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ABSTRACT

The purpose of this review is to summarize certain approaches toward investigating animal behavior proposed by physiologists, physicists, ecologists and others. The failure of classic reflex theory in the analysis of complex forms of animal behavior has been demonstrated. The peculiarities of the functional system theory, which is one of the most popular theories in neurophysiological circles of the USSR, have been described. The application of the functional system theory to an investigation of feeding behavior has been shown. The strong and weak points of the functional system theory have been indicated, and the place of this theory among other system theories proposed for an analysis of behavior has been discussed.

THE FUNCTIONAL SYSTEM THEORY OF AN ORGANISM AND ITS APPLICATION IN RESEARCH INTO SINGLEMINDED BEHAVIOR IN ANIMALS

CONDITIONS UNDERLYING CREATION OF THE FUNCTIONAL SYSTEM THEORY OF AN ORGANISM

One of the most widespread terms in the language of specialists working in the various scientific areas is "system." This does not occur by chance. The rapid increase in the number of state-of-the-art scientific publications may lead a scientist to feel a sense of overwhelming helplessness when encountering a flood of analytic data. Clearly, only the existence of some higher principle makes it possible to comprehend the logical connections among separate findings and to provide successful research planning at the highest levels.

The term "system" is applied to those isomorphic principles that penetrate all historically conditioned boundaries separating one science from another. Different sciences imply the investigation of intrinsically distinct classes of phenomena: organisms, society, machines, and so forth. However, exploration by use of a "system" as a higher generalizing principle for many phenomena is more than the simple application of analytical methods to the study of separate processes. There are efforts to explain the organizations of large biological systems by tying the behavior of an organism to the molecular level processes related to this behavior. There is also a persistent search for basic laws in the formation of "large-scale systems" in the fields of socio-economic phenomena, of machinery construction, and so forth. All this directs one's thoughts to the search for and discovery of new scientific laws, and it is precisely this aspect that comprises the most impressive achievements of that scientific movement which is called "systems approach."

In recent years, the development of this scientific movement has been marked by radical expressions of enthusiasm. At times the role of "system" in the development of science and society was elevated to such heights that some enthusiasts began to speak of the advent for science of a "systems era," believing that everything for which our era may boast has depended on a systems perception of regularities in nature. Also, there has been the tendency to view the systems approach as a science in itself--systemology.

Many systems theories have emerged with such pretentious titles as "general" and "universal" that they undoubtedly create confusion in the minds of scientists. For this reason I refer to a paper by Laszlo [24] which carries out a detailed analysis of objective and subjective difficulties encountered in undertaking a systems study. Laszlo shows the peculiarities of general system theory whose origins are connected with Bertalanffy, Weiss and Whitehead, the differences between a general system theory as well as numerous general systems theories. He works to clear up semantic confusion regarding the names of different systems theories. Referring the reader to this paper, I should like to underline what I consider the most important postulates for defining the position of a functional systems theory for an organism, both among systems theories in general and among the numerous theories from various time periods proposed in biology. Laszlo writes:

> General system theory is a general theory of systems. A general theory of systems includes special system theories as special cases. General system theory is not a theory of general systems, is not a generalized theory of some variety of systems, is not a theory of the most encompassing system, is not a metatheory. The empirical objects of investigation of general system theory are concrete systems [1, p. 20].

The theory of functional systems of an organism proposed by Anokhin is primarily a biological theory whose main principles and postulates were formulated as a result of years of analyses of various physiological processes in organisms themselves, and of external physiological mechanisms, that is, behavior. This theory is closely tied to evolutionary theory and is a creative development of reflex theory. Prospects for linking functional system theory of an organism to genetic theory have emerged in recent years. Thus functional system theory is basically biological theory, posited to explain and study different intrinsic processes occurring both within an organism itself and in the external manifestations of an organism's activity--its behavior.

The main goal of this paper is to demonstrate some peculiarities of interpreting animal behavior from the point of view of functional system theory, and to show the possibility for applying this theory in the construction of a "conceptual bridge" between the behavioral reactions of an organism, and the delicate physiological processes in the separate organs, tissues and cells that are the basis of such behavior.

There is no scientific task more complex or closer to human problems than the study of behavior. It is no accident, therefore, that analysis of the mechanisms and regularities of behavior has become the focus of attention not only of biologists but also of physicists, mathematicians and others. In biology the list of theories concerning animal behavior is the longest. In this regard we should mention both Loeb's tropism theory (1893 [26], 1918 [27]) with its incorrect conclusion that animals respond passively to external stimuli--or are forced by these stimuli, and also Descartes' classical reflex theory, the postulates of which he used to explain behavior in higher animals. Substantial contributions to the reflex theory were made by the Nobel Prize laureates Pavlov and Sherrington. In fact, it is with the name of Pavlov that the classification and intensive investigation of unconditioned and conditioned reflexes is associated, along with detailed analyses of various kinds of inhibitions in animal activity [37]. Sherrington's brilliant studies have made possible the determination of an anatomical basis for simple reflexes as well as the formulation of a concept regarding the integrating activity of the nervous system. These outstanding researchers have revealed a certain limitation to classical reflex theory, the basic principle of which may be summarized as stimulus-response, and the sturcture of the relex itself was understood to be an arc.

In 1916 Pavlov's objective was to study the most subtle and innermost workings of the human brain--the subject of the behavioral goals. Pavlov titled his most famous paper on this subject "Goal Reflex" [38]. It would seem that from this moment on there should have been intensive work in Pavlov's laboratory on this vital psychological subject. But it is well known that Pavlov never again dealt with this problem. Why was this? One on Pavlov's close colleagues, Anokhin, has written on the subject:

> It seems to me that Pavlov left this most important side of brain research because the fact of goal-directed actions stands in direct contradiction to the fundamental tenets of reflex theory. Pavlov undoubtedly thought about this and...saw that if he were to recognize the problem of goal-directed behavior, he would have to significantly rebuild that vast edifice which he had erected with such genius and difficulty over his entire life [2].

The concept of the reflex is built on the inviolable principle of progressive movement of excitation, point to point, along an entire reflex arc. In his study of goal-directed behavior Pavlov encountered an entirely unexpected principle for the functioning of the nervous system. At the initial stages of the spread of excitation, a model is created of the final result of the given act, that is, before the result itself will be obtained [2]. In reality, a person clearly knows that a goal or a striving to achieve some result precedes the attainment of this result, and the interval between these two moments may be minutes or years.

Feeling the limits of classical reflex theory, Sherrington wrote in 1906 that pure or simple reflexes do not exist in normally functioning animals "because all parts of the nervous system are connected together and no part of it is probably ever capable of reaction without affecting and being affected by various other parts, and it is a system certainly never absolutely at rest" [40]. In other words, whether or not a particular stimulus affects a response depends upon what Sherrington called "central inhibitory states."

Alexander writes that at present "in most of the world, however, with a few special exceptions such as Skinner (1938 [44]), learning theorists have toyed with the notion that complicated behavior ought to be viewed as no more than collections of reflexes, conditioned or otherwise" [1].

The dissatisfaction of researchers, trying on the basis of classical reflex theory to understand processes such as memory and simpleminded behavior, may be explained both as criticism of reflex theory and as a striving to create new concepts to explain behavior.

Alexander correctly notes that criticism of reflex theory is in part tied to the fact that "the anatomical basis for conditioning of a reflex has never been demonstrated, nor has a clear understanding been developed of the relationship between conditioning of simple reflexes and the nature of complex learning" [1].

There have been and continue to be many attempts to explain behavior and related physiological processes from opposing positions. In particular,

> ...the study of learning nevertheless became the study of behavior in the eyes of most social scientists of the western world, and learning itself came to be used essentially as if it were synonymous with epigenesis, or all of the events of ontogeny in which environment and heredity interact. In this interaction, environment was given the paramount role, almost to the exclusion of genetic variations as having any significance at all. Man himself, at the most advanced level of this supposed progression, was and sometimes still is pictured as Locke saw him, as a developmental blank slate upon which almost anything can be written with equal ease [1].

It is necessary to mention behavioral studies where the main accent has been on innate mechanisms. Freud's efforts, beginning in the 1920s to describe supposed instinctual aspects of human behavior and to uncover their ontogenetic and hereditary bases, were paralleled remarkably a decade or two later by Lorenzian ethologists. Both groups were attempting to understand high-level, complex behavior patterns, stereotyped in their makeup and with obscure ontogenetic antecedents [28,29].

At present close attention is being given to the possible role in behavior played by various genetic mechanisms [13,14]. This direction in research may be summarized by the following statement by Bullock:

> It seems at present likely that for many relatively complex behavioral actions, the nervous system contains not only genetically determined circuits

> but also genetically determined physiological properties of their components so that the complete act is represented in coded form and awaits only an adequate trigger either internal or external [13].

Brief mention is made of other biological trends in behavioral study which in their development also have become farther removed from the classical reflex theory. Some words should be said about peculiarities of the ecological approach based on Darwin's theory of evolution. With the advances of genetics, mathematics and logic, the modern ecologists have emphasized the population dealing quantitatively and precisely with changes at population and community levels [10,36,52]. Population genetics built their formulations upon the concept of population fitness. Behaviorists found justification for their tendency to consider foremost what is good for the population or for the species.

We finish our enumeration of some theories and tendėncies in biology connected with behavioral investigations. Our goal has not been to present detailed analysis; this has already been done sucessfully in Alexander's paper [1]. We want only to characterize the conditions (background) under which functional system theory of an organism appeared and is now developing. Also, we should like to underline our agreement with Alexander's remark about the demands placed by modern science on any theory proposed to explain behavior.

> It will not be easy, however, to build a sound theoretical view of behavior in general and of human behavior in particular. I believe we must realize that: 1) whatever we hypothesize must accord with our knowledge of evolution; and 2) a useful, predictive, general theory of behavior is unlikely to be constructed by building upward toward greater complexity from the engram, the reflex, or some simple unit of activity [1].

It is precisely in the light of these demands that we shall analyze the basic postulates of functional system theory and its implementation for explaining animal behavior.

CONCEPTUAL BASIS OF THE FUNCTIONAL SYSTEM THEORY

The peculiarity of functional system theory is determined first by the nature of the definition of "system." The term "system" is of ancient origin, and there is hardly a scientific discipline whose representatives do not use the term in one way or another. For instance, "blood circulatory system," and "respiratory system," have been held by some scientists as an expression of the systems approach. For the most part "system" applies to something collected together, regularized, and organized, and not to those criteria according to which components are collected, regularized, organized, and as forth.

Thus a system according to Bertalanffy (1956 [11]) is "a set of units with relationships among them"; according to Miller (in [14]) it is "a set of interacting units with relationships among them." A similar broad definition was given by Hall and Fagen: a system is "a set of objects together with the relationships between the objects and between their attributes" (1956 [21]).

Similar definitions of "system" could scarcely permit biologists to use "a system" as a methodological tool in the formulation of new research problems or in the interpretations of obtained data. As an argument we cite an eloquent characterization by the progressive-minded biologist Goodwin [19] on the state of affairs as they were in the middle of the 1960s. In his book The Time Organization of the Cell, Goodwin writes, "a central place in the biological sciences belongs to the concept of organization, although the idea of organization has no clear definition" (cited in [21]).

For the purpose of exactness we must allow that in recent years definitions of "system" have become more precise. For example, Weiss defined a system as a "complex unit in space and time so constituted that the component subunits, by 'systemic' cooperation, preserve its integral configuration of structure and behavior and tend to restore it after non-destructive disturbances, [4]" I personally prefer Mihram's definition of a system which is close to that Anokhin made two decades earlier. According to Mihram, a system is "a collection of interdependent and interactive elements that act together in a collective effort to attain some goal" [33]. This formulation, in my opinion, is the first definition of system made in the West that clearly emphasizes the goal-seeking attribute. It seems to us that "interaction" in the general sense as used often in definitions of "system" cannot organize a system of "multiple components"; thus it is not sufficient to mention "interactions" and "regularity" in formulating the idea of a system.

To define the word system, some additional aspects should be included that would supply the concept with concrete mechanisms for that which is an organized whole, clearly determined and logically perceived. More precisely, as Anokhin remarked, "we must discover those determining factors which release a system's components from redundant degrees of freedom" [2, p. 72]. Introduction to any definitions of the expression "regularized multiplicity" in no way corrects an initial defect and, perhaps even gives the definition a somewhat teleological flavor. Who really "organizes or regularizes" the multiple components of a systsm? What is the criterion of regularity? Obviously it must be a concrete factor which regularizes a system.

To answer these questions, we should observe the recovery, after certain disturbances (damages), of a simple and obvious function with a clear result (as, for example, the maintenance of the human body in a vertical position). Such an imperative factor that utilizes all possible systems is the useful result of a system (in the given instance, the vertical posture and the feedback formed by such posture).

It is precisely the adequacy or the inadequacy of the result that determines the behavior of a system: when adequate, the organism goes on to the foundation of another functional system with another useful result - the next step in a universal continuum of results. In the event of inadequacy of the obtained result there occurs stimulation of activating mechanisms; active selection of new components; change in degree of freedom for operating synaptic structures; and, after trial and error, creation of an entirely adequate adaptive result.

Treating "result" as an important link in any system is a departure from general widespread notions regarding systems, and sheds new light on probiems that are in need of deep analysis. First it is possible to present in full in terms of "result" both the entire activity of a system and all of its possible applications. This stresses even more the decisive role that result plays in the behavior of a system. This activity, as Anokhin pointed out, may be expressed in the following four questions that reflect various stages in the formulation of a system:

1) What result must be achieved?

2) When exactly must the result be achieved?

3) By means of what mechanisms must the result be achieved?

4) How does the system substantiate the adequacy of the achieved result?

The above allows one to understand the following formulation of system proposed by Anokhin. We may term a system only that complex of selectively involved components whose mutual interactions and interrelationships acquire the character of a mutual intercooperation of components aimed at obtaining a fixed adaptive result. The concrete mechanism of such mutual intercooperation among components is the components' freedom from redundant degrees of freedom not needed to obtain the given concrete result and, the preservation of all degrees of freedom which promote the achievement of the result. The result, in turn, through its own characteristic parameters (thanks to feedback) is able to reorganize the system, creating a form of mutual interaction among its components that will be most favorable for the attainment of precisely the programmed result.

The result is an integral and decisive component of the system, an instrument that creates regularized mutual interaction among all of its other components [2, p. 77].

A second important general question regards structure. A determination of structure is also important because at this point there occurs frequent interference between new ideas about system and all casually defined earlier notions of system. The criterion for using the term system was anything regularized in comparison to other various classes of phenomena (for example, the blood circulatory system, muscle system). In these examples the term "system" indicates the phenomenon's connection with definite types of anatomical formation, unified by the type of functions performed. Speaking of a system in this sense, we single out from an entire organism a certain part unified by a type of anatomical structure or function and we exclude any possibility to examine these isolated structures in a true systems framework. A blood circulation system could never exist as something separate, since this would be physiological nonsense. In an organism, the blood circulatory system always leads to some adaptive result (arterial pressure, rate of blood flow, etc.). However, not one of these results could be achieved with the work of the blood circulatory system alone; the nervous system, the endocrine system, etc. must also participate in order to obtain a result, and all of these components are united in the principle of mutual intercooperation.

It is essential to stress that the functional systems of an organism operate from dynamically mobilized structures at the level of the entire organism. The exclusive influence of an anatomical type of a participating structure is not reflected in the activity and final result of the functional systems. Moreover, the components of this or that anatomical origin are mobilized and involved in a functional system only in accord with their role in the process of obtaining the programmed result. That the "result" is a decisive factor in the formation of functional system and in its phase reorganizations indicated that the organism's systems are always functional systems.

Another important property of a system that is often overlooked by researchers is the sudden mobilization of structural units of an organism according to continuous functional demands which a function dictates to a structure. As this property of mobilization, we might consider the possibility of momentary construction of any combinations that could provide the functional system with a useful adaptive result.

In as much as the functional principle of selected structural mobilization is a dominant one in the predominant physiological processes of an organism, the Anokhin theory itself was named a theory of functional systems.

There is a connection between structural composition of a functional system and the increasingly important problem of system hierarchy. We have not truly isolated functional systems of an organism. Only for didactic purposes can we select a system which provides a result at a given level of a system's hierarchy. Therefore, while speaking about the structure of a functional system, we must keep in mind that any given functional system selected for study is located inescapably somewhere between the most subtle molecular systems and the highest levels of integrated systems, say, behavioral acts.

Two questions naturally arise as regards structural composition:

1) Is there any difference regarding the principle functional architectonic between elementary and very complicated subsystems? In other words, is there a similar architecture for systems of all levels, or are there differences in structure depending on the hierarchical level of the system?

2) What are the specific mechanisms that link subsystems together during the formation of a supersystem? Keeping in mind some modular mechanisms of the functional system, it is possible to refine this question: what specific architectonic mechanisms join subsystems in a supersystem?

In order to answer the first question, we should proceed from the conclusion reached while formulating the concept of system: the idea of result is central to the notion of system. In addition, a system cannot be stable unless the result itself, by means of the most essential parameters, influences the system with the aid of feedback. If this is so, then any system whatever its hierarchical level must submit to these rules.

All these considerations lead to a final and fundamental conclusion about the composition of a hierarchy: all functional systems, regardless of their organizational structure or number of components, have principally the same functional architectonic; the result is a dominating factor which stabilizes the organization of the system.

It is easy to answer the second of the above-mentioned questions following the postulation that the architectonics of the systems are essentially identical. If we suppose that some subsystems link up among themselves and contact each other by means of some intermediary mechanisms in order to obtain an adaptive result, it will be immediately clear that our supposition is wrong. In that case some subsystems would not be able to develop in their basic functional sense, i.e. to obtain a result; and thus the "system" itself could not be correctly called a system.

Thus the adaptive result of the system, regardless of how small, is the true contribution a system makes to the formation of a supersystem or a large system.

From the above considerations it follows that, during the organization of a hierarchy of systems, each lower level must somehow organize contact among results so that the next higher level of the systems may be organized, and so on. Obviously an organism formulates its systems in just this manner, and only in this way is it possible to organize the systems with a large number of components. "It is natural in this case that a 'hierarchy of systems' is transformed into a 'hierarchy of results' for each of the subsystems of a preceeding level" [2].

AN INTERNAL OPERATIONAL ARCHITECTURE OF THE FUNCTIONAL SYSTEM

It is not an exaggeration to say that one of the difficulties in the development of a systems approach is the debate that takes place about the level of the global properties of a system, that is to say "black box" discussions over the nature of systems. An overwhelming majority of scientists do not attempt to penetrate the internal architectonic of a system, and do not give a comparative evaluation of the specific properties of its mechanism. With such an approach, a system under discussion always appears homogeneous, with identical elements, components all of equal value, and with identical mechanisms.

The clearly worked out internal operational architectonic is one of the essential and probably decisive distinctions of functional systems theory [3]. Such an internal architectonic (Figure 1) expressed in physiological concepts is an indispensable tool for the practical application of a functional system to research work, even if this extends to the molecular level of the object under study.

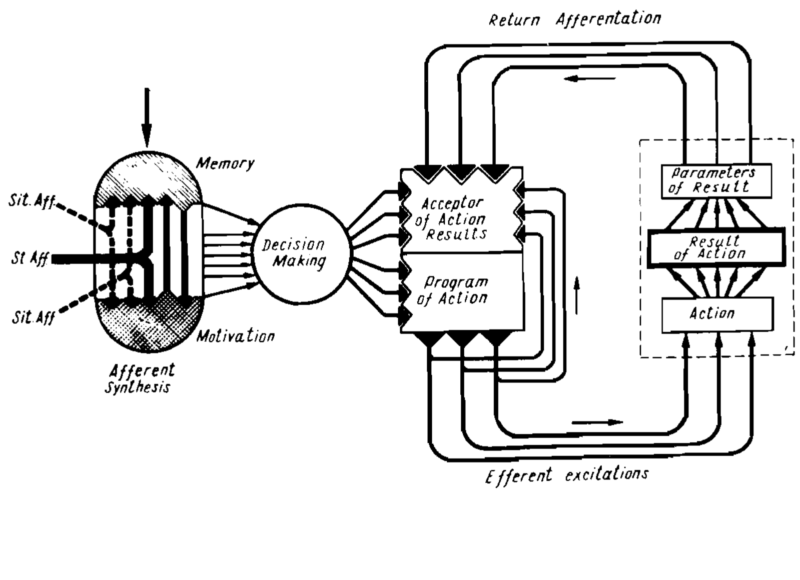

Figure 1. Operational architectonic of an Anokhin functional system according to Anokhin.

As has been noted, one characteristic of a functional system is that the problem of attaining the necessary result is solved within the system and on the basis of its natural mechanisms. This circumstance radically distinguishes a biosystem from a machine system--even the most complex machine system. For all intents and purposes, a machine's goal is established outside its own domain, and while it may attain a result not programmed by it, it can only exhibit a certain capability for self-organization. Even the simplest of biosystems can, on the basis of its own internal processes, determine by itself the result that is necessary at a given moment of its adaptive behavior. This problem is solved at the stage of afferent synthesis.

According to Anokhin [3] four decisive components of afferent synthesis must be subjected to simultaneous processing with simultaneous mutual interaction on the level of separate neurons. They are as follows: 1) the predominant motivation at the given moment; 2) external afferents that also correspond to a given moment; 3) trigger afferent stimulus; and 4) memory.

The basic condition of afferent synthesis is the simultaneous meeting of all four participants of this stage of a functional system. The uniqueness of this synthetic process (if it takes place at the level of a single neuron) is that it is realized on the bases of the central regularity of the brain's integrative activity, and of convergence of excitations at one and the same neuron. It should be emphasized that because of the simultaneous processing of all four excitations at the afferent synthesis stage, each of the above mentioned components acquires special physiological properties. It is precisely here that there occurs a freeing of the neuron from redundant degrees of freedom, thanks to the arrival of precisely these and not other excitations.

Thus it is afferent synthesis that brings an organism to answer the question: what result should be attained at a given moment? Afferent synthesis also provides the goal that the entire subsequent logic of the system will strive to attain.

Decision making represents one of the most interesting moments in the unfolding of systems processes. As seen from the above discussion, functional system theory makes "decision making" a full-fledged participant in the objective process of a system's organization. Here emerges an essential problem: where and how does decision making take place that aims at the attainment of one result to the exclusion of another?

The latest data from the Anokhin laboratory lead one to believe that evaluation of possible results for a given dominating motivation occurs at the afferent synthesis level [3]. However, these results are not obtained in real time but conditionally, they are evaluated with the aid of some mechanism we have yet to study.

That which happens during decision making is the result of a selection process, based on a long evaluation of various internally-formed results. In other words, "any decision making after the afferent synthesis stage has been finished is a choice of the most convenient degrees of freedom in those components which must form a working (efferent) part of a system. Those remaining degrees of freedom in turn provide the possibility to economically realize precisely those actions which must lead to a programmed result" [2].

It is necessary to point out that numerous experiments with animals with frontal lobes removed have shown convincingly that, at the moment of decision making, all information being processed is integrated precisely in the frontal part of the brain from which emanates the command to organize more optimal behavior structures [8,9,35,42,47].

The next link in the operational architectonic of a functional system is the acceptor of action result. Its formation destroys a traditional concept of classical reflex theory regarding the traditional movement of excitation along the central nervous system. "An acceptor of action result which is based on the multifaceted mechanism of afferent synthesis is not an expression of the sequential development associated with the entire chain of phenomena of a behavioral act. It anticipates the afferent properties of whatever result should be attained in relation to the decision that has been made. It correspondingly 'forestalls' the course of events between the organism and the external world" [3]. An acceptor of action result appears to be a very complicated apparatus. It must formulate certain delicate neural mechanisms that permit it not only to forecast the features of a result needed at a given moment in time but also to compare these features with the parameters of a real result about which the acceptor is aware thanks to feedback (Figure 1). It is this apparatus that allows an organism to correct a behavioral error or to complete incompleted behavioral acts. Here it should also be emphasized that various kinds of "searches" and compensations may also lead to an adaptive result through similar evaluation feedback.

Having shed some light on the conditions and on the "scientific climate" in which functional systems theory was born and developed, and having analyzed some of the principle links in its operational architectonic, let us now touch upon its practical application to the study of a complex problem such as animal behavior and show some of its other possible applications.

ANIMAL FEEDING BEHAVIOR FROM THE POINT OF VIEW OF FUNCTIONAL SYSTEM THEORY

As has been stated, the basic stress in functional system theory is that an organism like a system must have a final result. Of what does this consist, and how in this regard may one examine the behavior of an organism? To answer these questions, we must involuntarily touch upon the physiologist's idea about living processes. Here we should recall the following statement by Bernard made in the middle of the nineteenth century (before the development of the systems approach in biology): "The constancy of the internal state is the necessary condition of free independent life." Later this "constancy of internal state" was labeled by Carmon homeostasis. Since an organism lives in an obligatory interrelationship with changeable environmental factors, it is clear that: 1) an organism must be informed about changes of environmental factors; and 2) its physiological mechanisms in spite of environmental changes must maintain the "constancy of internal state," i.e. a complex of interconnected constants.

If we try to analyze the physiological mechanisms directed toward maintenance of homeostasis, we see that they may be divided conditionally into external and internal. In practice, an organism always has definite reserves that differ in the case of separate constants (for example, oxygen concentration in the blood, blood pressure, osmotic pressure), and allow an organism to maintain its homeostasis for some time using internal mechanisms alone. But an organism always (with difference only in time) resorts to external mechanisms, i.e. to behavior, in order to select in the environment all that is necessary for the maintenance of homeostasis. Thus in the broadest sense we can say that animal behavior is goal-directed and these goals are for the maintenance of the inner state of the organism. This point of view held by biologists promotes a more concrete study both of processes occurring within an organism and external manifestations of its vital activities.

It is useful to mention attempts that have been made to explain the behavior of organisms and even social (communal) behavior from the standpoint of thermodynamics. Such efforts are being made at present by supporters of the study of behavioral physics [20,31,32,50]. Broadly speaking, "the results of this direction of research would include: 1) a concept of temperature as a measure of average degree of emotional arousal in a group, and as an indicator of the direction of flow of emotional energy between interacting groups; 2) a concept of psychological entropy as a measure of the density of emotional states available to the members of a society with a given energy; and 3) a notion of the direction of change, generally toward increasing entropy" [20, p. 50].

One must hail such an approach to behavioral studies, while adding that there exists a great gap between the supporters of "physical" and those of "biological" interpretation of behavior. If we add to this attempts by certain philosophers, for example Burgers [15], to move away from determinism in nature, viewing initiative and creativity as fundamental to any unifying philosophical picture, then this gap widens to an even greater degree.

Thus singleminded behavior arises as a result of fluctuations of certain important constants within an organism, and of the need to normalize such constants. Motivational excitations play an important role in forming behavior. It is a peculiarity of motivation and its tie with purposeful behavior that motivation arises each time this or that useful adaptive result of a functional system changes and cannot be compensated for merely by the interval reserves of the organism [45,46]. Returning to the central architectonic of a functional system, we note that motivational excitation caused by changes in an organism's internal state represent an essential component of the afferent synthesis stage. Motivation itself will largely determine how an animal will react to environmental stimuli. No one would doubt that the basis of simpleminded feeding behavior in animals forms the corresponding motivational excitation accompanied by a subjective sense of hunger. Without going into detail about the hunger mechanism, we should like to mention the following factors: neural impulsation from the empty stomach; change of concentrations for various substances in the blood (for example glucose, lipid acids); and information from certain internal organs that serve as depositories for alimentary substances. In what way is afferent impulsation about changes in an organism's internal state transformed ultimately into a complex behavioral act directed toward food acquisition and a normalization of emerged deviations?

Modern neurophysiology has extensive data for the decisive role played by certain brain structures in the generation of feeding motivational excitations. First there is the lateral hypothalamic area whose neurons receive impulsation from various stimuli as well as show great sensitivity to chemical changes in the blood. The important role of the lateral hypothalamus in forming simpleminded feeding behavior is demonstrated by experiments on satiated animals using electrodes implanted in the brain (Figure 2). An electrical stimulation of only the lateral hypothalamic area (Figure 3) induces first an orienting reaction, then a searching reaction, and, finally, eating. Stimulation of surrounding areas gives no such clearcut reaction. An explanation of this phenomenon is simple. Local electrical stimulation increases the level of excitation of the hypothalamic "feeding center" (which in normal situations occurs because of natural stimulation from the empty stomach, from chemical changes in the blood, etc.); and the "feeding center" influences other brain structures, including the cerebral cortex, that finally leads to singleminded feeding behavior. Figure 4 shows electroencephalographic changes in various brain structures both cortical and subcortical, which are involved in these mechanisms of searching and feeding [53]. Thus it is feeding motivation excitation (naturally or artificially induced) which is one of the decisive conditions for the appearance of singleminded feeding behavior in animals. Motivational excitation, however, taken in isolation cannot force an animal to reach a necessary goal. "Hunger," as Setchenov writes, "can get an animal to its feet, lend a more or less passionate character to its search, but it has not elements that may direct movement in this or that direction or change this activity in accordance with the demands of environment or random encounters" [39].

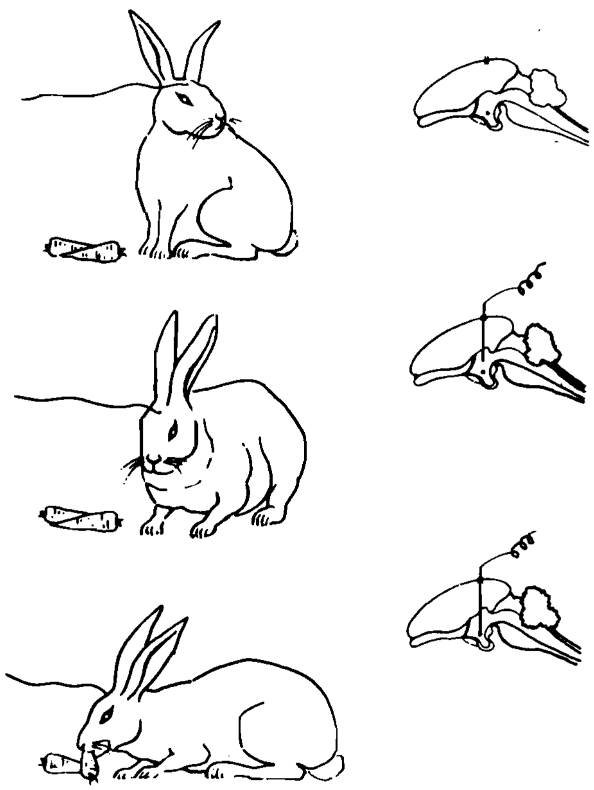

Figure 2. Method of investigation of hypothalamic feeding center in an awake rabbit.

Figure 3. Frontal section of rabbit's brain with electrode's tract in the lateral hypothalamic area (lift).

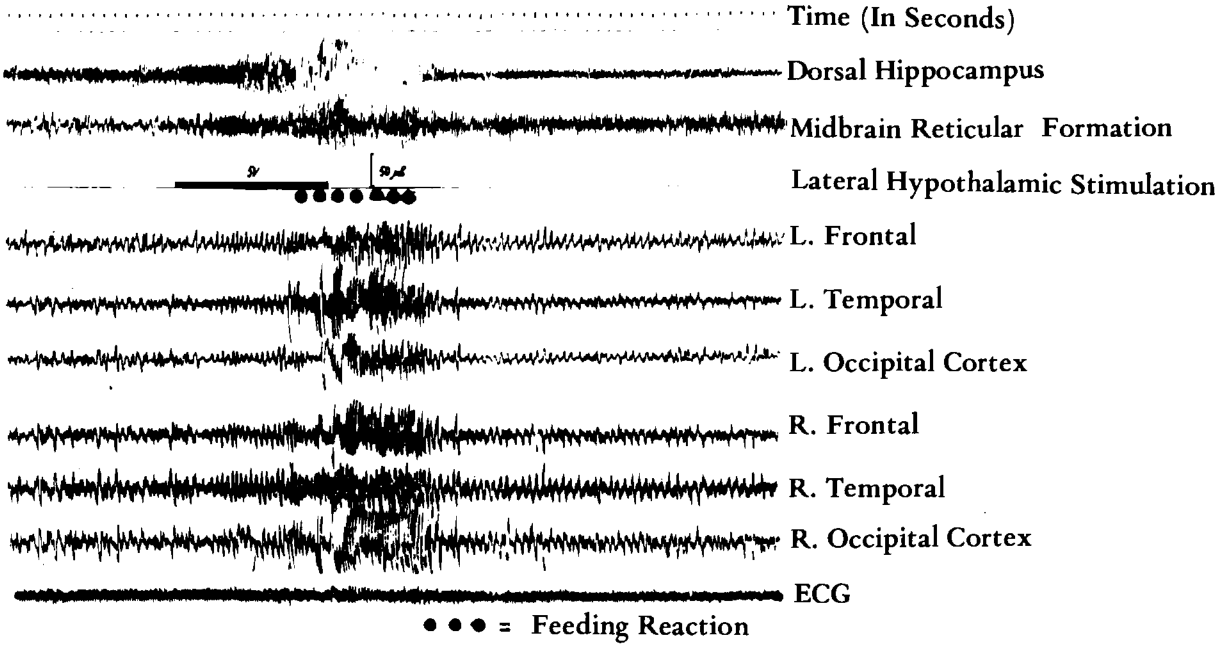

Figure 4. Electrophysiological record of feeding elicited by the stimulation of lateral hypothalamus of a satiated rabbit.

There is much evidence of the influences of environmental factors on the mechanisms formulating behavior. Thus the level of motivational excitation of animals may increase or decrease as a result of environmental changes [46]. That the level of "feeding" excitation may be changed has been proved by the following experiments in which animals have had electrodes implanted in certain cortical areas of the brain (Figure 5). A weak electrical stimulation of the frontal area increases several times the threshold of a rabbit's feeding reaction (elicited from the hypothalamic "feeding center"). Certain other cortical areas, for example, the occipital, facilitate conversely a feeding reaction in response to hypothalamic stimulation. At the initial stage of formation of singleminded animal behavior, motivational excitations as well as the environmental factors that have influences via the cerebral cortex, play an important role [52]. Figure 6 demonstrates that a single unit activity of the lateral hypothalamus (feeding center) can be changed in response to electrical stimulation of the brain's cortex.

Successful completion of the afferent synthesis stage must be realized with obligatory participation of the animal's memory mechanisms. And here again we should recall dominant motivation. At present we can affirm that memory operations for the implementation of singleminded behavior occur on the basis of motivational excitation.

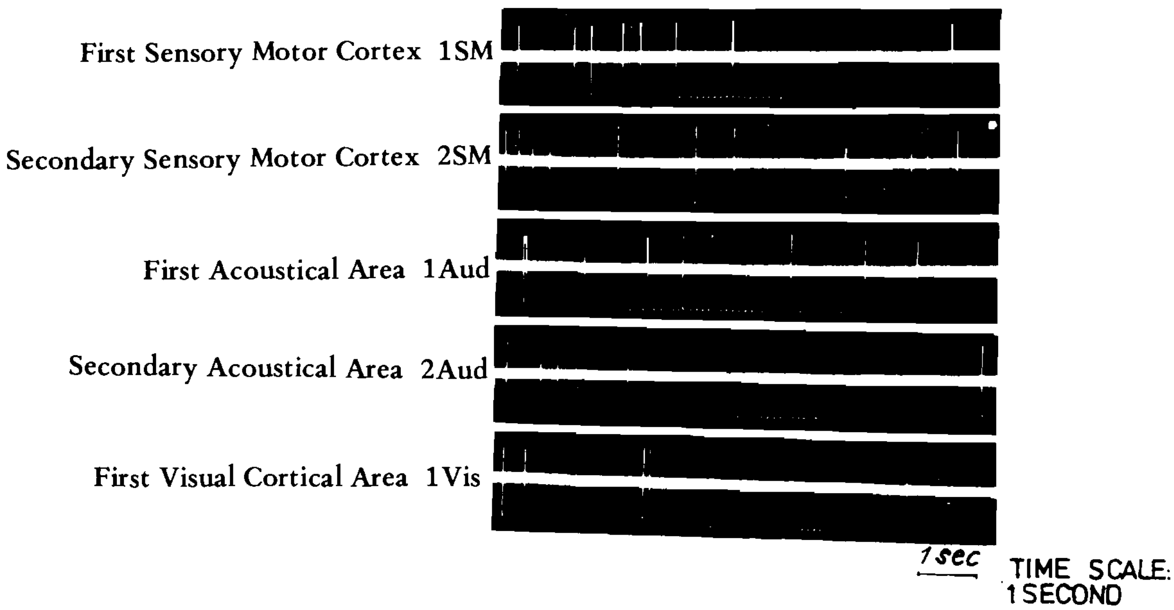

Figure 5. Example of lateral hypothalamic single unit response to the ipsilateral brain cortical stimulation.

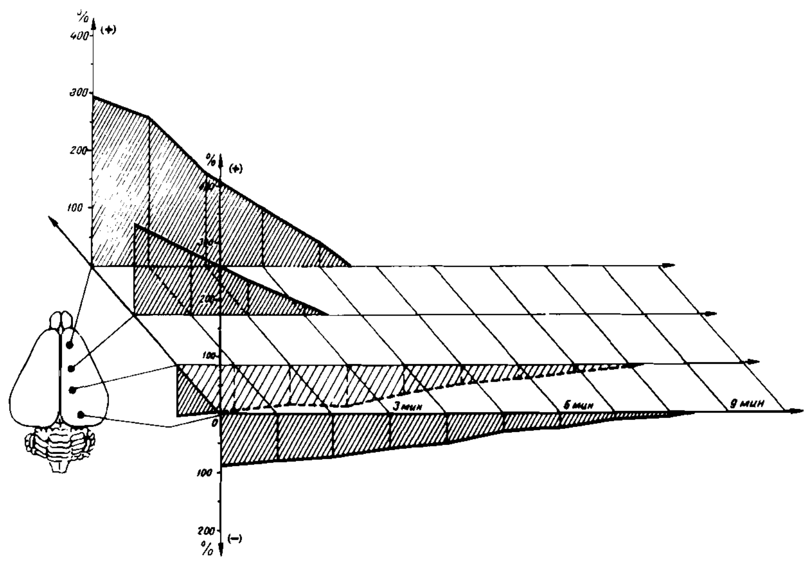

Figure 6. Changes of feeding threshold during electrical stimulation of some cortical areas. (Space above plate is increase of threshold and upper decrease.)

Thus the first stage of any singleminded animal behavior is exceptionally complicated, and must include the dominating motivational biological excitation at a given moment and the totality of environmental stimuli of the animal's location. In each case, the totality of these afferent stimuli create preparatory excitational integration which, in spite of its latent state, can be immediately revealed in response to a triggering stimulus. The physiological meaning of this triggering stimulus is that it reveals all the latent excitations just at a moment which presents the most convenient adaptive situation for an organism. Closely tied to afferent synthesis is the use of a memory apparatus. Afferent synthesis would be impossible were the totality of environmental and triggering stimuli not tightly tied to the animal's past experiences (preserved by the apparatus of memory).

What concrete neurophysiological mechanisms complete this complicated stage? Modern physiology gives the following answer:

> It is certain that as a functional event afferent synthesis cannot exist without the mutual interaction of all those excitations which are generated at receptors, emerge at the subcortical level and then in various combinations rise to the areas of the brain's cortex. It is precisely here, at the cortex, that there occurs the most synthetic mutual interaction of the afferent excitations. As a result of these interactions there is formulated the aim of obtaining one set of results in lieu of another [2,p. 223].

We demonstrated that the afferent synthesis stage is an inevitable one during which takes place integration of all excitations coming to the central nervous system and subsequent formation of efferent programs. At this time we mentioned the importance of the so-called intermediate stage of decision making. Decision making is a logical process of the functional system, and a result of definite physiological processes that are seriously in need of detailed investigation. Sumilina's experiments whereby frontal lobes were removed from dogs which then manifested singleminded feeding behavior showed conclusively that, at the moment of decision making, all information is integrated in the frontal cortex areas from which emanates a special command for the most optimal type of behavior. The decision making stage, which needs the greatest possible information in comparison to other stages, suffers the most seriously from various kinds of interference to the workings of the central nervous system [17,18,42].

After completing the decision making stage, an animal begins to realize an action's program. Electrophysiological methods demonstrated that until this second stage begins, an intensive activity takes place involving various subcortical structures, limbic reticular complexes in particular, as well as the neocortical area. The participation of limbic structures in feeding behavior is proved by changes in electrical activity (Figure 1), as well as through simulation of the dorsal hippocampus whereby even well expressed feeding behavior could be inhibited (Figure 7) [53].

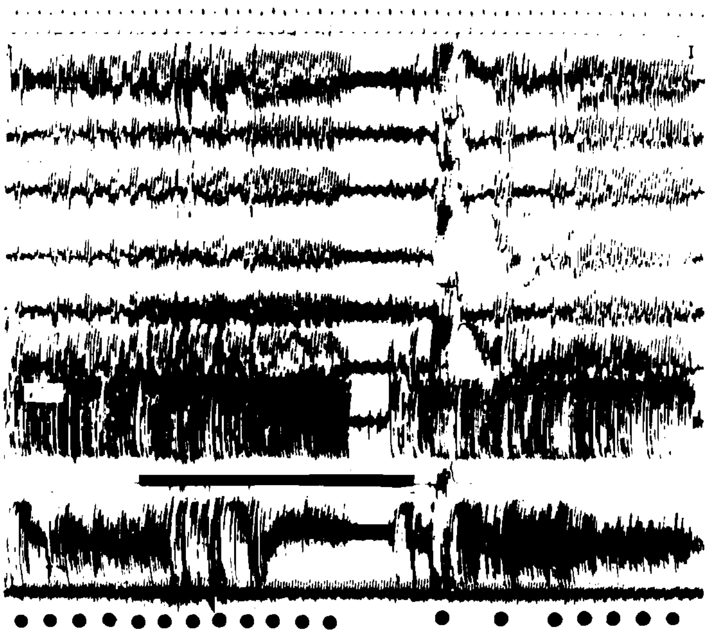

Figure 7. Interruption of feeding reaction during electrical stimulation of the rabbit's dorsal hippocampus.

The decision making stage and the output of efferent working excitations directed from the brain to the periphery form a vast complex of excitations in the central nervous system which "consists of afferent patterns of future result and collateral copies of efferent excitations going via a pyramidal tract to peripheral working apparatus" [3]. Depending on the time interval between statement of goal and its realization, additional excitations arrive at this complex of excitations that are engendered by real parameters of the obtained result. It is precisely here in the apparatus of the acceptor of action results that there is realized evaluation of the obtained result. This evaluation determines the subsequent behavior of the organism. If an achieved result corresponds to the result previously formed, an organism goes on to the next step of the behavioral continuum. If the parameters of the achieved result do not correspond to the properties of the acceptor of action results, then an orienting-investigative reaction is immediately induced. This reaction, while raising associative possibilities for the brain at a high level, provides an active choice of additional information. Pavlov's laboratory experiments have clearly demonstrated this phenomenon. Any change in the usual environmental conditions where an animal elicits a singleminded behavior (for example, a change in feeding time) is accompanied by a reaction clearly demonstrating that the obtained result does not correspond to a model of that result formulated in the mind of the animal [3].

The physiological mechanisms of the acceptor of action results has been investigated in detail at the Anokhin Institute of Normal Physiology. For example, it has been demonstrated that, at the moment when excitations spread centrifugally from the brain cortex there occurs a flow of nervous impulses; these impulses send a copy of the command via the pyramidal tract not only to that complex which evaluates results i.e. the cerebral contex, but also to the midbrain of the reticular formation by means of the collateral. The reticular formation, in turn, may provide in the centripital direction an activation of those excitation circles that must remain active until the moment when information arrives about attainment of the useful result via feedback.

OTHER POSSIBILITIES FOR THE APPLICATION OF FUNCTIONAL SYSTEMS THEORY

In our opinion; there is a positive side to functional systems theory that involves more than interpreting animal behavior. Functional systems theory of an organism brings a definite order to the data connected with brain research. For example, let us analyze visual afferentation. Visual afferentation is usually interpreted as a sensory modality, and from this analytical point of view its character is peculiarly optical. But what about visual afferentation from the standpoint of functional systems theory? A visual afferentation can be a "triggering" afferentation when, for example, it takes place in the event of a conditioned visual stimulus. For any other circumstance a visual afferentation may be an environmental afferentation; in this role it determines the latent integration of neural processes. Moreover, a visual afferentation can have a third functional meaning--it can be feedback for a system's evaluation of an achieved result. Thus "having formed the internal operational archetectonic of a system, we have changed our approach to usual notions and processes " [2, p. 105].

Functional systems theory has been useful for research into the embryonic development of functions [41]. The first studies in this direction were reported by Anokhin in a 1937 paper, "The Functional System as a Basis of Neural Integrative Processes in Embryogenesis" [3]. This, in fact, was the birth of a new evolutionary conception which Anokhin in 1945 formulated as a theory of systemogenesis [4]. The term "systemogenesis" describes a process that leads to the apperance of functions but not of organs. For example, the hand as an organ has not yet been formed with all of its components--in particular, the innervation of many of the forearm's muscles has not been completed; but an innervation of flexors that provides the grasping function has been completed. The main principles of systemogenesis (which range from moment of the first establishment of a system's components to the full fledged inherited adaptive functions that appear in newborns) have been formulated and are postulated as follows:

1) The principle of heliochronic establishment of a functional system's components. As has been proved [2], this principle implies that regardless of the complexity or the simplicity of a functional system's structure, all components, no matter how many, at the moment of birth form a functional whole--i.e. a functional system;

2) The principle of organ fragmentation in the process of embryonic development. Systemogentic type of development supposes the inevitable and non-homogeneity composition of an organ at each separate moment of its development. Those organ fragments will be first developed that provide from the moment of birth an organization for vital functional systems;

3) The principle of consolidation of functional system components that underscores the leading role of the central component of the system and supplies the final physiological architecture to the given system and;

4) The principle of minimal maintenance for a functional system. This tendency may be analyzed as a major achievement of evolution and in all probability it expresses one of the most perfect forms of successful achievement in the battle for survival. The essence of this regularity is that the functional system as found in an adult animal does not appear immediately in its fully developed form. First, those structural parts of separate components of the system are united which have already become mature at the moment of consolidation. As a result, the functional system while having begun the period of consolidation of its components has already become productive to a certain extent long before all of its links achieve final structural organization. Consequently, a functional system acquires an adaptive role in the life of a newborn before the system is fully and definitively mature.

The final generalization emanating from the physiological archetectonic of a functional system is a formulation regarding the integrated activity of the neuron. This formulation is based on new ideas that have recently come to light in modern physiology and results from subtle analysis of an afferent synthesis mechanism considered to be a nodular point of a functional system. The essence of the afferent synthesis is that excitations of various origins and physiological implications must be processed together and very often at the same time. The next crucial question arises: where can this meeting of excitations be organized as to provide an afferent synthesis of a functional system? There can only be one answer: on the same single neuron despite the many synapses and concentrations of information since the excitations are on their way to the cerebral cortex. This realization has resulted in a number of studies that at the initial stages form an idea as to the heterochemical properties of subsynaptic structures and, at the final stage, end with a new conceptual idea on "integrative neural activity" [6,47].

Some areas of physiology that have profited from applications of functional systems theory are: rehabilitation of destroyed functions, hypertension, emotional stress, etc. By adding the application of functional systems theory by teachers, physicians, musicians and by many other specialists, we can state with assurance that this system has grouped some universal features of functioning related to various classes of events [5].

In spite of indisputable achievements over its almost 40-year history, the functional system theory needs further creative development. Too complex and diverse are the problems that must be analyzed by the functional system theory, and there are too many scientific areas where this theory has yet to be used. Some aspects of Darwin's theory of evolution and altruistic tendencies in animal behavior [51] are examples of how animal social behavior may not be unequivocally considered as individual behavior, regardless of how carefully such behavior has been analyzed.

In considering the "intellectual inertia" that results from fixed ways of thinking, we should recall the words of Laszlo:

> Resistance to theories moving across disciplinary boundaries is stronger than resistance within the disciplines [24].

Taking into account "several additional factors, including indifference and fear" [24], functional system theory may be put alongside many other theories in biology about which a sceptic might say that only time and the future development of science will show definitively which of them is true.

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