d + \overline{\psi}_k - \overline{\psi}_n - \overline{\psi}_c) \le 0$$

or

$$\frac{d\overline{\psi}_{or}}{dt} \approx \frac{d\overline{\dot{q}}_{O_2}}{dt} \le 0.$$

The important consequence from (14) is that the $\overline{\psi}_k$ -function under a steady state of any organized system must be lower than it would be in the absence of regulation and control processes in the system. The principle of minimum energy dissipation in this case is carried out in a specific manner: dissipation is minimal, but it is less than it should have been in accordance with the physical and chemical properties of the system. In the scheme drawn in Figure 2, this peculiarity of organized systems is marked by the fact that under a steady state the ball is in the bottom of a certain hemisphere situated below the bottom of the cup. The conclusion shown in Figure 2 follows not only from the principle of minimum energy

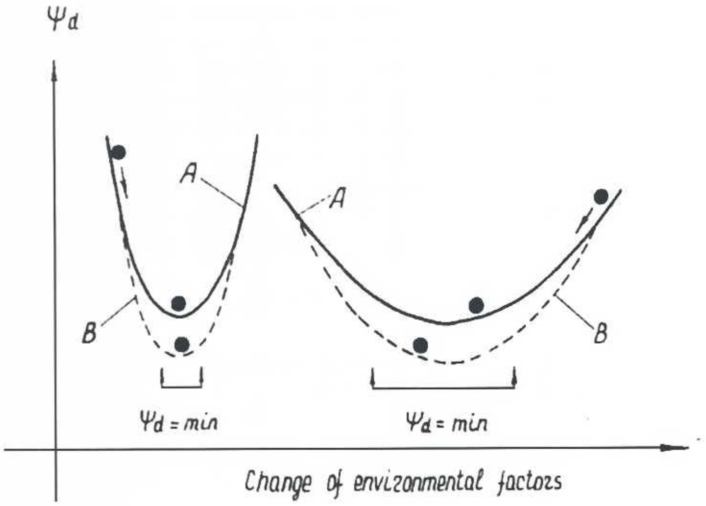

Fig. 2. Schematic model illustrating the principle of minimum energy dissipation for conventional (A) and organized (B) systems. *The ball in the cup bottom represents the stationary or steady state of the system. The arrows mark the opimal zone. (Zotin, 1990).*

dissipation for organized systems, but also from some other considerations (Zotin, 1990).

The second important consequence following from the principle of minimum energy dissipation for organized systems concerns the steady state processes. As one can see (Fig. 2), the ball position in the cup bottom corresponds to the most stable state of the system. Under different kinds of effect, it deviates from the stationary state, but if the effect stops it regains to the initial stable state. There are cases, however, when the system approaches to equilibrium or stationary state passing through a series of stationary states. Schematically such a stationary process is shown in Figure 3 where the ball is rolling along a trough every moment being under a stationary state. The trajectory on the trough bottom corresponds to minimum total energy dissipation and maximum stability of a steady state process. It is obvious that the developmental process is a steady state.

Principle of fastest descent

The Second Law of thermodynamics, even in the form of the Prigogine theorem (Prigogine, 19671), or the principle of minimum energy dissipation (8) does not show how and with what rate a non-equilibrium system is relaxed to the equilibrium or stationary state. It only shows the direction of changes and final value of entropy or external dissipation function. For characterization of the transitional process, a certain new principle is required. Attempts to formulate this principle were undertaken on the bases of the extreme principles of mechanisms and Second Law of thermodynamics (Ziegler, 1963; Presnov, 1973,1978; Shakhparonov, 1987; Swensen, 1989). This principle was formulated in the following way (Presnov, 1978): *during approach of a thermodynamic system to the equilibrium or stationary state the external dissipation function decreases in the fastest possible rate.* This principle can be also called "the principle of shortest descent" (Ziegler, 1963) or "principle of fastest descent" (Presnov, 1978).

If the principle of fastest descent is competent, we could understand causes of appearance of subsystems during movement of a large system toward the equilibrium, which move in the reverse direction and deviate from equilibrium. Moreover, the appearance of such subsystems is obligatory, since their movement toward non-equilibrium accelerates the movement of large system to the equilibrium. This follows from the Second Law of thermodynamics. Indeed, let the derivative of psid-function in time (5) be referred to such irreversible processes, among which the type (4) proccesses, are absent. According to Presnov (1978)

(18) $$\frac{d\overline{\psi}_d}{dt} = -\sum_{j=1}^{n}\left[\frac{dX_j}{dt}\right]^2$$

Let us designate (18) by symbol R_1. The derivative of psid-function in time for the processes, including irreversible processes of type (4), we will designate as R_2. For the latter type, we should subdivide the right part of equation (18) in two parts:

$$R_2 = \frac{d\overline{\psi}_d}{dt} - \frac{d\overline{\psi}_c}{dt} = -\sum_{j=1}^{n}\left[\frac{dX_j}{dt}\right]^2 + \sum_{k=1}^{m}\left[\frac{dX_k}{dt}\right]^2$$

The external dissipation function $\overline{\psi}_d$ decreases according to (7), while $\overline{\psi}_d$ — increases (4) as the system approaches the steady state or equilibrium. It is easy to show that

$$R_2 > R_1,$$

i.e.

(19) $$\frac{d\overline{\psi}_d}{dt} - \frac{d\overline{\psi}_c}{dt} > \frac{d\overline{\psi}_d}{dt}$$

since according to the Second Law of thermodynamics; for compensation of increasing in psid-function $\overline{\psi}_c$,the change of $\overline{\psi}_{d_c}$ should be more than,

$$|\Delta\overline{\psi}_c|, \text{ i.e.} |\Delta\overline{\psi}_{d_c}| > |\Delta\overline{\psi}_c|$$

Deviation of the subsystem from equilibrium can be realized only at the expense processes (4) inside maternal system. Moreover, according to the Second Law this compensation should be accompanied by appearance of entropy, i.e. the rate of external dissipation function decreasing should be increased on the whole by

$$d\left[|\Delta\overline{\psi}_{d_c}| - |\Delta\overline{\psi}_c|\right] / dt$$

The large system will move toward the equilibrium more rapidly than it would move if there is no deviation of the subsystems from the equilibrium.

In other words, for realization of the principle of the fastest descent subsystems should appear in the large system which deviates from the equilibrium rather than approaches it. The farther the subsystems deviate from the equilibrium, the lesser their state probability (10), the faster the system, as a whole, would move to the equilibrium state. Thus, the general system «is interested» in generation and maintenance of subsystems maximally deviating from the equilibrium state.

Concluding remarks

During ontogenesis, the continuous approach of the living system to the final stationary state occurs. This conclusion follows for organized and living systems from evolution criterion (15) and from a lot of experimental data which demonstrate that during development, growth and aging and the decreasing of respiration

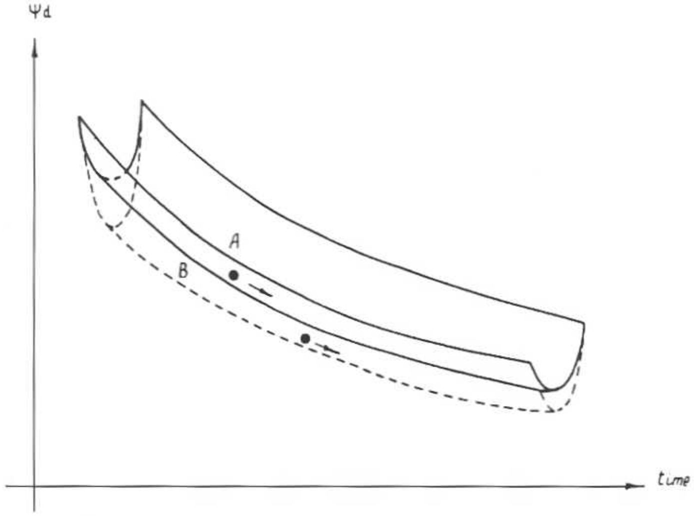

Fig. 3. Schematic model illustrating the stationary process for conventional (A) and steady state process for organized (B) systems. *The process, when the ball moves along the through bottom, corresponds to the most stable steady transition process. (Zotin, 1990).*

intensity and specific heat production takes place (Zotin, 1972; Zotin and Zotina, 1993). At the same time in "separate" time-periods of development, the organism is not submitted to criterion (15). According to these data certain periods of animal ontogenesis are characterized by deviations from the basic process (background of continuous approaching of the final steady state). Numerous data confirming this deviations are adduced in the monographs by Zotin and Zotina.

It is obvious that the phenomenological theory of ontogenesis may rationally explain the deviations from basic processes during animals ontogenesis. Besides, that phenomenological theory of ontogenesis must explain such phenomena as growth, differentiation and shape formation (accompanied by increasing of orderliness of organisms. These both aspects are quite explainable from the point of view of the thermodynamic principle of fastest descent. In accordance with this principle, growth, differentiation and shape formation are obligatory conditions of development. This principle explains also the separate deviations from basic process.

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