

EDITOR'S COMMENT: Konstantin Sudakov is a renowned physiologist who directs the institute in Moscow that is dedicated to P.K. Anokhin. Anokhin worked with Pavlov during the 1920s and became Professor of Physiology at the Gorky Institute. Professor Sudakov recounts the history of Anokhin's extension of Pavlov's theory of conditioned reflex to a concept of functional systems.

The Theory of Functional Systems: General Postulates and Principles of Dynamic Organization (dedicated to the Anokhin Centenary)

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Abstract—Dedicated to the Centenary of the outstanding Russian physiologist P.K. Anokhin, this article postulates the main principles of the general theory of functional systems. The system-formation role of useful adaptive results forming the functional systems of different levels is underlined. The peculiarities of mechanisms of self-regulation of functional systems, their isomorphism, holographic characteristics and selective inclusion into the functional systems of different organs and tissues are revealed. It is shown that interaction between numerous functional systems that form the whole organism is built on the principles of hierarchy, multiparametric interaction, sequential interaction, systemogenesis, and system quantization of life processes. The interrelation of reflex and functional systems is also considered.

FOR MORE THAN 300 years since Descartes, physiology has built its concepts of life on the reflex principle that is now generally recognized. The reflex is known to be a reflection—the body's response to a certain stimulus mediated by the nervous system. Russian researchers I.M. Sechenov and I.P. Pavlov have extended the applicability of this principle to human and animal brain activity, thereby making the reflex a universal concept explaining virtually all phenomena of life.

The reflex theory is known to rely on the following postulates: (1) the leading role and exceptional significance of stimuli in determining the reflex response; (2) propagation of excitation along the reflex arch from receptors to effectors along afferent nerve fibers, nervous centers, and efferent pathways; and (3) the reflected action is the final stage of the reflex, regardless of its complexity.

The Pavlovian theory of conditioned reflexes marked the whole epoch in the objective study of higher nervous activity. However, despite the remarkably universal nature of the

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reflex theory, it failed to provide a satisfactory explanation of many complex phenomena of life. This especially concerns goal-directed behavior during which the subjects not only respond to external stimuli, but also they persistently overcome various obstacles and can even sacrifice their lives in their search of appropriate environmental clues. Pavlov called such a form of activity the *goal reflex* (Pavlov, 1951). The term was not appropriate and had only a limited use. Indeed, the *goal* is an active stimulant of the subject's action, whereas the *goal reflex* means only a reflected action. The reflex theory also had a difficulty in explaining why living organisms are so skilled in inventing means to correct their behavioral errors, why their activity is not limited to responses to external stimuli and goes on until a certain vitally important result is achieved. The reflex principle could not satisfactorily explain the many facets of active instrumental activity of anthropoid primates.

New concepts of systemic organization of physiological functions emerged from the reflex theory. Pavlov was the first to note that certain properties of the dynamic stereotype reflecting a certain repeated sequence of conditioned stimuli were not characteristic of classical conditioned reflexes elicited by external stimuli.

A dynamic stereotype is a developed conditioned reaction of an animal to a stereotypically repeated sequence of conditioned excitations, for instance, light, mechanic stimuli, and sound. According to the law of physical force, a different amount of saliva is secreted under equivalent feeding reinforcement per every conditioned stimulus of different strength. In a developed stereotype, if instead of all previously used conditioned stimuli only light is used, it, on the location of other conditioned stimuli, will evoke conditioned reactions typical of those stimuli.

Thus, the significance of external (conditioned) stimuli as a reflex-triggering event is lost upon acquisition of the dynamic stereotype. The traces of previously experienced stimuli, that is, memory mechanisms, act as triggers of reflex actions. The law of the physical strength of the applied stimuli is no longer valid in these cases. In other words, the effect of an external stimulus (the main link of the reflex) is abolished in the dynamic stereotype. The concept of dynamic stereotype was Pavlov's first step toward the formulation of the general idea of the systemic nature of activity in living organisms; this idea was later applied to the whole human body (Pavlov, 1951).

Pavlov clearly showed that conditioned reflexes strongly depended on the typology of the animal nervous system. He was the first to note that reinforcement is necessary for conditioning. The founder of the theory of conditioned reflexes noticed that feeding conditioning was only successful in hungry animals. Conditioned feeding reflexes could not be elicited in satiated animals, that is, the conditioned feeding reflex did not appear despite the conditioned stimulus and other components of the reflex arch.

Over the last years of his life, Pavlov was especially interested in the higher nervous activity of anthropoid primates. He was prepared to study the animal activity that reorganizes their environment and to examine how animals acquire skills in using tools for satisfying their dominant needs. Pavlov, who thoroughly studied this kind of animal activity, was right when he noted that "... this activity cannot be called a conditioned reflex." He wrote that "... the animal grasped the relationship between things" (Pavlovian Wednesdays, 1949); however the nature of such phenomena remained obscure to Pavlovian laboratories.

The theory of functional systems, formulated by P.K. Anokhin, provided new solutions to unresolved problems of Pavlovian laboratories. This theory further develops Pavlov's ideas, especially those concerning the higher nervous activity of animals.

A.A. Ukhtomsky's theory of the dominant (Ukhtomsky, 1950), which postulated that

the internal state (dominant) of the human or animal organism can be a motive force of behavior and determine the subject's active attitude toward external stimuli, was the second source of the theory of functional systems. A.A. Ukhtomsky has shown that animals react not only to environmental stimuli, but very often their behavior is determined by dominants which take shape in the CNS and act as a behavioral incentive.

One more source of the theory of functional systems was the general systems theory (Bertalanffy, 1967). L. von Bertalanffy and his followers formulated the notion of systems as orderly sets of constituent elements: as soon as the elements unite they acquire a new quality.

In contrast to the general systems approach, P.K. Anokhin was the first to show the role of system-forming factors which consolidate a set of elements into active entities: functional systems.

Some functional systems determine the parameters of internal milieu, others the organism's behavior, its interaction with environment and fellow creatures. Some functional systems, especially those at metabolic and homeostatic levels, are determined genetically; others take shape as a current, e.g., behavioral need arises. The corporate action of these systems governs the activity of the whole organism.

The theory of functional systems has become more significant recently when many authoritative researchers, after several years of successful explorations on a molecular level, have persistently turned to the problems of integrative physiology (Giebisch et al., 1990; Natochin, 1992; Boyd and Noble, 1993; Folkov, 1994).

Integration of physiological functions was the main problem studied by P.K. Anokhin and his followers. Anokhin postulated that functional systems are units of the body integrative activity (Anokhin, 1974).

General Properties of Functional Systems

Result as a System-forming Factor

Adaptive results useful for the organism, rather than responses to stimuli, provide the basis for human and animal adaptive activity. In light of this, the functional system was defined as "dynamic self-regulating organizations whose activity is directed at securing adaptive results, which are useful for the organism" (Anokhin, 1979). Action results are the main factors of organization of functional systems at any level.

1. *Metabolic results.* These are produced by various metabolic molecular processes that generate products required for vital functions of the whole body, its tissues or organs. Alternatively, metabolic results can generate products that impair normal body functions and should be eliminated. Metabolic end products terminate or accelerate metabolic reactions and therefore can serve as useful results.

2. *Homeostatic results.* These are major parameters of blood and other body fluids, e.g., lymph and interstitial liquid. Homeostatic results produce a combination of homeostatic parameters such as the level of blood nutrients, gases, osmotic pressure, and pH. In conjunction with blood pressure, temperature and physiologically active substances (hormones, oligopeptides, neurotransmitters, etc.), these parameters ensure normal tissue metabolism and compose the dynamic internal milieu of the body.

3. *Behavioral results.* Certain forms of human and animal behavior satisfy the body's metabolic needs. Active metabolism produces a range of compounds which, when accumulated in the internal milieu, cause specific biological needs (feeding, sexual, defense, excretion, and so on). Many such needs can be satisfied only through active interactions

between the organism and the environment. Specific factors of the environment (food, water, comfort temperature, sexual partners, means of defense, etc.), which meet the subject's internal needs, are external results of behavioral functional systems. Another group of behavioral results is formed by factors that impair the subject's ability to satisfy metabolic and other needs. Such factors are actively avoided by subjects.

4. *Results of animal zoosocial activity.* When animals gather into communities, their individual needs are subordinated to the interests of the whole community. The results of animal zoosocial activity are presented by certain hierarchic relationships within populations, common shelter, and common activity that satisfy feeding, sexual, and other needs. Animals often display altruism in achieving zoosocial results, especially those concerned with the survival of the community. Zoosocial relationships often modify the animal's individual biological needs.

5. *Results of human social activity.* This group of adaptive results are specific of humans. Results of human social activity are primarily represented by achievements in learning, work, and everyday activity, as well as social protection measures, experience in culture and art, and so on. Social results are especially important for evaluating socio-economic relationships and work skills. Humans involved in working activity use their functional systems of metabolic, homeostatic, and behavioral levels to achieve socially significant results. The subject constantly interacts with the results in order to improve them. Human social activity is mainly organized by special functional systems that determine the subject's intellectual activity. The results of human mental functional systems are reflections of vitally important concepts and abstract ideas about external objects and their relationships, instruction, knowledge, etc., in the subject's mind. Joint efforts of humans are spent for creating social products, protecting the environment, society, and so on.

The multiplicity of useful adaptive results is indicative of a great number of functional systems that organize various facets of life of the whole organism. Certain functional systems determine various parameters of the internal milieu, whereas others are responsible for the interactions of the individual with the environment and conspecific relationships. There are genetically determined functional systems, especially those organized at the metabolic and homeostatic levels; other functional systems are formed according to the formation and satisfaction of metabolic and behavioral needs of the organism.

The System-organizing Role of Basic Needs

Functional systems are primarily caused by the current needs of subjects and are continuously formed by metabolic processes. In this respect, various needs of the organism can perform a system-organizing role. In addition, functional systems may be formed by special environmental factors (social environment is of prime importance for humans). Memory mechanisms can also cause the formation of functional systems, especially at the level of behavioral or mental activity.

Dominant biological and social motivations are products of internal needs and environmental influences and play the most important system-organizing role. Motivations selectively recruit elements from various levels in order to achieve results that are useful for an individual organism or population.

Deviations (varying in magnitude and duration) of parameters of the body's internal milieu from the level required for normal metabolism determine the actual internal biological or metabolic need of the organism. However, at any time there is a leading parameter of the total metabolic need, which determines the dominant need. The dominant need is

most important for survival of the subject, its relatives, or species. This need selectively organizes the dominant functional system and causes the behavioral act aimed at satisfying this need. When it is satisfied, another need, which is now most important for survival of the species or relatives of the subject, becomes the dominant need; it forms the appropriate dominant functional system, and so forth. This is exactly what the Russian researcher Ukhomsky formulated as the principle of dominant.

To achieve the result useful for an individual or population, the functional systems selectively bring together elements of different levels. In a living organism, these may be tissues of various organs, different levels of nervous or humoral regulation with their complex interactions (P.K. Anokhin's principle of "organ fragmentation"). The elements of such functional systems do not merely interact, they cooperate in achieving the useful result. Regulatory relationships permeate the entire dynamic organization of functional systems, securing the essential adaptive stability of their results and cooperation of separate elements in achieving the adaptive results. The theory of functional system renounces the organ-based approach to the body machinery. Any organ may have diverse facets of its metabolism selectively involved in various functional systems.

Self-Regulation: The Main Principle of Organization of Functional Systems

Self-regulation is a universal principle of dynamic organization of functional systems. Any deviation of their result from the level securing optimal living conditions of an organism or population will elicit a chain of processes tending to return the results to their optimal point. Such dynamic self-regulation ensures the stability of metabolic processes, essential for normal activity and equilibrium with the environment.

Functional systems whose self-regulatory mechanisms are responsible for the stability of the body's internal milieu are distinct physiological mechanisms of homeostasis. Their results can be regarded as dynamic constants of the body's internal milieu (blood pressure, osmotic pressure, temperature, pH, and so on). However, constant metabolic and external influences cause permanent or periodic changes in parameters of the internal milieu. Therefore, the mode of activity and parameters of results of metabolic functional systems constantly change. Self-regulation of functional systems is the only mechanism that maintains these parameters at the optimal levels. This means that the term *constant* is not exact when applied to living organisms. *Strict* constants are maintained at a certain level by appropriate functional systems. Any deviation of these constants from that level are fatal to the organism because of irreversible metabolic disorders. Other constants are *plastic* in that their levels can be shifted for a rather long period without disturbing the body's normal life conditions. Blood plasma osmotic pressure and pH belong to strict constants, whereas such constants as blood pressure, temperature and the level of nutrients in the blood plasma are plastic. The intensity of self-regulation in functional systems determines the endogenous life rhythms.

The rate of operation of the functional system maintaining the level of a metabolic parameter directly depends on the significance of this parameter for the survival of the organism.

Self-regulation maintains optimal levels of all parameters of the body's internal milieu that determine metabolic processes. Any deviation of the parameter from the level required for normal life of the organism immediately elicits (through feedback mechanisms or *reverse afferentation* after Anokhin), a sequence of processes that develop in central and

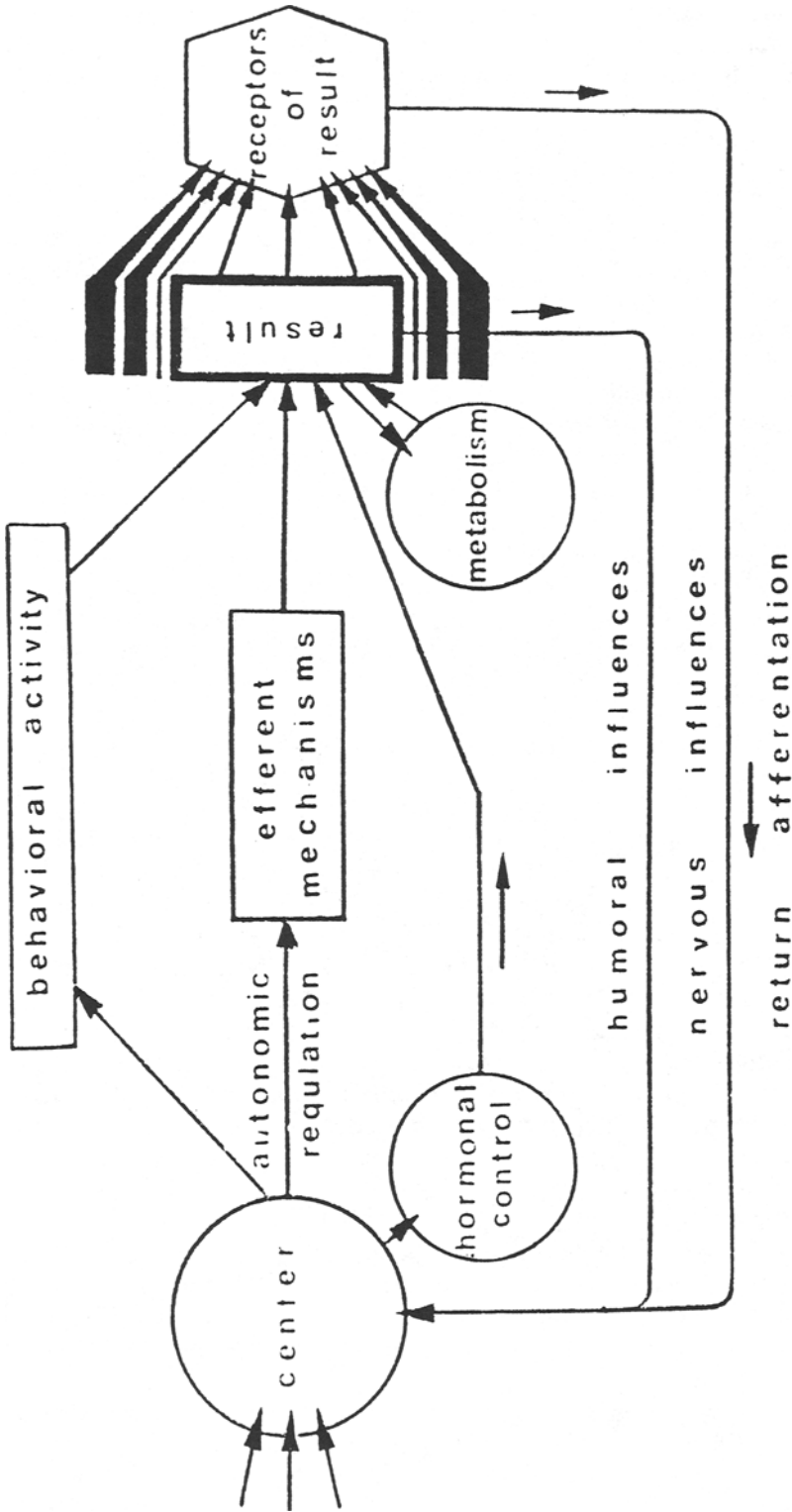


FIG. 1. General schematic presentation of the functional system after P.K. Anokhin. Here and in Figures 2, 3, and 5 the arrows indicate the direction of the self-regulation processes.

peripheral tissues in order to restore the optimal level of the given result. The same principle governs behavioral functional systems aimed at achieving certain biological or social results by the subject or community in the environment. In these cases, behavior is determined by the need experienced by the subject or community, and the results of action are permanently tested (by self-regulation based on feedback principles) for their consistency with the satisfaction of that need. In addition, behavior is determined and corrected by a multitude of external factors (the so-called disturbance-stimulated control), as well as by the genetic and individual experience of the subject. Note that the environment is incorporated as an intrinsic component into certain functional systems of the living organism. These functional systems achieve their adaptive results useful for the organism only through interaction with the environment. This is most clearly demonstrated by functional systems formed at the social level in order to satisfy human social needs.

Self-regulation is inherent in functional systems of any level. This principle maintains the optimal level of any parameter of the internal milieu and metabolic process. Behavior is also governed by the principle of self-regulation. Behavior is initiated by an internal need, and its results are constantly tested for their consistency with the satisfaction of that need.

In terms of the general theory, functional systems are self-organizing, dynamic central-peripheral complexes that selectively integrate the central nervous system with peripheral organs and tissues by means of nervous and humoral regulatory mechanisms. This integration is performed in order to achieve adaptive results which are useful for the system and the whole organism.

Isomorphism

Every functional system, according to P.K. Anokhin's concept, has a uniform (isomorphic) organization, including some universal peripheral and central key mechanisms: (1) useful result as a leading element of the functional system; (2) receptors of the result; (3) reverse afferentation from the receptors to central structures of the functional system; (4) central architectonics, which is represented by nervous elements selectively recruited by the functional system from various levels of the nervous system; and (5) effector components (somatic, autonomic and endocrine), including goal-directed behavior (Figure 1).

The integration of all these key mechanisms in a functional system determines the result, which should be useful for the whole body metabolism. The result and its deviations from the optimal level are monitored by appropriate receptors. The signal (reverse afferentation) generated by the receptors is directed to appropriate nervous centers, and, in accordance with the principle of self-regulation, causes the functional system to selectively involve new elements from various levels in order to organize the effector activity that would restore the result required for the body normal metabolism.

All functional systems, irrespective of the complexity of their organization, have uniform central architectonics (Figure 2). The central architectonics of functional systems consists of the following key stages arranged in sequence: afferent synthesis, decision making, acceptor of action results, efferent synthesis, action, and finally, the evaluation of results achieved by the system.

Afferent synthesis is the initial stage of the central architectonics of functional systems. At this stage, the central nervous system synthesizes excitations caused by the internal metabolic need and situational and triggering afferentations with genetic and individually acquired memory.

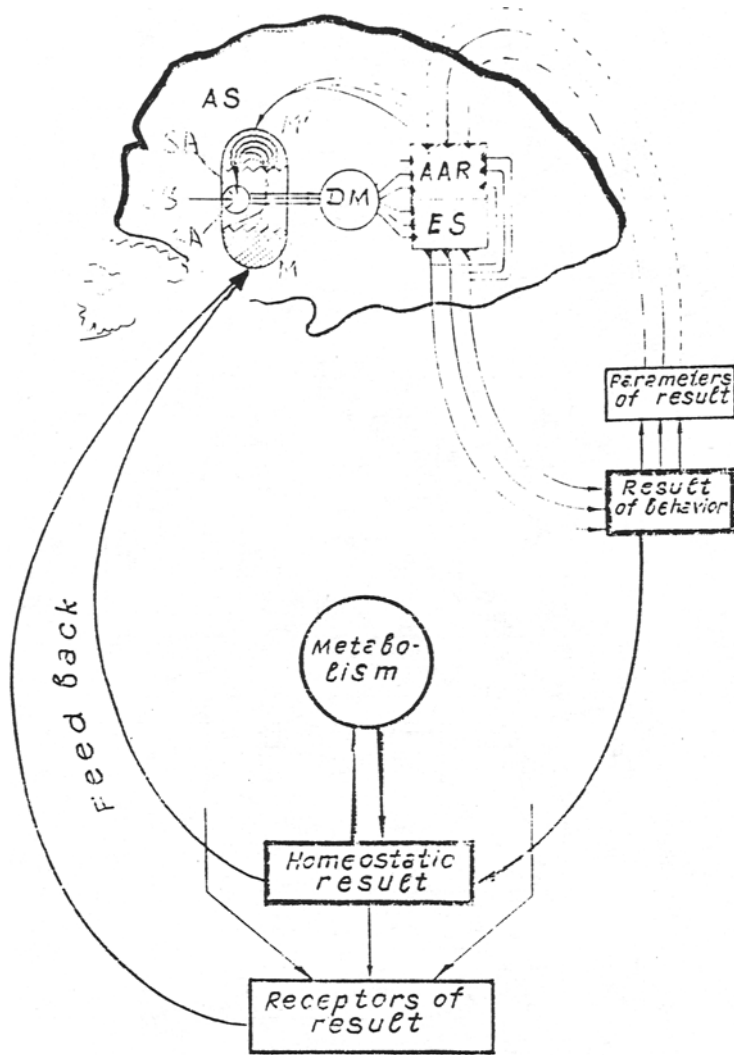


FIG. 2. Central architectonic of the functional system aimed at achieving the behavioral result. AS, afferent synthesis; M, motivation; M', memory; SA, situational afferentation; CS, conditioned stimulus; DM, decision making; AAR, acceptor of action result; and ES, efferent synthesis.

Afferent synthesis prepares the stage of *decision making*, whose physiological role is to limit the degrees of freedom for the activity of functional systems, leaving only one dominant line of effector activity directed at the satisfaction of the dominant need of the organism formed at the stage of afferent synthesis.

The next stage of the dynamic development of the central systemic architectonics occurs simultaneously with the formation of the effector action. This is the *acceptor of action results*, which anticipates the required result of action of the functional system. At this stage of central organization of the functional system major parameters of the required result are programmed with due account of the genetic and individual experience, and the

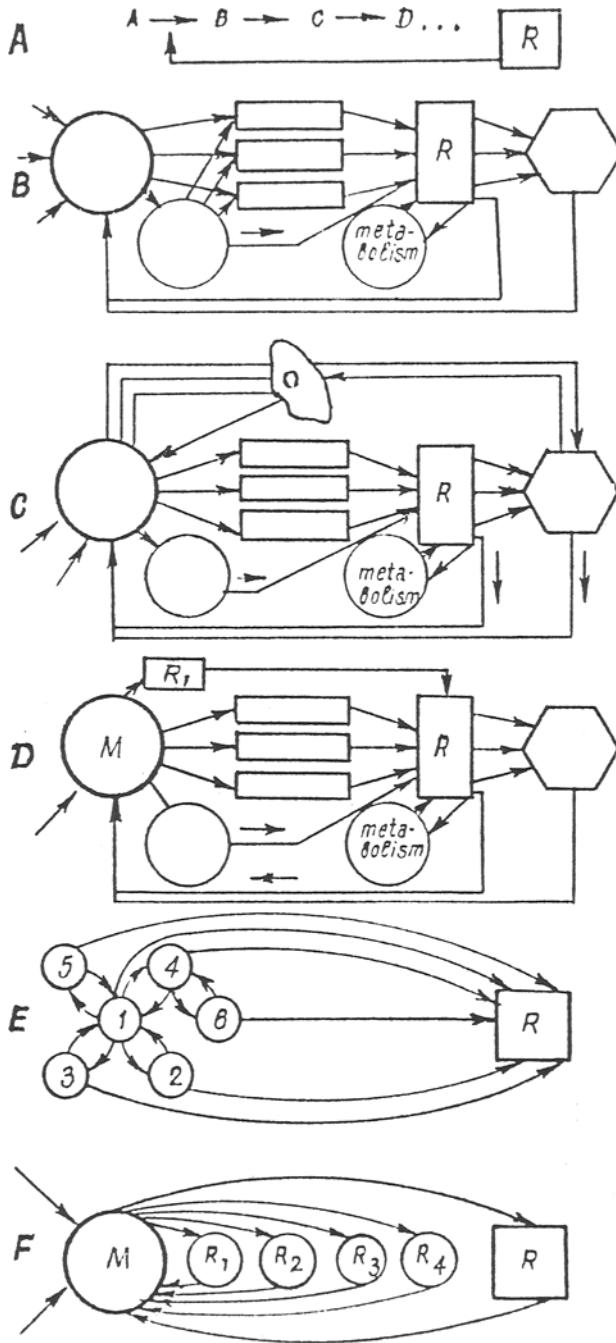


FIG. 3. Isomorphism of functional systems organized at various levels. A, metabolic level; B, homeostatic level without an external self-regulatory link; C, homeostatic level with an external self-regulatory link; D, homeostatic level with an external active (behavioral) link of self-regulation; E, population level; F, social level; M, motivation; and R, result of action of the functional system. See the text for explanations.

parameters of actually achieved results are continuously evaluated (through reverse afferentation) in relation to the anticipated results.

The activity of the functional systems decreases when the achieved useful result is sufficient for satisfying the dominant need of the organism. In contrast, the discrepancy between parameters of the actual result and those anticipated by the acceptor of action results causes a searching response that initiates the process of restructuring the afferent synthesis. A new decision is then made in order to activate the functional system and direct it at achieving a new result that would meet the dominant need.

All these stages of achieving the useful result of behavioral activity are continuously evaluated through reverse afferentation that is generated by appropriate receptor stimulated by external factors and through humoral signals received by structures involved in the acceptor of action results. Reverse afferentation is the main determinant of self-regulation in all functional system. Through reverse afferentation, the central nervous system can regulate the adaptive reactions of the whole organism in accordance with its needs and environmental conditions.

Thus, the architecture of all functional system is represented by a cyclic, closed-loop, self-regulatory organization. The adaptive result useful for the organism is its key point. Any deviation of this result from the level required for the normal activity of the organism immediately stimulates the appropriate receptors and selectively mobilizes special nervous structures through nervous and humoral channels of reverse afferentation. These structures use effector mechanisms (including behavioral, autonomic and hormonal responses) to bring the result back to its level required for normal metabolism. Such processes occurring an uninterrupted sequence with continuous information on the success in achieving the useful adaptive result (the principle of self-regulation).

Despite such isomorphism, the self-regulatory organization of functional systems occurring at various levels may vary (Figure 3). Metabolic functional systems have no central architectonics.

Most homeostatic functional systems are represented only by internal genetically determined self-regulation mechanisms. The useful adaptive results of these functional systems are mainly achieved by autonomic mechanisms that cannot be voluntarily controlled. This structure is characteristic of functional systems determining the metabolically optimal blood volume, amount of blood cells, blood plasma pH, and blood pressure. Other homeostatic functional systems may have an external self-regulating link that mediates the interaction of the organism with the environment. For example, the functional system of respiration, in addition to an internal self-regulatory link, has an external link (which is passive until the environment provides insufficient amounts of respiratory gases) that inhales gases into lung alveolae, takes up oxygen, and releases carbon dioxide. The functional system of excretion and several others also have external self-regulatory links.

The third type of homeostatic functional systems features an active external self-regulatory link that includes goal-directed behavior of the subject in the environment. This behavior often transforms the environment through active efforts of the subject. As a rule, such functional systems are initiated by internal metabolic needs of the organism and satisfy these needs by organism interacting with certain environmental factors. The goal-directed behavioral activity caused by these functional systems is governed by special motivations organizing the brain structures, including its higher levels. Such functional systems regulate the optimal level of nutrients in the body, osmotic pressure, the level of metabolic products, and body temperature.

In functional systems organized at the population level, the role of functional ar-

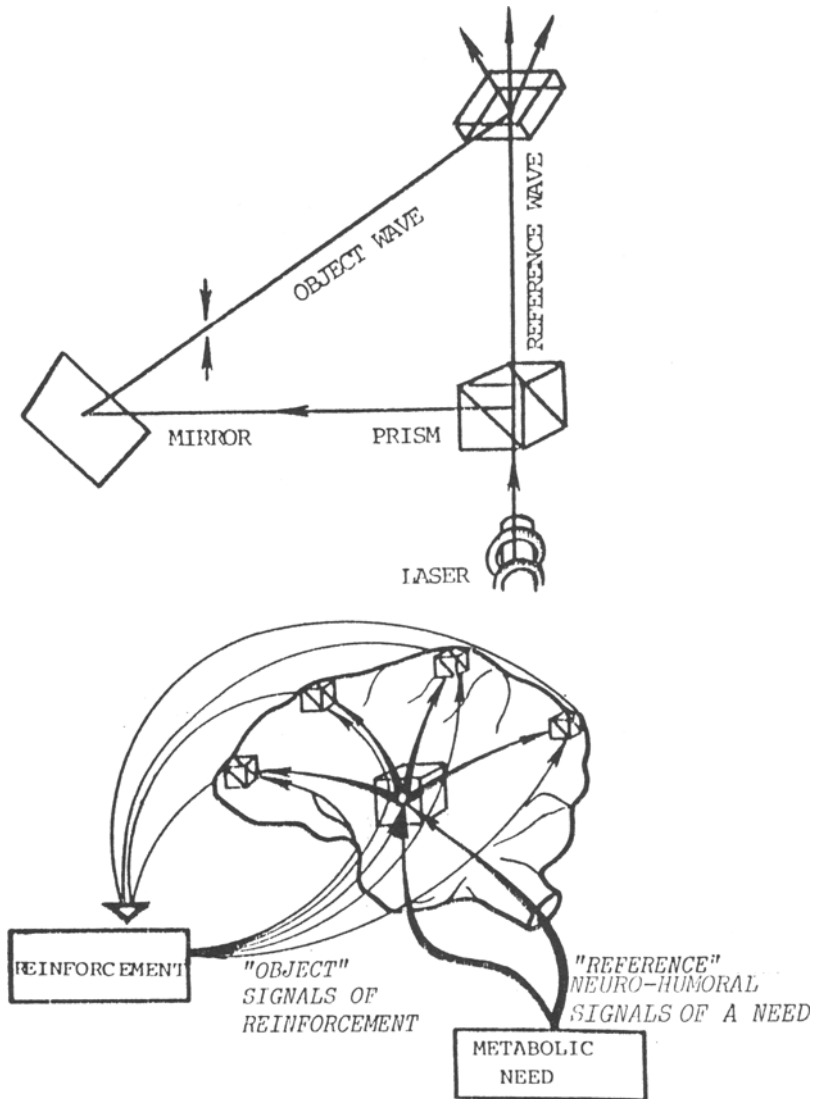


FIG. 4. Analogy between physical holography (upper panel) and the interaction of metabolic need with reinforcement (lower panel).

chitectonics is performed by dominant specimens. In functional systems organized at the level of group or society, as well as in functional systems of human mental activity, the result, which is usually found outside the body, is often not directly related to metabolic needs but may subserve them in an indirect way. Such functional systems can be determined by coordinated activity of several humans, their brain functions, and behavior (which depends on the brain functions) that achieve the adaptive result useful for humans. Creative work (designing and assembling a machine or writing a book), in which humans achieve results that are socially important for the subject and society, provide examples of such functional systems.

The result of mental functional systems may not be transferred outside the brain (e.g., in creative thinking).

It is clear that functional systems organized at various levels may have certain qualitative traits but always conserve the isomorphism of self-regulatory organizations that produce adaptive results useful for the functional system and the whole organism.

Holographic Principle of Organization of Functional Systems

One of the basic principles of dynamic organization of functional systems is the holographic principle. The activity of every element involved in the functional system reflects the state of the system's adaptive result (Sudakov, 1996). Thus, the initial need of the organism as well as its satisfaction are reflected in the activity of all the elements, constituting the functional systems. Making an analogy with physical holography, signals from the need can be regarded as a reference wave and signals from parameters of the result as object wave (Figure 4).

This principle allowed designing physiological experiments for objective demonstration of functional systems of various levels of organization. Experiments performed by B.V. Zhuravlev et al. (1991) showed that the distribution of interspike intervals of neurons clearly reflected the involvement of these neurons in various functional systems. For example, neurons involved in the feeding functional system of hungry rabbits displayed a dominant pattern of interspike intervals within the band of 10–20, 150 and 1,000 ms. Neurons involved in the functional system of seeking water in water-deprived rabbits displayed a dominant pattern of interspike intervals at 20–30 and 150 ms. Neurons involved in the functional system of defense behavior displayed dominant pattern of interspike intervals at 40–50 and 150 ms. After feeding, water intake, or removal of threatening stimuli, these neurons adopted a different, regular pattern of activity with only one dominating interspike interval. These findings suggested that the activities of neurons involved in various functional systems reflect the state of their adaptive results.

There is considerable evidence that the rhythm of any organ (e.g., heart, respiratory organs, esophagus, or stomach) reflect its involvement in a distinct functional system of the body (Kromin, 1989).

Selective Involvement of Organs and Tissues in Functional Systems

The results of functional systems *selectively involve* various organs and tissues in the integrated structure of the functional system. Every functional system selectively recruits tissue elements of various levels occurring in various anatomical structures in order to achieve its result useful for the whole organism. Various functional systems may use the same or different organs for achieving their adaptive results. For example, various parameters of heart activity can be used for maintaining constant blood pressure, gas metabolism, optimal body temperature, nutrient homeostasis, and so on. Kidneys can be used, in addition to their excretory function, for regulating optimal pH, osmotic pressure, body temperature, and so on.

Within every functional system, elements are easily interchangeable, and their effector mechanisms readily compensate each other. When one or several effector mechanisms of a functional system fail, other components can still achieve the adaptive result. Effector components can be subdivided into fast-operating and slow-operating (strategic) groups. For example, when blood pressure increases, arterial lumen, heart rhythm, and blood flow

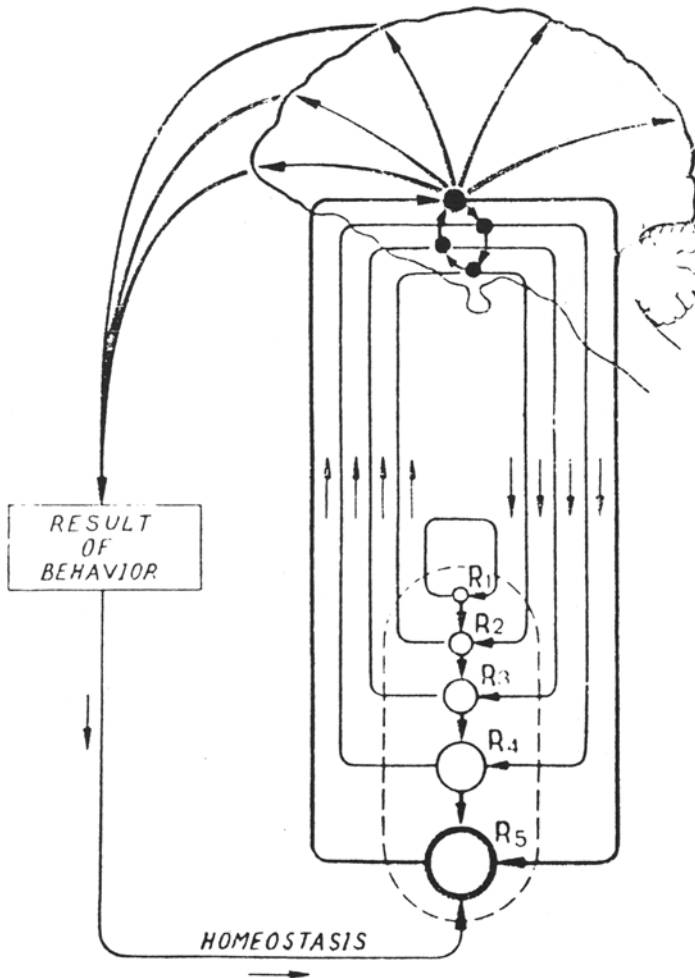


FIG. 5. Hierarchic interaction between behavioral and homeostatic functional systems. R_1, \dots, R_5 , results of homeostatic functional systems.

change almost immediately. The volume of circulating blood and its properties change considerably later. Renal functions and eritropoiesis, synthesis and degradation of blood elements are involved at even later stages.

The involvement of various organs in functional systems always obeys the principle of cooperation, that is, each element is not a passive part of the functional system; rather, it is active in interacting with other elements of the system in order to facilitate achievement of the useful adaptive result. The joint action of individual tissue elements and organs in functional systems is always performed in order to achieve an adaptive result, which is useful for the system and the whole body.

The selective involvement and cooperation of elements of functional systems is most clearly observed in nervous elements of various levels of the central nervous system involved in a functional system.

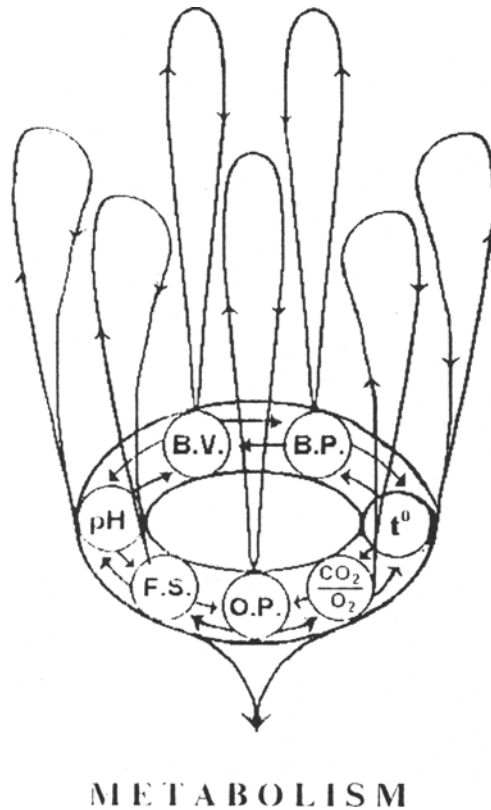


FIG. 6. Multiparametric interaction of functional systems at the homeostatic level.

Systemic Organization of the Whole Organism

The whole organism is a complex of numerous functional systems. They interact using several principles: hierarchy and multiparametric interaction, sequential interaction, systemogenesis, and systemic quantization of activity.

Hierarchy of Functional Systems

The activity of every organism at any time is determined by the functional system that dominates because of its value for survival or adaptation to the environment. The dominance of functional systems in the whole organism is determined by their biological (in humans, primarily social) significance.

In relation to the dominant functional system, all other functional systems form an hierarchic range (from the molecular level to the levels of the subject and society) in accordance with their respective biological value and significance for human social activity (Figure 5). After a dominant need is satisfied, another need becomes dominant in the order of their social and biological value; this need forms the dominant functional system. Other systems form the hierarchic range in relation to that functional system, and so forth.

One dominant functional system is changed for another in a dynamic process during the whole life of the subject, reflecting the nature of continuous changes in the body metabolism and interaction with the environment.

Multiparametric Interactions between Functional Systems

This principle of multivariate regulation means that functional systems interact in their final results (Yumatov, 1976). The principle determines the joint action of different functional systems (Figure 6). As a rule, the change in one parameter, which is the result of one functional system, immediately affects the results of other functional systems. Alternatively, any change in a single parameter of the complex result of a functional system changes its other parameters.

The principle of multiparametric interaction is valid for virtually all homeostatic parameters and integrates the activity of various homeostatic functional systems into a common functional system of homeostasis responsible for dynamic regulation of the whole body's internal milieu and controlling its changes due to metabolism and activity of the organism in the environment. The common action of functional systems of individuals is most evident in the results of a population's activity.

Sequential Interactions of Functional Systems

The whole organism displays a *continuum of action* of various functional systems: their activities follow each other in time. This principle is most clearly demonstrated in the continuum of processes of feeding and digestion (Figure 7). The succession of events of food intake and processing of nutrients clearly demonstrates the dynamics of consecutive functional systems and their distinct adaptive results. The functional system that governs the search for food is changed (upon food ingestion) by that controlling the treatment of food in the oral cavity. The latter functional system is terminated by the important result: the act of swallowing. Mechanical and chemical treatment of food in the stomach and the appropriate final result (transport of food into the duodenum) are controlled by the activity of the next functional system. The treatment of nutrients in the small intestine results in their absorption. After this, digestive functional systems are changed for the system controlling the formation and elimination of fecal masses; defecation is its final result. Importantly, the whole sequence of these functional systems regulating the body feeding is strictly controlled by the genetically determined mechanisms in the central nervous system.

The succession of digestive functional systems is governed by the anticipatory principle. Each result of action of a functional system organizes the mechanism that anticipates the result of action of the following functional system. This mechanism evaluates the achieved result by means of nervous and humoral feedback signals, and then a new functional system supersedes the previous system.

Similar phenomena of a sequence of functional systems are observed in the dynamics of respiration, excretion, blood circulation, as well as in behavior.

Systemogenesis

Systemogenesis is the selective maturation of certain functional systems or their parts during pre- and postnatal ontogeny (Anokhin, 1974; Sudakov, 1996).

Systemogenesis determines the sequential development, operation, and interaction of

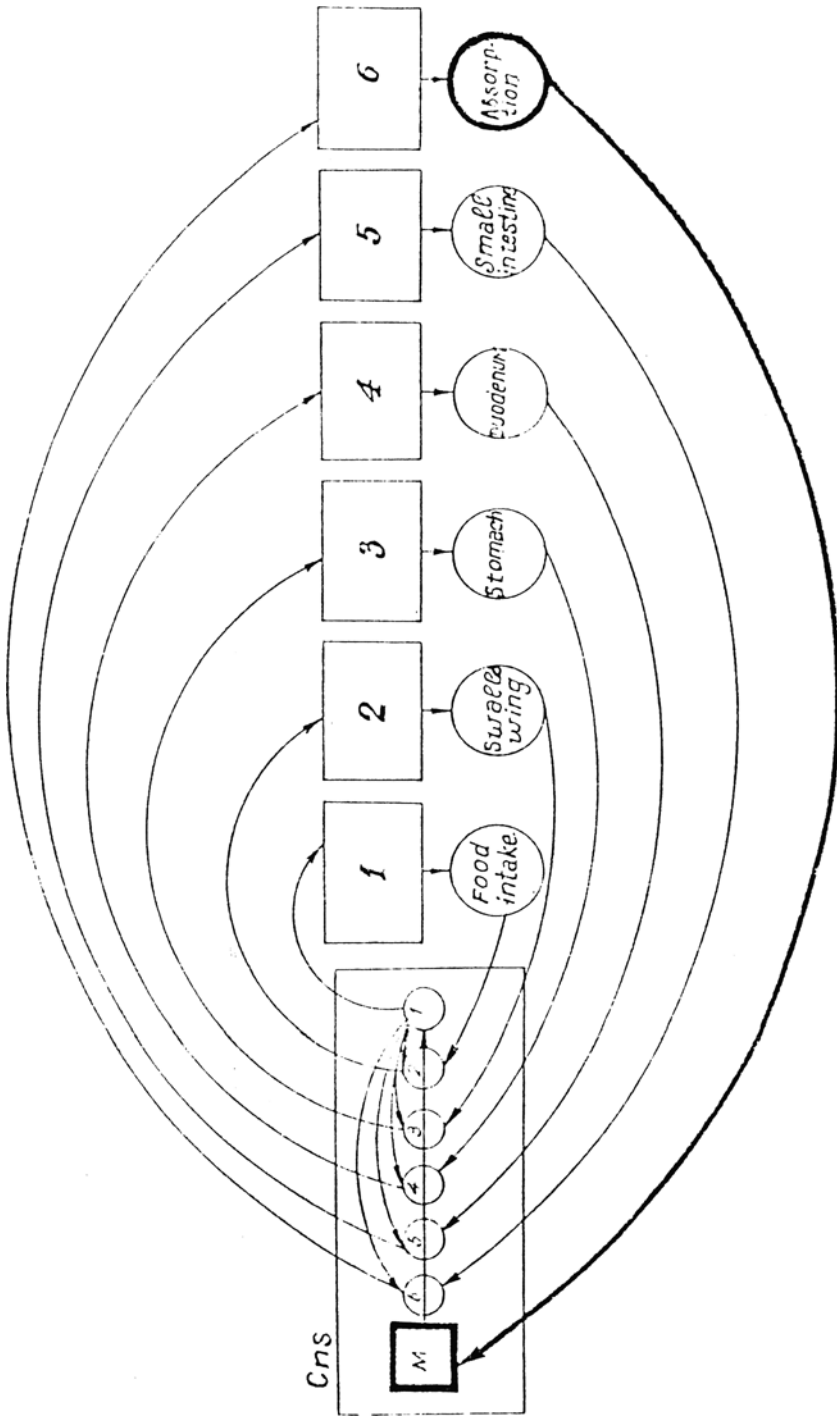


Fig. 7. Sequential interaction of functional systems that control: 1. food seeking and ingestion; 2. treatment of food in the oral cavity; 3. passage of food through the esophagus; 4. treatment of food in the stomach; 5. treatment of food in the duodenum; and 6. treatment of food in the colon. M, motivation. See the text for the explanation.

functional systems, as well as their decay over long-term periods of individual life. Special observations clearly demonstrated the selective maturation of fetal homeostatic functional systems during prenatal development.

Over the last years, the concept of systemogenesis was expanded and now includes the dynamics of maturation, transition to the automated behavioral activity, and the loss of the diversity of goal-directed acts terminated by final behavioral results during the subject's individual learning. This section of the theory of functional system is termed as the *systemogenesis of behavioral acts*.

Systemogenesis appeared to embrace nearly the whole period of individual life, from birth to senescence. This is the field of *systemogenesis of aging*.

N.N. Kokina (1987) considered the principles of formation of systemic relationships in groups of animals as the area of *population systemogenesis*. V.P. Praznikov (1989) showed that systemogenesis, in addition to maturation of functional systems, includes the selective involution of functional systems during senescence and the appearance of previously eliminated functional systems under stress conditions. This section of the general theory of functional systems, especially senile systemogenesis, is still poorly investigated.

Systemic Quantization of Activity

Metabolic needs that emerge in living organisms at certain time points transform their life continuum to a discrete form. The diversity of a life event is broken into a range of consecutive fragments. We suggest that every such fragment of life determined by a functional system with its results is a systemic *quantum* (Sudakov, 1992).

Systemic functional quanta are found at various levels of life processes. At the level of homeostasis, systemic quantization is clearly seen in physiological processes of digestion, respiration, excretion, blood circulation, sexual functions, and so on. For example, respiration contains the following systemic quanta ending with distinct results: inhalation that fills alveolae with a required amount of air; diffusion of gases into lung capillaries; transport of oxygen to tissues; diffusion of gases from capillaries to tissues and from tissues to blood; transport of gases to lungs; alveolar gas exchange; and exhalation. Blood circulation displays the following sequence of processes: cardiac cycle that ends with ejecting a certain amount of blood; movement of blood in arteries at a certain rate; microcirculation that allows the exchange of substances between tissues and blood; venous blood flow; and regional quanta in lung and peripheral circulation.

Each functional quantum of life is ended by its useful result for the organism and is only terminated after receiving the complete reverse afferentation from the result of the previous quantum.

Behavior of living organisms also obeys the principle of systemic quantization. The theory of functional systems explains human and animal behavior by the following sequence of events: the emergence of a dominant biological need, formation of a dominant motivation based on this need, interaction of the motivation arousal with situational excitation and memory in the central nervous system, decision making and organization of the acceptor of action results in order to initiate goal-directed behavior, and finally the interaction with the environment in order to achieve behavioral results that satisfy the initial need.

Every behavior quantum includes intermediate (stage) results and final results that satisfy the initial need. Various parameters of results of behavioral activity are continuously evaluated by means of reverse afferentation from various receptors to the central nervous system (Figure 8).

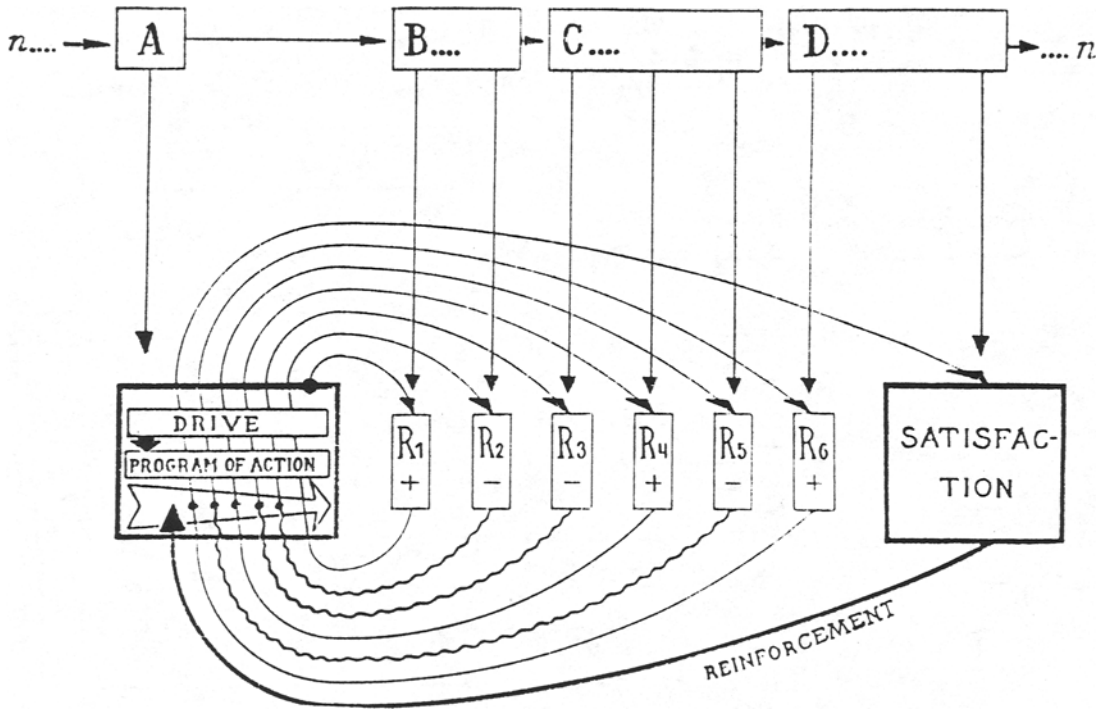


FIG. 8. A systemic quantum of behavior: $n \rightarrow A \rightarrow B \rightarrow C \rightarrow D \rightarrow n$ is the sequence of environmental events; $R_1 - R_6$ are stage results. Plus and minus signs indicate the results that facilitate and hamper, respectively, the achievement of the final result (satisfaction).

Systemic quantization of behavior obeys the principle of self-regulation and is effected through permanent evaluation by the subject of stage results and the final result that satisfies the subject's dominant need. Each stage of behavioral activity and the effects of various external factors on the organism are evaluated in terms of satisfaction of the dominant need of the organism.

For the organism to be adequately adapted to and survive in the environment, its dominant needs (especially metabolic needs) should be satisfied. The inability to satisfy the dominant metabolic need is often fatal to the subject, and the inability to satisfy sexual needs in the extinction of the species. The inability of a human subject to satisfy his/her social needs results in the loss of prestige and economic damage.

Each behavioral quantum terminates upon satisfaction of the need, and the behavior of the human subject or the animal are since then determined by a new need that forms the next behavior quantum, and so on. Systemic quanta of goal-directed activity can be formed with biological (metabolic) and social (especially in humans) needs.

Genetic and individually acquired memory allows living organisms to anticipate the properties of external stimuli that satisfy the emerging metabolic need. Behavioral quanta emerging from dominant needs are essentially aimed at achieving future results of behavior that must satisfy these needs. This mode of programming the quanta is determined by mechanisms of the acceptor of action results of each functional system that underlies the quantum. These mechanisms of the acceptor of action results that anticipate the actual life

intermediate problems should be solved, each having its own result. Similarly, the achievement of socially or personally important results in sports requires perfecting the performance of certain stages of the task, including, e.g., the initial position, posture, and special skills.

The Mixed Type of Quantization

This type of behavior includes a number of stages at which there is either sequential or hierarchic quantization. Such mode of quantization is observed throughout the human life, from birth to death, including sleep and rest. Quanta of important mental activities alternate with those organized by biological and other needs.

The wide applicability of general principles of functional systems to various natural and social phenomena suggests that functional systems are an objective reality (Sudakov, 1985).

The whole organism represents at any time a concerted interaction (horizontal and vertical integration) of various functional systems arranged by the principles of hierarchy and multiparametric (simultaneous and sequential) interaction. This determines the normal course of metabolic events. Disorders in this integration, when not compensated by special mechanisms, result in diseases and may eventually be fatal to the organism.

Results of action of functional systems appear as manifestations of various phenomena providing evidence for their objective existence. The result evaluation becomes a potent factor of human interindividual and social (industrial) relationships.

Man created mechanical and electronic automated devices operating in accordance with the principle of self-regulation through evaluation of the action results. Importantly, any result of action, however complete may be its evaluation by the machine, is finally reevaluated by humans. The permanent evaluation of results of their own activity and work was a potent factor of evolution of living species, including humans. The permanent evaluation of results of work and perfecting the work tools is a major determinant of evolution of human society.

Reflex and Functional System

The discovery of general principles of systemic organization of physiological functions strongly suggested that these functions are governed not only by the reflex principle (from stimulus to action) but also by the principles of self-organization and self-regulation. In contrast to the reflex, all forms of which are the body responses to a certain stimulus, functional systems that control homeostasis or behavioral acts display new features. They not only respond to external stimuli but use the feedback principle for correcting the shifts in their controlled vital results. In addition, functional systems form mechanisms that anticipate actual events and correct the results by comparing their parameters with those required by dominant needs of the organism.

As distinct from the reflex theory, the theory of functional systems proceeds from the following postulates.

1. It is not the proper action but the useful result for the system and the whole organism that determines the activity of the functional system.
2. Functional systems are formed by dominant needs of the organism, environmental influences, and the mechanisms of genetic and acquired memory.

3. Every functional system is organized according to the principle of self-regulation, which determines that any deviation of the result of the functional system from the level required for normal metabolism provides stimuli that mobilize the appropriate systemic mechanisms in order to achieve the result that would satisfy the dominant need.
4. Functional systems selectively recruit various organs and tissues in order to achieve the result of action.
5. Functional systems permanently evaluate the results of action by means of reverse afferentation.
6. Systemic integration of functional systems of any complexity displays a more complex architectonics than central mechanisms of the reflex arch. It includes such stages (absent from the reflex arch) as afferent synthesis, decision making, anticipation of the needed result (acceptor of action results), efferent synthesis, and the multicomponent action proper. The reflex arch is only a component of the systemic organization of self-regulatory physiological functions.
7. In addition to the linear principle of propagation of excitation, the central structure of functional systems performs a specific integration of anticipatory excitations that foresee the parameters of the final result. The mechanism that anticipates the needed results and compares them with those actually achieved (acceptor of action results) is the most important part of the central architectonics of functional systems.

As distinct from the reflex theory, the theory of functional systems puts forward certain new ideas.

1. It denies the prime importance of external stimuli in behavior. The behavior of a living organism is determined, in addition to external stimuli, by internal needs, genetic and individual experience, and effects of situational stimuli that create the *pre-stimulus integration of excitations*, which is activated by the triggering stimulus.
2. Systemic excitation that forms the goal-directed behavioral act does not unfold in a linear manner; rather, it involves the anticipation of actual results of the behavioral activity. This mechanism compares the parameters of actually achieved results with those programmed from the subject's past experience and allows the subject to correct errors of the behavioral act.
3. The goal-directed behavioral act is not terminated after the action, as suggested by reflex theory; rather, it continues until the useful adaptive result satisfies the dominant need, and the appropriateness of reverse afferentation is evaluated by the acceptor of action results.

Essentially, all reflexes use a preexisting dominant functional system of the organism (Figure 10). Functional systems caused by dominant needs determine, the activity of living organisms that transform their environment.

Taken together, these data suggest that the theory of functional systems, born within the bounds of the reflex theory, is now a distinct line of research in physiology.

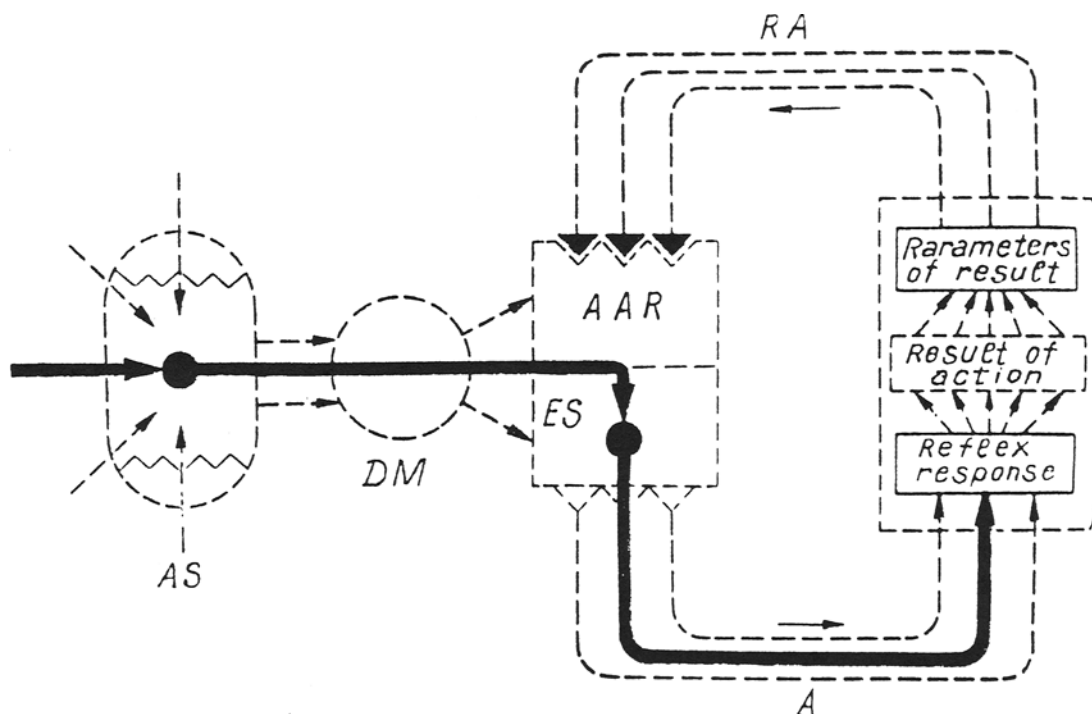


FIG. 10. Relationship between the reflex arch and systemic architectonics of behavioral acts: AS, afferent synthesis; DM, decision making; AAR, acceptor of action result; ES, efferent synthesis; A, action; and RA, reverse afferentation.

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