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Translation

NEUROPHYSIOLOGICAL STUDY OF SYSTEMIC MECHANISMS OF BEHAVIOR

By

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NEUROPHYSIOLOGICAL STUDY OF SYSTEMIC MECHANISMS OF BEHAVIOR

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ANNOTATION

This study deals with analysis of behavioral mechanisms from the standpoint of functional system theory created by P. K. Anokhin, and it substantiates the need for the systemic approach to investigation thereof. From the point of view of P. K. Anokhin's theory, the elementary behavioral act is considered as a cycle of "exchange of information" between the environment and the organism. Mechanisms of involvement of an individual neuron in the system of the behavioral act are examined. There is discussion of correlations between mental, systemic and neurophysiological processes in behavior.

INTRODUCTION

The behavior of living organisms is the subject of investigation of many disciplines, in each of which special aspects of behavior are studied. This circumstance, as noted by R. Hinde (1975) in the preface to his book, does not allow us to define the concept of "behavior." However, for many areas of research, including neurophysiology and psychology, behavior in the most general sense can be defined as the relations of an organism and the environment. For this reason, the study of behavior should include analysis of both the environment and processes within an organism, and interaction between the organism and environment. The concept of "behavior" should pertain to all forms of interrelations between the organism and environment, including those that are reflected in the psychological aspect of the organism.

At the present time hardly anyone will deny the role of the psychological factor in behavior. Yet, it is obvious that behavior is based on physiological functional processes of specific morphological structures of the organism. The correlation between mental and physiological processes constitutes the so-called psychophysiological problem.

The materialistic thesis of unity of behavior and the psyche rules out the possibility of gaining full knowledge about the mechanisms of behavior without determining the role of mental processes in behavior. Any behavior theory that "throws out" or excludes mental processes is not, in our opinion, consistent with reality, since it is expressly through mental processes, through informational correlations that the external environment determines behavior, as reflected in the theses of reflecting and regulatory role of the psyche in behavior. At the same time, the unity of behavior and the psyche implies that it is impossible for mental processes to occur apart from behavior, i.e., certain physiological processes. Thus, a given solution to the problem of mechanisms of behavior of necessity leads to a given solution of the psychophysiological problem as well.

The psychological problem cannot be solved solely on a physiological or solely on a psychological basis; consequently, neither physiology nor psychology can offer a complete description of behavior. Nor can this be achieved by means of direct correlation of mental and physiological processes. As validly noted by A. N. Leont'yev (1975, p 7), "the fact of the matter is that no direct correlation of mental and cerebral physiological processes solves the problem. The theoretical alternatives that arise with such direct comparison are well-known: there is either a hypothesis of parallelism which inevitably leads to interpretation of the psyche as an epiphenomenon, or a thesis of naive physiological determinism with the ensuing reduction of psychology to physiology, or else, finally, there is a dualistic hypothesis of psychophysiological interaction, which assumes that the nonmaterial psyche affects tangible processes occurring in the brain. There is simply no other solution for metaphysical thinking, only the terms change to refer to the same alternatives."

It is presently becoming obvious that synthesis of psychology and physiology to describe behavior is possible only on some higher basis common to both disciplines. The systemic approach is such a basis, and it is now being developed in many areas of knowledge (Anokhin, 1973a; Kedrov, 1974; Kuz'min, 1976; Lomov, 1975, and others). Of the many variants of the systemic approach, functional system theory, which was developed by Academician F. K. Anokhin (1935-1974) appears to us to be the most adequate to the problems of physiology and psychology and the task of their synthesis in the description of behavior. This theory proceeds from the most general biological theory, theory of evolution, to explain behavior.

Indeed, unlike many variants of the systemic approach in biology, which propose to study the properties of systems on formal models (Mesarovich, 1970), functional system theory is entirely based on biological facts, and it uses the concept of survival, or useful adaptive result, as the foundation for the method of isolating the system. Like all fundamental initial concepts (Kedrov, 1962), the concepts of system and result are defined in functional system theory through the relationship between them. The result is a state of the environment that allows the system to survive. The system is an aggregate of elements so organized as to achieve this result. Survival is the main result that is ultimately reached by biological systems. Hence, the behavior of biological systems is goal-oriented, and any behavior occurs to reach some useful adaptive result that ultimately leads to survival.

Of course, there are very diverse forms of interactions between an organism and the environment; behavior can be defined as interaction, in which both the organism and environment are whole. Then behavior will appear as a two-way exchange of organization or information between the environment and organism, which can occur only by means of informational or specifically systemic processes that cannot be reduced to separate physiological processes or separate effects of the environment.

Systemic processes describe the state of both the organism and environment; for this reason, a neurophysiological or psychological description of behavior is a particular description of the same systemic processes of correlation between the integral organism and environment.

From this point of view, the description of the correlation between the organism and environment in terms of systemic processes should constitute the special subject of "systemology." Correlations between systemic and elementary neurophysiological processes are the relations between information and its material carrier, since systemic processes are distinctive informational processes (Ferster, 1964; Gorskiy, 1974). But the correlations between mental and systemic processes are the relations between internal and external ifnormation. External information is the organizational attribute of environmental elements, while internal information is that of organization of elements of the organism. Thus, one can compare neurophysiological and mental processes only through qualitatively unique systemic processes, which exist in the organism as processes of organization of various elements into a single whole, a functional system.

Since systemic processes, one aspect of which is the psyche, are represented in the organism by processes of expressly organization of physiological functions, this view avoids equating mental and physiological processes. It also avoids psychophysiological parallelism, since systemic processes are processes of organization of expressly physiological functions and the psyche is the product of the brain. Since internal organization is determined by organization of the environment, i.e., its object structure, the psyche cannot be excluded from analysis of mechanisms of behavior. Finally, since systemic processes "consist" exclusively of physiological processes and a new quality is attained exclusively as a result of their organization, physiological and psychological determination of behavior is inseparably united and the two do not exist without one another, which precludes any psychophysiological interactions.

Evidently, this point of view is consistent with conceptions of correlation between the psyche and brain as information and its carrier, which are being developed from the philosophical point of view (Ponomarev, 1967; Dubrovskiy, 1971, 1976). Thus, functional theory system serves as the basis on which one can find an experimental solution to both the problem of mechanisms of behavior and the psychophysiological problem. From the standpoint of this theory, neurophysiology of behavior and the psyche can be interpreted as the study of systemic processes of exchange of organization between the integral organism and objective environment using neurophysiological methods.

In research on behavior, the problem of elementary phenomenon was always considered the key one, which determined all subsequent theoretical developments and direction of research. Since the times of Descartes, the organism's reaction to some environmental agent was always considered to be an elementary manifestation of behavior. There is a certain interval between a "stimulus" and the "reaction" to it, and in different aspects it is referred to as "delay," "reaction time," "reflex time," etc.

The polemics on the subject of processes that occur in this interval gathered, or concentrated, all of the contractions in psychology, physiology and other disciplines that deal with the brain and behavior. The problem of determination of behavior, the psychophysiological problem, the problem of localization of functions, cybernetic problems of information coding and regulation of the organism's relations with the environment, and all other general biological problems of behavior and the psyche are related in some way or other to determination of the mechanisms of the elementary behavioral act.

From time immemorial, such mental processes as perception, comparison [collation], remembering, etc., have been attributed to this interval also. Measurement of this interval in different experimental modifications is widely used to describe the most diverse mental processes and states; and it is even believed that "the method of measuring reaction time is the best method for studying higher functions, and it has a great future" (Shoshol', 1966, p 316).

In spite of the complexity and diversity of processes that one relates to elementary behavioral acts, for a long time the neurophysiological interpretation of processes occurring between the "stimulus" and "reaction" amounted to conduction of stimulation from receptors to effectors, as was dictated by reflex theory.

The conception of the behavioral act as a reflex was not based on direct studies of neuronal mechanisms of behavior and not on physiological facts or even anatomical conceptions, but exclusively on the ideas of mechanistic determinism. In his "Answer of a Physiologist to Psychologists," I. P. Pavlov wrote: "It is generally accepted that the concept of reflex originates with Descartes; but what was known about the detailed construction of the central nervous system or about its activity in the times of Descartes? Physiological and anatomical separation of sensory nerves from motor nerves occurred only in the early 10th century. Obviously, the idea of determinism was for Descartes the essence of the concept of reflex, hence his conception of the animal organism as a machine. This was the interpretation of reflexes of all subsequent physiologists, who related different activities of the organism to different stimuli, gradually isolating elements of neural structures in the form of various afferent and efferent nerves, and in the form of special pathways and centers of the central nervous system, and finally also gathering the typical dynamic features of the last mentioned system" (1949, p 495).

Even at the moment of its inception, the idea of reflexes "made the first breakthrough in the strong wall of mystical and religious conceptions that separated the researcher from real facts" (Anokhin, 1945, p 6). The principle of determinism, contained in the reflex concept was not only used to fight against interpretation of behavior from the teleological positions of idealism, but served as a natural methodological basis for experimental research on the nervous system. The contemporary advances in neurophysiology became possible only on the basis of the analytical approach, which enabled neurophysiologists working with local processes or substrates to use the same approach that had been used and glowingly justified itself in mechanics.

At the present time, the principle of "mechanistic determinism" (also qualified as "linear" and "naive physiological") as applied to interpret biological processes and behavior is being critized from the most varied positions, including philosophical (Dubrovskiy, 1971; Serzhantov, 1974), cybernetic (Menitskiy, 1975; Svinitskiy, 1976), psychological (Lomov, 1975), biological (Oparin, 1964) and neurophysiological (Burns, 1969; Belenkov, 1975, 1976; John, 1973; Sudakov, 1976, and others).

Although it was obvious to many, rather long ago, that the reflex interpretation of the elementary behavioral act was unsatisfactory, for a long time more constructive solutions of this problem were delayed by the fact that considerable revision of the entire system of conceptions that had been formed would be necessary to reject century-old reflex traditions in physiology. As noted by B. Burns with reference to one of the earliest and most striking critics of the reflex, "Lashley's argumentation was weak ... because ... Lashley quantitatively tested the reflex or telephone theory of behavior and found it to be invalid, but did not offer any other promising system of concepts" (1969, p 19).

Functional system theory created by P. K. Anokhin provides such a system of concepts. V. F. Serzhantov believes that "acceptance of this conception leads to certain consequences for the entire theoretical system of biology and psychology: the principle of functional system permits deeper interpretation of biological and psychological concepts formulated in science to this time; hence the need to reorganize the entire conceptual structure of these areas of science" (1974, p 74).

Application of the conceptual apparatus of functional system theory to problems pertaining to the elementary behavioral act alters radically the very methodology of research. For this reason, analysis of the neurophysiological mechanisms of the elementary behavioral act from the positions of functional system theory requires preliminary consideration of behavior in the terms of this theory.

We shall make such an examination as compared to known and customary conceptions of reflexes; however, our main goal will not be to compare the two approaches, but to define the subject of investigation and formulate concrete problems, for which experimental neurophysiological solutions must be found.

CHAPTER 1. SYSTEMIC DESCRIPTION OF THE BEHAVIORAL ACT

Qualitative Distinction of Behavior From Elementary Physiological Processes

The psychological description of relations between an organism and the environment includes such concepts as memory, motivation, perception, action, emotion, etc., i.e., concepts that characterize the organism as a whole, as a subject. The environment is also described in psychology as "objective" [object-related], and the correlation of an integral organism and objective environment emerges as the correlation between a subject and object. As validly observed by L. M. Vekker, "the ultimate, final characteristics of any mental process in the general case can only be described in terms of properties and relations of external objects. Thus, perception or a conception ... cannot be described in other than terms of shape, size, consistency, etc., of the perceived or imagined object. Thought can be described only in the terms of the features of objects, the relations between which it discloses; emotion can be described in terms of attitude toward events, objects or individuals that induce it, while voluntary decisions or a volitional act cannot be expressed in other than terms of the events in relation to which the action or deed is performed" (1974, p 11).

Thus, psychology describes the relations between the organism and environment in terms of properties and relations of expressly environmental elements. This is an extremely important aspect of behavior; however, psychological concepts do not describe internal processes at all, i.e., processes that take place in the organism, since "phenomena of subjective reality constitute information given to the person so to speak in 'pure form'" (Dubrovskiy, 1976, p 54).

Internal processes have always been referred to the area of physiology, which has its own conceptual system. From the very beginning, physiology developed as an experimental and analytical science. Neurophysiological concepts, such as stimulation, excitation or inhibition, afferentation or efferentation, etc., were created to describe processes occurring in different, morphologically distinguishable organs or nerves. For many reasons, for a long time experimentation was possible only on preparations of animals, in which, of course, there is no behavior.

In undertaking development of physiology of behavior, I. P. Pavlov introduced into the practice of physiological experimentation work with integral organisms. It is expressly to I. P. Pavlov that we owe formulation of the task of physiological study of behavior, which has not lost its meaning to this day. Already in 1903, he observed: "The tremendous complexity of higher, as well as lower, organisms continues to exist as a whole only so long as all of its elements are finely and precisely linked, balanced with one another and with the surroundings. Analysis of this balancing of the system constitutes the first and foremost task and goal of physiological research as purely objective research" (1949, p 337).

However, having formulated the task of studying integral behavior, nevertheless the Pavlovian school first concentrated its experimentation on the study of actual function of a single salivary gland, rather than mechanisms of integral behavior, and this was of decisive significance to development of the entire conceptual system of the teaching on higher nervous activity. Having concentrated its efforts expressly on analysis of brain function, the teaching on higher nervous activity used the analytical concept of "reflex," which already existed in physiology and was developed to describe processes demonstrated in preparations, i.e., expressly beyond integral behavior, as the foundation for conceptions of the mechanisms of the integral behavioral act. For this reason, the descriptions of behavior of an integral organism and processes occurring in preparations turned out to be identical.

With reference to adaptive behavior, I. P. Pavlov wrote: "... adaptation is based on a simple reflex act, which is initiated by certain exogenous conditions that affect only a specific kind of endings of centripetal nerves, from which stimulation passes over a specific nervous pathway to the center, from their to a gland, also over a specific pathway, thus causing specific function in it" (1949, p 334). Application of the analytical concept of "reflex" to analysis of mechanisms of integral behavior resulted in setting aside from the main line of physiological research the qualitative specifics of expressly integral behavior.

Confusion of concepts describing the function of disconnected physiological mechanisms and the integral organism made it impossible, for a long time, to see the actual problem of integrity, since "excitation of neurons" ultimately produced "excitation of a center" and even "excitation of the brain," while "inhibition of a reflex" was attributed to "inhibition of neurons" of the corresponding centers. This "energetic" description of processes occurring in the organism and implementing behavior also required an "energetic" description of the environment as an aggregate of different "stimuli" or "irritants." The correlation between the organism and environment with reference to behavior was actually reduced to conformity between elements of stimulation and elements of reaction.

Application of the analytical concept of "reflex" to description of integral behavior appeared to disclose the possibility of describing internal processes of behavior in traditional physiological concepts describing the state of different organs and tissues. However, this approach also closed the way for relating "properties and relations of external objects" to processes within the organism. Indeed, if, as is assumed in reflex theory, relations between the organism and environment consist of element-by-element conformity between stimuli and reactions, some sort of special concepts would be utterly superfluous to describe "properties and relations of external objects" and processes of correlation between expressly the integral organism and objective environment. As we know, this circumstance had dramatic consequences with regard to the contact between physiology and psychology, and made it impossible to develop a conceptual system common to these two disciplines that describe behavior.

Development of the ideas of I. P. Pavlov concerning the systemic nature of higher nervous activity led to creation of functional system theory (Anokhin, 1935-1974), which reflected the qualitative uniqueness of mechanisms of integral behavior, as compared to reflex mechanisms of spinal preparations and anesthetized animals. As observed by V. F. Serzhantov, "functional system theory grew from reflex theory in its Pavlovian interpretation, it is a continuation of the latter, but at the same time it is also a negation thereof in a certain sense. However, this is dialectical negation" (1974, p 70).

P. K. Anokhin expounded functional system theory on the basis of physiological facts that disclosed the qualitative specificity of processes of integration of different physiological processes into a single whole, the functional system of integral behavior. This disclosed an absolutely new type of processes in the integral organism, a type of systemic processes or "processes of organization of physiological processes."

Discovery of systemic processes in the organism automatically leads to a certain interpretation of both the environment and correlation between the organism and environment. According to functional system theory, unlike material-energetic relations between a local stimulus and local reflex reaction occurring in anesthetized or spinal preparations, behavior is a means of two-way informational correlation between the organism and environment.

Highly organized organisms exist in an organized environment; in the course of evolution they had to adapt to such environmental factors as behavior of the prey or predator, availability of material to build a nest, behavior of sexual partner, etc. All these adaptations required integral evaluation of different material-energetic factors and attitude toward their specific organization as to a whole, i.e., an object.

The environment affects different receptors of the organism in the form of different, separate energies; the object, i.e., organized aggregate of environmental elements, may even find passive reflection only in organization of activity of many receptors, when the organism emerges as a whole. There is reflection in behavior of the environment, not only objectively, but actively; the organism constantly searches for and obtains the information it needs, unlike a preparation which is indeed "submitted to the effect of a stimulus."

Processes within the organism referable to behavior can also not be reduced to energy processes of "excitation and inhibition." Any aggregate of excited elements per se does not create the phenomenon of behavior. It is expressly processes of coordination of specific elements and organization thereof in a single whole, in which everything is "finely and precisely related, balanced within itself and with external conditions," expressly these processes of organization constitute the essence of internal mechanisms of behavior of the integral organization, and not "stimulation of cells of a functional organ" per se.

The systemic approach compels one to consider behavior as the correlation between organization of the environment and organization of processes within the organism. And determination of behavior by the external environment emerges as determination of organization of processes within the organism expressly by organization of the environment.

Just as "life is characterized by a special, specific combination of properties, rather than any particular properties" (Oparin, 1924, p 36), so behavior is not referable to some special processes, but to specific organization of processes on the physiological level. Processes of organization are qualitatively specific and bilateral: environmental organization determines organization of processes in the organism, which in turn leads to organized influences of the organism on the environment and new organization of the environment, etc. This entire, continuous cyclic process is designated in systemic terminology by the general term, "behavior."

As we know, biological existence of an organism is implemented by absorption of organization, or "negentropy" of chemical bonds (Schroedinger, 1947). This principle is common to all living things, regardless of complexity of the organism. The behavior of multicellular and particularly highly organized organisms can be viewed as development of this capacity and use by the organism, to maintain its integrity and organization, not only of organization of chemical bonds, but other, higher forms of organization of the environment. In this regard, "adaptation of organisms to it acquires a qualitatively new form, which is related to reflection of objectively object-related reality" [Leont'yev, 1972, p 49).

Thus, behavior as a qualitatively specific form of adaptation of the integral organism to the objective environment is based on systemic mechanisms of organization of different physiological processes into a single whole, a functional system.

Functional system theory provides the basis for describing behavior in terms of systemic processes proper, i.e., processes of correlation between external and internal organization. Exchange of organization between the organism and environment can only be described by systemic categories, which characterize the environment and processes in the organism from the standpoint of correlation [comparison]. The environment must be characterized not only by a specific organization of its elements in time and space, but existence in the organism studied of the capacity to make use, in some way or other, of this organization of environmental elements in behavior. In turn, processes in the organism must characterize not only a specific organization of elements of the organism, but the link between these organization and certain exogenous events. Therefore, the concepts of functional system theory, such as "goal" or "result," "memory" or "motivation," refer both to specific organization of the environment and specific organization of elements within the organism.

At the present time, actually only the "skeleton" of the systemic conceptual apparatus has been created, and different concepts will be constantly defined; however, such definition must be made on the basis of concrete factual material. Description of these processes in terms of "properties and relations in objective-object-related reality" is the subject of psychology; their description in terms of activity of endogenous elements of the organism is the subject of behavioral neurophysiology.

As noted by K. Lashley, reflex theory "has the advantage of simplicity, which explains its popularity as a slogan" (1933, p 188). Systemic categories do not have this advantage. They are not referable to traditional or intuitively obvious categories; nevertheless, for the methodological considerations stated above, the objectives of neurophysiological studies of behavioral mechanisms should ensue expressly from a systemic description of behavior as exchange of organization between the organism and environment.

Goal Orientation of the Behavioral Act

The purposefulness of behavior of living organisms has actually never been completely denied, since even mechanicism, which considered a "reaction" to be the immediate consequence of a "stimulus," was also compelled to recognize at least "seeming" purposefulness of behavior. This recognition ensued from the adaptational nature of behavior directed toward survival of the organism. While rejecting the concept of "goal" to interpret a specific behavioral act, not a single biologist could deny that "all life is the pursuit of one goal, namely of preserving life itself" (Pavlov, 1951, p 33).

The conviction taken from mechanics, that the only scientific interpretation is interpretation in terms of linearly related "causes" and "effects," and at the same time the obvious orientation of behavior of organisms toward reaching the goal of "surviving" generated numerous attempts at explaining the purposefulness of behavior without using the concept of "goal." This situation was cleverly described by the expression: "Teleology is a lady, without whom not a single biologist can live, but he is ashamed to appear in public with her" (quoted in: Mesarovich, 1970).

The law of Thorndike's effect, which postulates that there is a retroactive effect of the result of action on the "stimulus" and "reaction" link, the conceptions of the Pavlovian school about "copying" an unconditioned (already adaptive) reaction to a conditioned signal, as well as the inborn permissive [or resolving] mechanism of ethologists--all these are attempts to explain purposeful behavior through cause and effect relations between "stimulus" and "reaction." This desire is attributable to exclusively general philosophical considerations, since any behavior is a continuum of behavioral acts, and in reality it is much more convenient to classify natural behavior according to "actions" and "results," as is done by zoologists (Chauvin, 1972), rather than according to "stimuli" and "reactions." The independence of reflex formulation of the problem of behavior from the subject of research proper can be very graphically seen in the book by R. Hinde (1975).

While indicating the considerable advantages of describing behavior according to the results attained and noting that "a description according to consequences is often absolutely necessary for a complete description of behavior" (p 21), R. Hinde nevertheless views the problem of behavior as "establishing a link between the phenomena studied and events and conditions that immediately preceded them. Such analysis is usually called 'causative analysis'" (p 12).

Both the natural forms of behavior, such as "food searching," "nest building," "sexual" and "instrumental" behavior observed in experiments, and such facts as the relationship between chemistry of saliva and composition of future food, demonstrated in the classical experiments of I. P. Pavlov--all these observations were a direct indication that both the integral behavioral act and any behavioral reaction are directly governed by future, rather than prior, events.

The obvious link between a given form of behavior and future events, or results, also failed to serve as the theoretical basis for analysis of behavior exclusively for general, philosophical considerations, since it required an utterly different methodological approach.

The critical comments directed toward reflex theory and "causative analysis" of behavior, which became particularly numerous in the last decade, made it absolutely obvious that mechanistic determinism (also called linear, naively physiological, etc.) could not explain the behavior of living organisms. However, as noted by P. K. Anokhin (1962b), rejection of mechanistic determinism led to teleological conceptions, which were found to be idealistic, since in the history of science, as a rule the recognition of purposefulness in living nature was set against materialistic determinism.

The conceptions of purposeful behavior fell into the stream of philosophical systems that extended the concept of "goal" to nature as a whole, which led to "vitalism," finalism," recognition of "entelechy," etc.

One can find a critique of these conceptions in recent philosophical works (Volkova,et al., 1971; Ukraintsev, 1973, 1976, and others). Demonstrating the inapplicability of philosophical teleology, the authors arrive at the conclusion that the goal-oriented approach to analysis of biological phenomena is justified and absolutely mandatory.

Behavioristic theories such as "symbol -- what it designates" (Tolman, 1951), as well as conceptions of "extrapolation reflexes" (Krushinskiy, 1967), of behavior guided by images (Beritov, 1961), "TOTE unit" type of concepts (Miller, Galanter, Pribram, 1965), cybernetic behavior theories (Ashby, 1962; George, 1963), made a significant contribution to interpretation of determination of future by future events, but all of these conceptions recognized purposefulness of behavior, along with the reflex, which appeared to be a satisfactory explanatory principle, at any rate, at least on the level of some physiological mechanisms.

The "firmness" of the reflex in physiology was in contradiction to purposefulness of behavior as a whole, which led some to maintain that it was "premature to physiologize" to interpret behavior (Tolman, 1951) and others to use reflexology even to explain human behavior.

At the present time, there are apparently few who would question the purposefulness of human behavior, although there have been both philosophical and physiological attempts to interpret human behavior from successively reflex positions, a summary and critique of which can be found in the book by Ye. A. Budilova (1972).

At present, it is imperative to have the goal category in an explanation of human behavior (Leont'yev, 1975; Gal'perin, 1976; Bekhtereva, 1974). However, for some authors, an obstacle arises when the conclusion of purposefulness of behavior is extended to animals, which consists of consciousness of human activity, the "humanitarian nature" of the concept of "goal," or "anthropomorphism" of such extrapolation. These obstacles appear contrived, since the concept of "goal" in its application to analysis of animal behavior can be used without the adjective "conscious," using this term to refer to the future, for which the behavior occurs. In this interpretation, the concept of "goal" can apparently be used with equal significance to describe both the behavior of a man who goes shopping in a store, and of the earthworm who crawls up to the earth's surface for leaves and grass.

The systemic "goal" category refers to an event for which behavior occurs. Like all systemic categories, "goal" characterizes the relationships between an integral organism and organized environment; for this reason, this category also refers to a specific organization of the environment, as well as specific organization of elements of the organism.

Functional system theory extended the principle of purposefulness to all levels of analysis of behavior and all physiological mechanisms, on which behavior is based. Successive application of the principle of purposefulness permits solving a number of "paradoxes" and creating a unified and orderly system of concepts to explain both integral activity of the organism in behavior and elementary neurophysiological processes contained in behavior.

The purposefulness of all biological processes is related to the very history of appearance of life on earth. Observing that "the analogy drawn by mechanists between organisms and machines cannot by any means explain the very thing it is called upon to explain, the 'purposefulness' of organization of living beings," A. I. Oparin stresses that differentiation of integral multimolecular systems from the primeval soup could only occur by virtue of the fact that the association of several molecules enabled this structure to interact with the environment as a whole and to preserve integrity. "By virtue of their differentiation, the emergence of such systems does not represent anything unique: at first these were simply isolated regions in the primeval soup." And "any, even scattered chemical processes taking place in a drop, let alone some combination or other thereof, were not indifferent to its subsequent fate"(1964, p 27). Some of them aided in, while others prevented retention of the integrity of multimolecular systems. "This is the route, already at the early stage of evolution of coacervates, along which a form of selection arose of the primitive systems, according to the feature of conformity of their organization with the objective of preserving a given drop under conditions of its continuous interaction with the environment. It is expressly on the basis of this new pattern, which emerged in the very process of inception of life, that there was formation of the metabolism inherent in all living things, a combination of different reactions that, as an aggregate, was 'purposeful,' for constant self-preservation and self-reproduction of living systems under prevailing environmental conditions" (1964, p 28).

The purposeful organization of different chemical processes constituting metabolism became enriched during evolution with more and more, also purposeful additions. This is how D. Kenyon and G. Steinman describe how metabolism became more complex in evolution: "There had to be a time when the most easily assimilated nutrients (A) would be entirely used up; then the eobionts (primitive prototypes of living cells), which were capable of producing A from other available compounds (B) gained the advantage. When, in turn, the amount of secondary nutrients (B) diminished, it became necessary for A and B to form from C, and so on. Acquisition of the appropriate catalysts to accelerate these reactions determined the degree of complication of this process" (1972, p 269).

All subsequent evolution and all, even qualitative, complication of organization of biological systems and those derived from them were thereby guided by the same "system-forming factor" (P. K. Anokhin), the result that increased their chances of survival. This "patent" significance of the result to determination of purposeful behavior of systems with different levels of organization was constantly stressed by P. K. Anokhin: "The very appearance of stable systems with elements of self-regulation became possible only because the first result of such self-regulation emerged in the form of stability itself, capable of withstanding exogenous factors. Consequently, the regulatory role of the result of the system was the first moving factor of development of systems, which accompanied all stages of prebiological, biological and social development of matter" (1975, p 339).

In any concrete study, we find contemporary organisms at a certain phase of evolutionary development, when their structure reflects the entire history of their survival. Since only purposeful forms of activity of organisms were selected and structurally fixed in the course of evolution, the genetic memory of organisms could only contain potentially purposeful behavioral acts which, under any conditions, led ultimately to survival of the organism. Individually acquired behavioral acts were superimposed over innate ones in accordance with the same evolutionary principle of survival.

The aggregate of all innate and acquired acts constitutes the general stock of adaptive behavior of animals, which differs in different species and specimens. This stock is life experience, or memory of the organism. The systemic "memory" category refers to the aggregate of specific organizations of elements of the organism that corresponded in the past to some behavioral acts.

Aside from learning processes, adaptive behavior can be gleaned only from the store of memory. For this reason, behavioral acts cannot in principle be other than purposeful. According to functional system theory, the selection of some particular goal out of all the material in memory and of one behavioral act conforming with this goal occur under the influence of several factors, designated as "motivation," "situation" and "triggering stimulus." The interaction of these factors is referred to as "afferent synthesis."

On the level of highly organized animals, the main goal of life, to survive through the demands of tissular metabolism and homeostatic mechanisms, is manifested in the form of motivations of behavior. Adaptational behavior cannot be unmotivated. Functional system theory makes full use of the idea, voiced by I. M. Sechenov: "Vital needs generate desire, and then it leads to action; desire will then be a motive or goal, while movement will be the action or means of reaching the goal. Movement would be senseless in general without desire as a motive or impulse (1952, p 516).

Motivation as a systemic category is concrete definition of the goal to survive. "Motivation retrieves all (behavioral) acts from memory that had at one time been related to satisfying this motivation" (Anokhin, 1974b, p 23). Since the same motivation (for example, the motivation of hunger) can be satisfied by means of reaching different, even more concrete, goals in the form, for example, of a specific type of food, further reduction of potentially attainable goals and potentially feasible behavioral acts occur under the influence of the situation, which permits only the behavioral acts whose goals are attainable only in this situation. This state preceding the triggering stimulus was named preliminary ["pretriggering"] integration. These conceptions are illustrated in Figure 1.

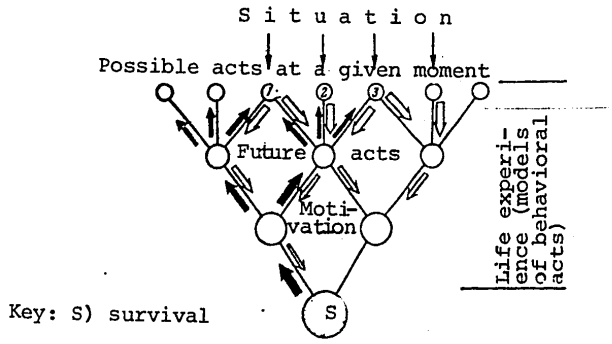


Figure 1. Correlation between motivation and situation in preliminary integration. The circles refer to behavioral acts constituting the organism's life experience. The links between them reflect their position in the hierarchy of goals. Arrows show the direction of influences of motivation and situation determining the priority (circled numbers) of behavioral acts in a state of preliminary integration. The circles without numbers refer to "reduced degrees of freedom."

In highly organized animals, attainment of the main goal of survival is mediated by many hierarchically organized intermediate goals. Separate, interrelated events serve as these goals, and the successive occurrence thereof can lead the animal to satisfying its movitvation. These events form the "tree of goals" of a specific motivation in the entire logic net [system] of life experience. In different situations, the same goal can be reached by different actions; at the same time, under different conditions, the same action is used to reach different goals. The final choice of one goal and one behavioral act out of the many possible ones in a given situation is made at the time when an event occurs in the environment that favors one of the goals already chosen by motivation and the situation. This event is called the triggering stimulus.

Only events included in the hierarchy of goals are actively "pursued" or "expected" by the organism, can guide the animal in choosing one concrete goal out of all those that could be attained with the motivation at hand in a given situation, and lead to survival. In actuality, trigger stimuli appear only as a result of prior behavioral acts in the continuum of behavior. Any unexpected events immediately interrupt goal-directed behavior and induce an orienting-exploring reaction. The process of selection of one goal and one action out of all the material in memory, under the influence of all elements of afferent synthesis, is referred to as "decision making." Separation of afferent synthesis and decision making only means that there is isolation of determinants, on the one hand, and output functions of a single process, on the other, which translates the orderliness of the environment into an orderliness of elementary physiological processes in the functional system of behavior.

One goal, selected in the process of afferent synthesis and decision making, is referred to as the "acceptor of action results." The model of this goal, which exists as a certain organization of elements extracted from memory, in turn determines the organization of actuating mechanisms of the behavioral act, i.e., organization of physical influences of the organism on the environment. This organization of actuating mechanisms is referred to by the term "program of action," while the organized influences on the environment are referred to by the term "action."

Action is a means of altering the correlation between the organism and the environment, a means of "translating" the expected event--"goal" into a real event--"result"; for this reason, action is totally determined by the model of a future event, rather than the trigger stimulus that directly precedes the behavioral act. Determination of action by the goal, i.e., "anticipatory reflection of reality" (P. K. Anokhin) makes it possible to eliminate the so-called time-related paradox, which arises in reflex interpretation of the behavioral act, in which the orientation of action toward reaching future events does indeed appear paradoxical, since the stimulus that directly preceded action is believed to be the cause of action.

At present, conceptions of purposefulness [goal orientation] of behavior are becoming widely recognized. Even such a strong proponent of reflex theory as E. A. Asratyan devoted part of his paper at the 21st International Psychological Congress to a discussion of "neurophysiological mechanisms of goal-directed nature of motivational motor acts" (1976, p 18).

One can find a discussion of some conceptions of goal orientation (E. S. Russell, W. Thorpe, G. A. Deutsch and others) in a special chapter of the book by R. Hinde (1975), in which objections to these conceptions are also cited.

R. Hinde believes that "behavioral activity directed toward a certain goal will attenuate as the goal situation is approached," and he sees an objection to this thesis in the fact that "rats run fastest when coming close to the goal" (p 669). In actuality, these view is wrong in its first premise. Since "approaching the goal situation" is possible only as the systematic attainment of more important goals in the hierarchy, any "attenuation" of behavioral activity half way to the ultimate goal is not justified in any way.

Another objection is due to the fact that R. Hinde relates the goal orientation of behavior to its determination by an "error signal," i.e., discrepancy between the real and "goal" situations, and he concludes: "... there is no conclusive evidence that, for example, the reaction of a wasp to damage to its nest is a reaction to the difference between the damaged and intact nest, rather than a reaction to the edges of the hole" (p 669-670). However, according to functional system theory, a discrepancy between a real and goal situation by no means serves as the cause of goal-directed behavior. A discrepancy between the goal and a real event can only induce a general orienting-exploring reaction. But goal-directed behavior is determined by the goals themselves, i.e., models of future situations extracted from memory; these models precede actions and determine them.

A concrete model is compared to the result only after the action, i.e., a comparison is made of the informationally equivalent real situation to the model of this same (and not future) situation. For this reason, from the standpoint of functional system theory, in the example discussed by R. Hinde, the goal included in the hierarchy and ultimately leading to survival is the intact nest, and behavior is directed expressly toward this goal, rather than the "difference between damaged and intact nest."

With such interpretation of the mechanisms of goal-directed behavior there is in general none of the contradiction mentioned by R. Hinde, since elimination of the hole serves as the more concrete goal of an intermediate behavioral act in the sequence of acts of nest-building behavior.

Thus, the general conclusion of R. Hinde, that the goal approach "should be limited to cases, in which behavior includes reactions to inconsistency between the existing and goal situations" (p 675), cannot be deemed warranted. Inconsistency between the existing and goal situations is demonstrable only as an inadequate result, and it elicits "orienting" behavior which disrupts the ongoing goal-directed behavior. The goal approach is mandatory for all cases of behavior, since there simply are no unpurposeful acts in the animal's prior experience.

The other objections are probably based on pure misunderstandings. For example, R. Hinde writes: "It is important to stress here that behavior may be goal-directed on one level of integration and not on another. At the early stages of nest-building behavior, the typical movements of the weaver are directed and coordinated so as to obtain a finished "stitch," but these stitches are not directed so as to lead to building the nest. The lowest levels are probably goal-directed, but behavior is not directed toward completing building of the nest" (pp 672-673). R. Hinde does not explain which mechanisms are involved in appearance of individual goals--"stitches," and how precisely a nest and not something else is created in integral nest-building behavior.

From the standpoint of functional system theory, any concrete goal may be formed exclusively as concretization of a more general goal and ultimately the main goal of survival, which is an inalienable property of everything living.

We should also mention the instances of obviously useless and "senseless" animal behavior under inadequate environmental conditions as a frequently raised objection to goal-directed behavior. Such behavior is inherent even in mammals, For example, a fox or sled dog "buries" uneaten food by scratching a wooden floor with its paws and, of course, does not produce a result (V. Fishel', 1973). In our opinion, these findings are in contradiction to the purposefulness and success of behavior, rather than goal orientation, and they are apparently attributed to the fact that both the goals and actions to reach them can be retrieved only from memory, while the store of memory cannot be adequately used in an inadequate situation. If, however, training is included in such situations, which broadens the store of prior experience, behavior may change radically and become quite purposeful.

As a rule, examples of unpurposeful animal behavior are cited to illustrate its difference from human behavior. However, all elements of human behavior are also extracted from the store of memory, and man's behavior in psychological experiments demonstrating the conservatism of thinking have much in common with the behavior of a fox that is placed in a cage. The experiments of Lachins, for example, offer a striking demonstration of this (see Liper, 1963, pp 301-302).

Our description of the thesis in functional system theory of the goal-orientation of behavior is only a scheme, and does not presume to have offered all of the arguments in favor of goal-directed behavior, let alone complete discussion of the mechanisms of goal-directed behavior. It was necessary only to show that recognition of purposefulness of behavior is not in contradiction to the principle of causation in explaining behavior, but develops it. Indeed, functional system theory considers the immediate cause of action to be a goal, the information model of a future event retrieved from memory. Although the goal serves as a model of the future, it already exists in the form of specific nervous activity even prior to action and, consequently, has the main property of a cause: it precedes its effect, i.e., action. It also has another property of a cause: it consistently induces its effects--actions, which were related in the past with reaching it.

At the same time, functional system theory discloses the causes and mechanisms of goal formation proper. The goal emerges as a consistent consequence of processes of choice and formation from all elements in memory of the model of only one event required for survival, and this choice is made under the influence of both endogenous (motivation) and exogenous (situation) factors. The trigger stimulus is considered to be the result of prior behavior and one of the exogenous factors of choosing the goal. For expressly this reason, the link between a stimulus and action that follows it is stochastic, and the occurrence of the same action following the same stimulus is merely a special case.

Thus, functional system theory removes the seemingly unresolved contradiction between the principles of causation and goal orientation in explaining behavior.

Appearance of the result, i.e., a new event in the environment, leads to a situation of conformity between the result of action and "acceptor of result of action," thereby indicating the end of one cycle of exchange in orderliness between the organism and the environment, and the start of the next one.

Isolation of the Behavioral Act in the Continuum of Behavior

In order to investigate the neurophysiological mechanisms of systemic processes in the behavioral act, it is absolutely mandatory to be able to isolate the behavioral act in the continuum of behavior.

In the reflex interpretation of behavior, it is assumed that any behavior is made up of different reflexes. The unit of behavior is a single reaction to a single stimulus. R. Chauvin calls this the "atomistic" approach and observes that reactions "are never isolated; separation thereof leads to impossibility of any interpretation of either these reactions or behavior as a whole. For ethologists, the concept of reflex in the narrow sense is, we are not afraid to state, senseless" (1972, p 11). Successive behavior in the reflex interpretation is viewed as a "chain reflex," i.e., a successive series of reactions to corresponding stimuli, which appeared as a result of prior actions. P. Milner observes that "in many reactions, the same movement is performed several times, but in each instance it is followed by different movement; then the problem arises as to how two different movements can be induced by the conditioned reflex mechanism, by the same feedback signal. Of course, we can follow several routes to bypass this difficulty, but the simple basic theory does not hold up under the burden of the required additions and changes" (1973, p 121).

Because of the methodological convenience of delivering stimuli and recording reactions, the usual artificial sequence of events in physiological experiments (stimulation, delay, change in observed parameter) was taken as the natural course of events. One can indeed detect such a sequence in preparations (anesthetized animals, with severing of the brain and spinal cord, or with the use of curare), i.e., in cases where we are dealing with "machine-like" factors and there is no adaptive behavior.

In a waking animal, the concepts of "stimulus" and "reaction" do not enable us to unequivocally isolate a behavioral act. The presence of behavioral acts without obvious exogenous stimuli ("false starts," "motivational reflexes," "intersignal reactions," "reactions to time," etc.) indicates that the processes determining action appear long before the stimulus, and this complicates significantly determination of the actual moment that the processes referable to a given behavioral act begin. As for the "reaction," this is not so much a reference to some definite, qualitative reality of behavior, as it is a synonym for the philosophical category of "effect," which is meaningless apart from its relation to the stimulus. In some studies of behavior, electromyographic activity or some autonomic parameters or other are taken as the reaction, in others movement of some part of the body, in others yet, an event such as making contact by means of a telegraph key, etc.

Thus, the concepts of "stimulus" and "reaction" are philosophical, and they may include any changes in the environment (stimuli) and any changes in the organism that follow the stimulus (reactions). This diffuseness of the concepts of stimulus and reaction does not permit isolation of expressly one behavioral act. Indeed, to describe elements of behavior one must resort to such terms as, for example, "swallowing reaction," "running reaction," etc. On the one hand, they reflect the methodological principle of mechanistic determinism, according to which the behavioral act is a "reaction"; on the other hand, isolation of the behavioral act is accomplished with actual disregard of this principle.

Indeed, "the run" characterizes a segment of behavior only from its phenomenological aspect, regardless of whether some stimulus is present. Introduction of a stimulus still does not lead to unequivocal isolation of a "stimulus-reaction" pair, since one can consider the turn of the animal's head in the direction of the feeder and running toward it, as well as taking feed and salivation, change in respiration and change in cardiac activity, etc., as a reaction to a conditioned alimentary signal, for example. At the same time, the run may be interpreted as the reaction to turning the head and taking feed as a reaction to the run, etc. It is only the proposed "neural link" between specific anatomical structures (for example, between the "eye and salivary gland") that would permit isolation of some reflex, but then a vicious logic circle is formed: for we cannot study the mechanisms of a phenomenon isolated solely on the basis of a hypothetical mechanism.

Thus, there are objections to the reflex approach, which separates behavior into reflexes induced by separate stimuli, not only when compared to the continuum of behavior: isolation of a behavioral act to study the neurophysiological mechanisms of behavior cannot be performed unequivocally when it is considered as a reaction to some stimulus or other, since neither the stimulus nor the reaction can be unequivocally defined in the continuum of behavior.

From the standpoint of functional system theory, an individual behavioral act is directed toward achieving a certain result, and it can be isolated expressly by its result, i.e., by the event that it causes in the environment and to achieve which it is performed. The result has very specific properties and meaning in the functional system, which are isolated according to different criteria (Anokhin, 1968; Serzhantov, 1974). Here, we shall discuss only those of its features, according to which it can be defined by external observation of behavior.

Since we are dealing with behavior which, in the broadest sense, can be defined as the "balance between the organism and environment" (I. P. Pavlov), the first property of the result of expressly a behavioral act is that the result is a specific correlation between the organism and environment, i.e., event. Any behavioral act elicits numerous changes in the environment, which may be indifferent and occasionally even harmful to the organism. In accordance with the terminology of functional system theory, let us call the result of the behavioral act expressly events, i.e., organized aggregates of environmental elements that can be used in behavior. Let us call all incidental changes in the environment the effects; we shall not discuss them in this work. The fact that "events" characterize expressly the correlations between the environment and organism, and that any concrete special goal is included in the hierarchy of goals and, consequently, in the structure of memory or life experience of the organism, automatically render the concept of "result" applicable only to "familiary" organized sets of environmental elements. All so-called meaningful stimuli may be a result: inborn "releasers" or acquired conditioned signals.

Since, according to functional system theory, behavior is goal directed and all actions are determined by the goal, which is "translated" by action into a result, the second decisive property of a result is also the fact that a result is an event that stops actions directed toward reaching it.

Since goals are hierarchically organized in the structure of experience and any exogenous factors become goals only if they bring the organism closer to reaching the goal of survival, in the continuum of behavior, achievement of any result enables the animal to move toward achievement of the next goal. For this reason, the third essential property of a result is that it initiates the next behavioral act, which is determined by the next goal in the hierarchy of goals leading to satisfaction of a concrete motivation and achievement of the goal to survive. For expressly this reason, a stimulus, i.e., result of prior behavior, is only a trigger of subsequent behavior, whereas the specifics of the latter are determined by the model of a future event, i.e., goal.

These three properties of a result enable us to define, quite unequivocally, some of the results of behavior and, consequently, to single out individual acts in the continuum of behavior. In our opinion, this idea was very well expressed by V. F. Serzhantov: "A performed functional act that ends with a specific result causes the organism to move to other similar acts. Thus, each separate act is qualitatively circumscribed in time, being separated from both preceding and subsequent phenomena of vital functions. As life moves from one result to another, there is distinctive expression of its rhythms on the level of the organism" (1974, p 73).

Thus, according to functional system theory, the behavioral act can be isolated as a segment of the behavioral continuum from one result to another.

These acts, which take place successively in time, do not form a "chain," but an hierarchy, since the goals are hierarchically organized in accordance with the general goal of "survival" and any result turns out to be made up of more concrete results, and itself is part of a more general result. In the above example of behavior, occurring after use of a conditioned alimentary signal, the portion of food serves as a rather major result, to the achievement of which all of the behavior discussed is directed. It is achieved, in turn, through the successive achievement of more special results, which refer both to the change in situation when the head is turned and change in position of the animal in space as it runs.

At the same time, the portion of food serves only as a special result of behavior directed toward satisfying the hunger motivation. Description of the real hierarchy of goals would require knowledge about the entire subjective life experience of the animal; however, as an example, we can confine ourselves to listing only some of the obvious events included in the hierarchy of goals and results: "to be satiated"--"to eat a portion of foot"--"to be near the feeder"--"to see the feeder"--"to receive the conditioned signal." The goal "to eat a portion of food" contains all of the preceding goals and is itself contained as an element of the system with the more general goal "to be satiated."

According to this arbitrary hypothetical hierarchy, the result (for example, "to be near the feeder") is reached by all prior behavior, including turning the head, which leads to a special result, "to see the feeder."

Thus, by introducing the conception of hierarchic organization of goals in the structure of the organism's experience, functional system theory makes it possible to isolate a behavioral act no matter how minute, in accordance with the result it achieves, without removing it from the continuum of behavior and without breaking behavior down into separate "atoms."

At the same time, functional system theory permits retention of all the methodological conveniences of delivering stimuli and recording reactions. Indeed, in the case of integral behavior, a stimulus is, from the standpoint of functional system theory, the result of prior behavior, since it even has all of its external features: it is familiar, it stops activity preceding it and causes the action to start that is determined by the next goal in the structure of experience on the road toward satisfaction of motivation.

It is not the next, but prior behavior, which led to appearance of a stimulus, that is informationally related to this stimulus, which exists beforehand as a goal, in the form of a certain "anticipatory reflection" (Anokhin, 1962). All those who work with animals by the conditioned reflex method know that dogs literally require a conditioned signal facing the experimenter and barking. Training alters this behavior, since "stimulus-result" are attainable by means of "passive anticipation," which the experimenter specially develops by reinforcement with a conditioned "calm background" signal.

As we have already stated, a stimulus serves only as one of the guidelines of future behavior, which permits the selection of one goal out of the many possible ones according to motivation and situation, by means of a model thereof in the structure of experience. Since this goal can be reached by different means, depending on other conditions, for example, initial position, it is understandable that different actions may follow the same "stimulus."

Since, by virtue of the complexity of organization of experience, the same goal can be selected under various exogenous conditions, it is understandable that action may be performed in the absence of a given stimulus, whereas other conditions make it possible to reach this goal (evaluation of this possibility by the animal may also be wrong). The distinct appearance of the same action following the same stimulus is a special case of goal-directed behavior, when a constant goal in a specific situation can be reached by the same means and only in the presence of the same prior "result--stimulus."

This situation is the most convenient for the study of neurophysiological mechanisms of systemic processes, since in the case of a constant stimulus--result of prior action and stimulus--result of next action it is easy to isolate the interval between the two results, in which all of activity is directed toward reaching only one goal, i.e., we can isolate a single behavioral act.

Organization of Physiological Functions in the Behavioral Act

Functional system theory also alters conceptions of organization of different physiological functions in behavior, in accordance with conceptions of determination of behavior by the goal.

In physiology, the concept of "function" was related to a specific structure for a long time. A reflection of this approach is seen in such concepts as "spinal functions," "cortical functions," "functions of the liver" or "salivary gland." At the present time, the limitation of such an approach for analysis of integral activity of the organism is obvious (Anokhin, 1940; Luriya, 1962; Menitskiy, 1975, and others).

Conceptions of reflex mechanisms of behavior were closely linked with conceptions of reflex mechanisms of different physiological functions, down to the functions of a single neuron. Synthesis of "little" reflexes could not yield anything but a "big" reflex: "... some receptor nerve unit is hit by some agent of the outside world or inner world of the organism. This hit is transformed into a neural process, into the phenomenon of neural excitation. Excitation travels over nerve fibers, as if they were wires, to the central nervous system and from there, by virtue of established links, over other wires to the functional organ, in turn changing into a specific process in the cells of this organ. Thus, any agent consistently is related to some activity of the organism, like cause and effect" (Pavlov, 1949, p 553).

Although this conception of the reflex has occasionally been labeled as oversimplified or even "caricatured," it has not become enriched by any basic changes in the last 70 years. As validly observed by D. N. Menitskiy, "in spite of the enormous advances of natural sciences and modern technology, as well as psychology and neurophysiology, the basic tenets of conditioned reflex theory remained without appreciable change until recent years.... The categorial structure, i.e., set of problems, principles and concepts of the classical direction of physiology of higher nervous activity remained the same" (1975, p 71).

Nor could these conceptions change, remaining reflex-oriented, since the above quotation of I. P. Pavlov serves as an excellent definition of the physiological concept of "reflex," reflecting real physiological processes in spinal preparations and anesthetized animals. We believe that authors who object to this definition of reflex do not actually uphold successively reflex positions to interpret integral behavior, and they put some other content into the distinct physiological concept of "reflex."

The conceptions of reflex mechanisms of physiological functions were based on factual data, which continue to be submitted to this day. They appear absolutely reliable with the use of modern investigative methods. For example, the arcs of spinal reflexes can presently be described with exhaustive accuracy and thoroughness (Eccles, 1959; Kostyuk, 1971). However, all these data were obtained esclusively on preparations (spinal, pretrigeminal, anesthesia, muscle relaxants, etc.), i.e., expressly in states that preclude goal-directed behavior.

This circumstance, i.e., demonstration of reflexes in the absence of integral behavior, was noted by I. P. Pavlov as far back as 1904, at the very inception of conditioned reflex theory: "... amazingly, after transection of all sensory nerves of the tongue, most substances that reach the mouth when eating or forced in lead to absolutely the same salivation as before they were severed. One has to resort to more radical measures, to give a toxic agent to the animal, remove the higher branches of the central nervous system, to become convinced of the fact that there is not only a mental, but purely physiological link between substances that stimulate the mouth and the salivary glands" (1949, p 348). This link is also demonstrable in clinically important reflexes.

In states that preclude goal-directed behavior, the effects of stimulation do indeed appear "automatically" ["machine-like"], since they are caused by stable and in essence "dead" morphology, although it is purposeful, which the experimenter actuates with stimulation. Under such conditions, stimulation does indeed serve as the cause of all processes occurring in the preparation. The assumption that the animal uses certain morphological elements in behavior just as they are used by the experiment in a preparation was accepted without proof, since there simply was no methodological possibility, for a long time, to examine the activity of the nervous system in behavior.

In the case of integral behavior, in the presence of "spontaneous" nervous system activity, even the primary nature of afferent processes in relation to efferent ones is found to be related to interpretation of the behavioral act as a reaction to a stimulus. The constant flows of impulses in both directions make it possible to consider either direction as the first (Bernshteyn, 1966) or render such a choice generally impossible, since one cannot single out the moment when there would be only afferent or only efferent activity. The fact that behavior is a continuum of constant cyclic correlations between the organism and the environment relegates the question of which is first, afferentation or efferentation, to problems of the "egg and chicken" type.

The conception of action as efferent activity and specific processes in "functional organ" cells appears to be just as unjustified. As repeatedly stressed by P. K. Anokhin, "the conception that any exogenous stimulus can produce a 'reflex on a muscle,' 'reflex on a gland' or 'reflex on the heart' is more an expression of the technique used to evaluate reactions than of our knowledge about the mechanisms of reactions" (1975, p 148). Even as a phenomenon, the behavioral act exists when and only when there is organization of various processes into a single whole. P. K.

Anokhin observed that only the deepest bias could enable one to see reflexes in the behavioral act. "Consider a kitten," he wrote," that performs rhythmic scratching movements to remove some irritant from the ear. This is not only a commonplace 'scratching reflex,' this is consolidation, in the true meaning of the word, of all parts of the system for a result. Indeed, it is not only the paw that extends toward the head, in this case, i.e., to the point of irritation, but the head extends toward the paw. The cervical muscles on the irritated side are selectively tense, as a result of which the entire head is bent toward the paw. The trunk is also curved in such a manner as to make free manipulations with the paw easier. And even the three paws that are not directly involved in scratching are so placed as to assure the success of scratching, from the standpoint of position of the body and center of gravity. As we see, the entire body is turned toward the focus of the result; consequently, not a single muscle of the body remains uninvolved in reaching a useful result. We are dealing, in the true sense of the word, with a system of relations that is entirely subordinated to the achievement of a result that is useful to the organism at a given time" (1975, p 3..5).

This integration of activities of anatomically different structures and subordination of any physiological process contained in the behavioral act to the general result rules out the possibility of performing any physiological function included in behavior as an independent "reaction" to some separate factor, and this can be observed on preparations. It is only organization as a whole that determines the form of activity of each structure, and "the components referable to some anatomical system or other are mobilized and involved in the system only to the extent that they aid in obtaining the programmed result" (Anokhin, 1973a, p 35).

Functional system theory makes it possible to extend the concept of purposefulness to all levels of organization of physiological functions, which leads to a revision of the content of the concept of function itself. According to functional system theory, goal-directed behavior of the entire organism is organized from also goal-directed activities of its elements, and the result of the entire integral behavior is achieved by reaching the more elementary special results. Consequently, it is possible to make any division of activity of the integral organism into parts, i.e., into separate functions, only in accordance with the hierarchy of the results. Achievement of some result in the organism is a function, i.e., part of the general [overall] work, while the organized aggregate of activities leading to attainment of this result is a functional system. "We interpret functional system as a combination of processes and mechanisms which, being formed dynamically in accordance with a given situation, necessarily leads to an ultimate adaptive effect that is beneficial to the organism in this very situation" (Anokhin, 1962b, p 77).

From this systemic thesis, not only any function is multistructural, but any structure is multifunctional, since it is not one function, but all those that could take place with the use of this structure that are fixed in the structural distinctions. For example, such a result as moistening food in the mouth is achieved by an entire functional system, including the activity of many neural, muscular, vascular, glandular and other morphological elements.

At the same time, the same process of salivation and activity of the same structure, the salivary gland (for example, in the dog), can be used to achieve different results: not only to moisten food and submit it to primary enzymatic treatment, but for heat regulation, licking a wound, etc.

One could use the term "function of structure" to designate all these functions, since the entire set of functions, in which the salivary gland can be used in general, with only part of these possibilities being used in each individual functional system, is fixed in the structural distinctions of the salivary gland.

Thus, according to functional system theory, all functions contained in the functional system of the integral behavioral act are, in turn, organized as functional systems of a lower order of complexity.

Functional systems on different hierarchic levels were analyzed in detail in the school of P. K. Anokhin. For example, many studies dealt with functional systems of regulation of respiration (Golubeva, 1971; Polyantsev, 1969; Yumatov, 1976), position (Shumilina, 1949; Agayan, 1970), arterial pressure (Anokhin, 1947; Shumilina, 1961), autonomic elements of behavior (Shidlovskiy, 1969), integral food-obtaining behavior (Sudakov, 1971; Shuleykina, 1971; Khayutin and Dmitriyeva, 1976) and many others, as can be seen, if only from the bibliography compiled by D. G. Shevchenko (1972).

Functional systems on the lowest level of complexity are functional elements of more complex functional systems. The behavioral act is performed as the immense hierarchy of functional systems on different levels of complexity: "Of course, the correlation between actin and actomyosin constitutes a well-circumscribed functional system, with regard to its operational architectonics, which ends with a positive result that can be formulated as the contraction of a muscular fibril. But such a functional system is merely an intermediate system between even finer molecular correlations of muscle cell protoplasm and between movement, for example, of a hunter in the forest in search of game, since this movement is also ultimately performed by means of actin and actomyosin. How wide the range is, which contains numerous functional systems making up this immense hierarchy of systems!" (Anokhin, 1973a, p 37).

An enromous number of various means of organizing elements is possible in this hierarchy. However, it does not contain all possible combinations, and is limited only to inborn and acquired integrations, since the very formation of some organization or other in philogenesis or through learning is possible only under the system-forming influence of the result, and it is already the "purposefulness" of the morphological structure of the organism that reflects the restriction of "degrees of freedom" of different combinations. Still, even the variants of organization, which had, in principle, at some time led to an adaptive result on some level of complexity or other and therefore were fixed in the inborn or acquired experience of the organism, are present in sufficient number to make the necessary selection and organization of elements on each hierarchic level to reach an individual result.

Thus, from the standpoint of functional system theory, performance of any function is related to organization of specific activities, rather than activity or a substrate per se. This link was determined already in the course of inception of life. Since the main goal of biological systems, to survive, is actually the goal of preserving integrity and organization of metabolic processes, the entire hierarchy of goals of highly organized animals is a hierarchy of organization of physiological processes ultimately leading to preservation of integrity and organization of metabolism within the entire organism. And only those of the more elementary functional systems, the results of which form the result of a larger system, are involved in some large functional system. Thus, the interrelations of elements in the system are subordinated to the result of the entire system. "The term 'system' can be used only for a set of selectively involved elements, in which interaction and interrelations acquire the nature of interaction of elements to achieve a focused useful result" (Anokhin, 1975, p 37).

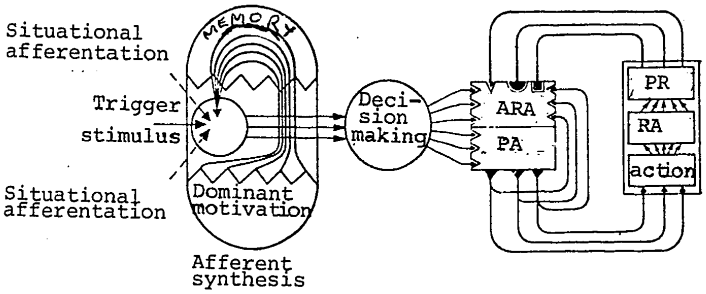
Consequently, the neurophysiological study of systemic processes in the behavioral act is the study of processes of organization in behavior of the activities of separate brain structures and separate neurons.

Operational Architectonics of the Functional System in an Elementary Behavioral Act

The orderliness of the environment, both present and past, which makes up the memory of an organism, is used to put in order the relations between elements in the functional system of a single behavioral act. The correlation between this order of environmental elements and processes of organization of elements of the organism is implemented through the operational architectonics of the functional system of a behavioral act. According to the theory of P. K. Anokhin, the structure, or operational architectonics, of a functional system of any degree of complexity is comprised of systemic mechanisms, or stages, of afferent synthesis and decision making, and then the acceptor of results or goals of action and action program; performance of action; achievement of results and comparison of feedback from the parameters of the results to the acceptor of action results (Figure 2).

In an elementary behavioral act, these systemic processes, i.e., processes of interrelation between current and past information, and organization of the system, are directly superimposed over the time structure of the behavioral act, and they can be precisely determined in time. There are various systemic processes involved in a behavioral act, singled out as a segment of the behavioral continuum from one result to another, at different phases of its development: afferent synthesis and decision making become involved between the result of the preceding act and start of actuating mechanisms of the next one; the start of the actuating mechanisms of a behavioral act already coincides with implementation of the program of action and acceptor of results of action, while achievement of the result marks the time of occurrence of feedback and comparison thereof to the acceptor of results of action (Anokhin, 1973b).

All these processes, or stages, of organization of elements into a system exist in functional systems of all levels of complexity; however, they present a number of distinctive features in an integral behavioral act, which are related to the fact that behavior "equilibrates" expressly the entire organism with the object-related [objective] environment.



Key: ARA) acceptor of action result
PA) program of action
PR) parameters of result
RA) result of action

Figure 2. Operational architectonics of a functional system after P. K. Anokhin (1973a)

Even the first living systems were open (Anokhin, 1975, p 333) and included interaction with the environment. The result, in this sense, is part of the system brought out into the environment, or part of the environment contained in the system. Organization of the system can be maintained only by means of organization of the environment (Ferster, 1964), and the very first living things had to utilize "negentropy" from the environment (Schroedinger, 1947). For this reason, the results on the level of biochemical systems were specific chemical substances, organization of the relations of which was used to maintain metabolism. On the level of highly organized organisms, an event in the environment that became a result could also consist of only a specific organization of the environment. This organization of the environment, or information flowing and already fixed in memory, ultimately determines the selection and organization of elements and physiological processes on all levels of complexity in the functional system of the integral behavioral act.

In order to form an hierarchy, the "operational architectonics" of systemic processes must be basically invariant on all hierarchic levels of the systems (Anokhin, 1973a). The functional system of the integral behavioral act is made up of subsystems on the physiological level, each of which undergoes a stage of afferent synthesis and decision making, and includes its own acceptor of results of action and program of action. Of course, on the level of physiological subsystems, all these processes take less time than processes of organization of the entire system of the behavioral act. This is related both to the lower volume of elements in physiological systems and partial morphological fixing of some organizations "refined" in phylogenesis or ontogenesis.

At the same time, an individual behavioral act is always only one of the subsystems on the behavioral level in the functional system whose goal is to satisfy motivation, in which each systemic process may involve many elementary behavioral acts. Thus, the functional system of an integral (and, at the same time, elementary) behavioral act must result in an even, i.e., correlation with the environment of the entire organism, and consists of subsystems of only the physiological level, the results of which are certain changes within and without the organism, constituting part of the events, but not correlating the environment and organism as a whole.

We have already noted that, according to functional system theory, the choice of one goal and one behavioral act out of the entire store of memory take place with the involvement of motivation and situation. It actually signifies a choice of an enormous amount of subsystems on all hierarchic levels and organization from them of a specific integration, or even an entire hierarchy of integrations of physiological processes. The purposeful coordination of functions of different elements into an integral system takes place by means of eliminating "superfluous" degrees of freedom from the elements (Anokhin, 1973a, 1974a), related to the possibility of using the same element in different systems.

Since exchange of orderliness between the organism and environment takes place constantly, at any given moment motivation and situation make it possible to implement only a small number (probably about seven) of behavioral acts (Chuprikova, 1978). Motivation and situation reduce the degrees of freedom of all subsystems used in behavior, so that in the presence of one motivation and in a specific situation only limited sets of elements can unite into the functional system of the behavioral act. This preliminary selective organization of elements is what constitutes "preliminary [pretrigger] integration" (Anokhin, 1968). The latter concept is referable to the next act, and in the continuum of behavior preliminary integrations of future behavioral acts are formed and change during current behavior, which is the expression of one of the preceding preliminary integrations.

The process of translation of preliminary integration into a behavioral act, i.e., final elimination of all superfluous degrees of freedom of all subsystems of the physiological level and organization thereof into a single, purposeful functional system of the integral behavioral act, occurs with appearance in the environment of some result of prior behavior, on which depends the choice of a concrete goal and a means of reaching it.

Since there is no information in the environment as to expressly which subsystem organization will lead to satisfaction of motivation, while memory of the organism consists entirely of such information, exogenous information in the course of afferent synthesis and decision making is used expressly for selection from memory of specific information, from which a concrete goal is set (acceptor of results of action), which is reached through a single act and adequate motivation and situation. These processes of organization of elements into a system take up the interval between the result of the preceding behavioral act (stimulus) and start of purposeful action (reaction).

The acceptor of results of action, which appears after decision making, can be theoretically related only to the programs of action that had led to achievement of expressly this result in the past, and this determines the purposefulness of any action. Since actuating mechanisms of the behavioral act are determined by the acceptor of results of action and retrieved from memory, where they are coordinated beforehand, the program of action arises immediately after decision making as an "efferent integral" (Anokhin, 1968).

Reverse organization of system elements into a new order of environmental elements occurs already by means of the systemic process of action, when the organized work of actuating physiological subsystems is performed and real results of integral behavior are achieved. Action is now manifested as the coordinated function of selected subsystems, and until the result is achieved coordination occurs only on the subsystem level, whereas the correlations between the integral organism and organization of the environment are predetermined until the next result is achieved. Upon completion of action and achievement of results, information about the parameters of the real results is compared to the information of the acceptor of results of action and, in the event they coincide, the organism is able to move to the next purposeful behavioral act on the road toward satisfying motivation; whereas in the case of noncoincidence, this induces a universal orienting-exploring behavioral act.

Thus, the integral elementary behavioral act is an elementary cycle of correlating organization of the integral organism to the objective environment. We can examine this cycle starting, for example, with action: action leads to a result, i.e., specific organization of elements of the environment which, along with motivation and situation, is used to organize elements of the organism in processes of afferent synthesis and decision making; the organization formed after decision making conforms with the acceptor of results of action and related program of action. "... Decision making is a transitional factor, after which all combinations of stimulai acquire an actuating, efferent nature ... immediately after making a decision there is formation of the integral of efferent stimuli, which must first implement a peripheral action and then achievement of the results of action. There is a precise, i.e., equivalent, informational link between all these stages of formation of the act proper.... If we were to examine the results of action as consequences of organized centrifugal flows of stimuli, these deterministic relations can be continued further, in the direction of information about the results obtained" (Anokhin, 1968, p 233).

Now that we have discussed this elementary cycle in terms of systemic processes, we can undertake the neurophysiological study of systemic processes of the elementary behavioral act.

Our objective should be to try to disclose the neurophysiological content of such systemic processes as afferent synthesis and decision making, acceptor of results of action and program of action. All these concepts are related to the concepts of "organization" and "information," which cannot be unequivocally defined at the present time (see, for example, Abramova, 1976; Kremyanskiy, 1976).

Perhaps, as the relevant neurophysiological data are accumulated, it will be possible to define these concepts both in philosophical and cybernetic terms. However, this will require that the systemic principle be the guiding one in neurophysiological studies of behavior. When it is disregarded, a situation is formed in neurophysiology that is quite vividly described by G. Somyen: "... when it is a matter of the central nervous system, we are rich in facts but poor in theory. Data are accumulating with incredible speed, but they form an amorphous mass, rather than an organized structure. Advancement is inevitably retarded and the route becomes confused whenever there is an abundance of facts but not enough guiding principles (1975, p 235).

We should like to end this chapter and, at the same time, give warning in the words of K. Lashley: "The point of view of nervous activity described here apparently does not give us the simple and clear explanations that are possible if we recognize the reflex hypothesis. But this clarity was attained at the price of distorting the truth, and we prefer to admit our ignorance and be accused of vagueness, instead of shutting our eyes to the most important problems (1933, p 196).

CHAPTER 2. ELECTROPHYSIOLOGICAL CORRELATES OF SYSTEMIC PROCESSES IN THE ELEMENTARY BEHAVIORAL ACT

Electrical Activity of the Brain in Behavior

Electrical activity of different brain structures and neurons is the most accessible and widely used parameter of processes occurring in the central nervous system in performing behavior. Since the functional system of the goal-directed behavioral act is formed by the coordinated activity of many structures and neurons, it is equally important to neurophysiological studies of systemic processes to determine the time characteristics of neurophysiological processes in each separate structure or neuron and the correlation between these processes.

Of course, the systemic significance of time and space characteristics of electrical activity of different brain structures can be disclosed by comparing them to the time intervals of the behavioral act and systemic processes occurring in these intervals.

As we have already noted, there must be general systemic processes of afferent synthesis and decision making in the elementary behavioral act, in the interval between the stimulus and start of action, i.e., processes of coordination of activities of many elements on the scale of the entire organism; there must also be general systemic processes of implementation of the acceptor of results and program of action between the start of action to achievement of the result, when activity of the organism as a whole is already coordinated and goal-directed, while coordination processes take place only on the level of physiological subsystems of the integral behavioral act.

Systemic processes can be determined only in time, and they cannot be localized in some structure, since systemic processes are processes of interaction between many constantly functioning afferent and efferent central and peripheral structures that are coordinated in a specific way to achieve a concrete, adaptive result.

At the same time, it is apparent that local processes in separate structures, which perform different functions, must be related to expressly these specific functions. Electrophysiological phenomena are usually compared to specific functions, since they are always recorded in some concrete local structures. For example, with derivation from the visual cortex, all electrophysiological parameters are compared to the properties of visual stimuli and assessed as the correlates of visual information processing, whereas with derivation of potentials from motor structures they are compared to movement and considered as correlates of specific motor functions.

When analyzing the significance of electrophysiological phenomena from the positions of functional system theory, the question arises as to how special and systemic processes are related and to what extent they are reflected in electrophysiological phenomena. This question is also closely linked with the problem of origin of electrophysiological phenomena. Do they reflect processes specific to the morphological structure and relations of a specific structure, or processes of coordination of activities of elements situated in different structures?

If electrophysiological parameters are correlates of processes related to specific structure and physiological functions of specific brain structures, they must be peculiar to each structure. But if electrophysiological indicators are related to systemic processes and reflect coordination of activities of elements "referable to different anatomical systems," these parameters must be similar for different structures, but specific to a specific behavior.

According to current data, the activity recorded with a macroelectrode in some point of the brain represents the sum of many processes occurring in adjacent tissue. Overall electrical activity reflects both synaptic potentials (Jasper, Stefanis, 1965; Frost, Gol, 1966) and dendritic ones (Purpura, 1963; Klee et al., 1965) and, perhaps, glial ones (Roytbak, 1965), as well as circulatory and tissular metabolic processes (Aladzhalova, 1962); and the active elements do not remain constant, so that the overall effects owe their origin to different neurons in different time segments (Elul, 1972).

The complexity of electrogenesis of total activity, which is also increased by anisotropism of brain tissue and presence of dipole relations in oriented structures, does not enable us to relate the characteristics of overall activity to the activity of some specific structural elements of brain tissue. However, total electrical activity of specific brain structures can serve as an indicator of the state of these structures and dynamics of processes in macrostructures.

It is for this purpose that one usually records overall electrical activity of different brain structures in relation to behavior. At the present time, there are very many works dealing with analysis of the EEG of activity in behavior. As noted by V. I. Gusel'nikov, at the first stage "there was a great desire to see, in the dynamics of the overall EEG, a reflection of the classical conceptions of the main patterns of brain function, which led at best to repetition of the general schemes already proposed for them by I. P. Pavlov" (1976, p 8).

However, already visual evaluation of overall activity according to the change in frequency and amplitude of oscillations made it possible to determine that during performance of behavioral acts, in response to a conditioned signal, activation is observed in many structures of the brain (Gasteau, Roget, 1962), and there is selective involvement in activation of various structures with various forms of behavior (Shumilina, 1959, 1961b). These facts already warranted reference to systemic organization of processes in the brain during performance of behavioral acts (Shumilina, 1965; Naumova, 1968).

With the appearance of a possibility to assess more precisely the frequency and time characteristics of overall activity, it was found that the oscillations of potentials become synchronous in various structures during behavioral acts (Livanov, 1962, 1972). Synchrony is also observed in selectively related structures, rather than all of them (Anokhin et al., 1973), and the set thereof changes with change in form of behavior (Ioshii et al., 1969).

Special experiments conducted in the laboratory of M. N. Livanov (1972) revealed that synchronous activation of different structures is closely linked with behavior. On the one hand, a correlation was established between the probability of movement of a rabbit in response to a flash and level of spatial synchronization of the cortical EEG (Luchkova, 1971); on the other hand, there was a link between spontaneous movements and level of EEG synchronization (Trush, Korol'kova, 1974). A correlation was also established between human reaction time and level of spatial synchronization of cortical activity (Vasil'yev, Trush, 1975).

Thus, studies of overall electrical activity revealed that, in performing behavior, there is activation of an entire system of structure, the composition of which depends on the form of behavior; electrical processes are synchronous in many structures; synchronization of processes is referable to a specific set of structures, and it is necessary to behavior.

All these data already indicate that, in behavior, cerebral processes have systemic, rather than linear, organization. However, the EEG describes processes occurring in a particular structure in only the most general features; moreover, evaluation of changes in the overall EEG requires rather long time segments, and changes in the overall EEG may be referable to large segments of the behavioral continuum.

Separate oscillations of overall electrical activity, which are referred to as "evoked potentials" (EP), "generated potentials," "premotor potentials," "motor potentials," as well as "wave of anticipation" or "conditioned negativeness," in relation to exogenous events or movements, are more suitable for comparison to systemic mechanisms of the elementary behavioral act.

Like overall activity, EP constitute a complex phenomenon reflecting the state of many different elements at the point of derivation. The configuration of EP recorded in a given point probably also depends on both synaptic (Purpura, 1963) and dendritic (Kullanda, 1964) potentials, and perhaps glial ones as well (Roytbak, 1965), and the location of the macroelectrode in relation to orientation of dipoles also plays a role in polarity and amplitude of components (Gusel'nikov, 1976). EP are used in behavioral experiments and clinical examinations as a parameter of the dynamics of rather rapid processes in local points of derivation.

Synchronism and Similarity of Configuration of EP of Various Structures in Behavior

For a long time, EP were studied on animals anesthetized with barbiturates. Under such conditions, the oscillations of potential in response to afferent stimulation were recorded from relatively local "focuses of maximum activity," and they were stable in amplitude and configuration (Chang, 1959). This circumstance caused wide use of the EP phenomenon in studies of the morphology of relations in the central nervous system and publication of numerous studies dealing with a search for the pathways and structures through which particular oscillations are "conducted." Reflex or "commutator" conceptions of the mechanisms of behavior determined the same approach to the study of EP in integral behavior as well. However, already the use of chloralose (Buser et al., 1959) and muscle relaxants (Buser, Borenstein, 1959) revealed that, in response to the same stimulus, EP can be demonstrated in many structures of the brain, while responses to different stimuli can be recorded in the same structure.

EP were found to be very generalized (Kogan, 1965; Shul'ga, 1965) and unstable in both localization and configuration in waking animals and man, which made it necessary to use the averaging procedure. Destruction of different brain structures in waking animals did not eliminate EP in others (Chow et al., 1966; Cohn, 1969), while the observed EP changes were brief and could not be unequivocally explained (Cherkes, Lukhanina, 1972). Nevertheless, debates continue concerning the links between EP components and conduction of afferent excitation over some "projection" and "nonspecific" pathways or other.

Already in the early studies involving recording of EP in response to stimuli requiring a behavioral reaction it was found that there is very early oscillation of potentials in cortical regions that were unrelated to the stimulated analyzer (Artem'yev, 1956, 1959). All researchers working on development of conditioned reflexes observed a phase of generalization, when EP were demonstrable in virtually all leads (Shumilina, 1965; Naumova, 1968). E. R. John and his coworkers compared, in an entire series of experiments, the time parameters and configuration of EP in many different brain structures, and demonstrated in many of them synchronous EP, similar in configuration, in response to a stimulus that induced behavior (John, 1969; John, 1972). In these studies, a comparison was made of configuration of EP averaged for many deliveries of a stimulus, which permitted elimination of EP instability in any structure, which is common in waking animals. Analysis of the activity of neuronal "ensembles," recorded with the same "quasimicroelectrodes" used for EP revealed that impulse activity of neurons of many anatomically and functionally different structures was similarly organized in time when submitted to statistical evaluation (John, Morgades, 1969). These data served as one of the bases for "statistical configuration theory" (John, 1973).

The synchronism and similarity of EP configurations in response to a stimulus that evokes behavior do not extend to all structures of the brain. In addition to the fact that EP are specific in configuration and distribution for different behavioral acts (for example, food-searching and defense behavior), they are also variable and individual for each animal (Myshkin et al., 1968). The question of individuality of EP has been best studied in man. It was demonstrated, for example that, other conditions being equal, EP of twins have marked similarity (Dustman, Beck, 1965); some of the individual characteristics of EP are beginning to be used in differential psychophysiology (Rutman, 1974; Rusalov, 1974, 1975).

All of these distinctive features of EP do not make it possible to introduce a nomenclature of EP components that would apply equally to all conditions (Rutman, 1974) or to outline the typical topography of their derivation. Under some conditions, marked EP may be recorded even from "extracranial" structures (Prichard et al., 1965), under others they are depressed and not demonstrable at all (Coquery et al., 1972).

In our laboratory, we also observed synchronism of EP in different brain structures in response to a flash of light, in the case where the flash triggered the rabbit's run to the feeder.

Experiments were conducted (with S. S. Trofimov) on five rabbits in a special chamber (Figure 3). A flash of light from the flash lamp of a Soneclat stimulator (0.3 J, 50 μs) was delivered from the ceiling of the chamber (70 cm above the floor). There was a 1-s interval between the flash and automatic delivery of a feeder with 10-30 g of cabbage or carrots.

The EEG of the right and left visual, right and left sensorimotor, right auditory cortex, hippocampus, hypothalamus and reticular formation of the mesencephalon was derived monopolarly by means of implanted electrodes. The silent electrode was placed over the frontal sinus. A Polygraph-XVII, with concurrent recording on a Magnetor XIV, was used to record the EEG, as well as EMG of cervical muscles and relevant marks. The bandpass constituted 0.3-200 Hz for the EEG channels. The EP were averaged by reproducing the tape for 25 runs on an NTA-512B analyzer (bandwidth 2 ms, period ["epoch"] of analysis 512 ms or 1024 ms).

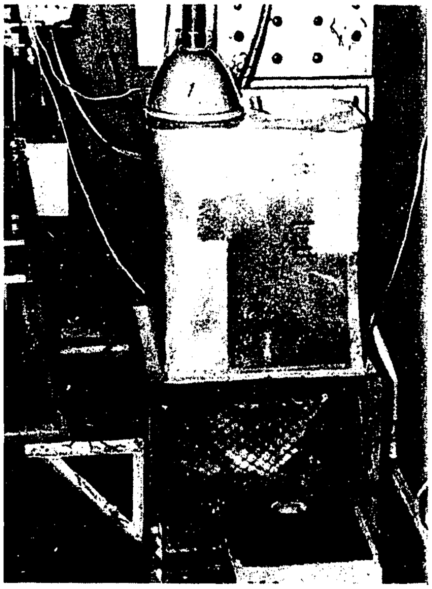


Figure 3. General view of experimental chamber

1) flash lamp
2) feeder with automatic delivery of 10-20 g cabbage
3) contacts

Figure 4 illustrates the tracing of total electrical activity of different regions of the brain in a single behavioral act. It was demonstrated that EMG activity marking the start of functioning of actuating mechanisms appears on the rear front of the negative component of EP. On the left are averaged evoked potentials (AEP) in different structures of the brain corresponding to 25 such acts.

Figures 5 and 6 illustrate AEP of different regions of the brain in response to a light, which triggers orienting-exploring behavior in one situation (a) and purposeful movement toward the feeder in another (b) for two different rabbits (in Figure 5, the tracings were obtained for rabbit No 2 and in Figure 6, for rabbit No 4). These same figures illustrate histograms of latency periods of EMG activation during the corresponding acts.

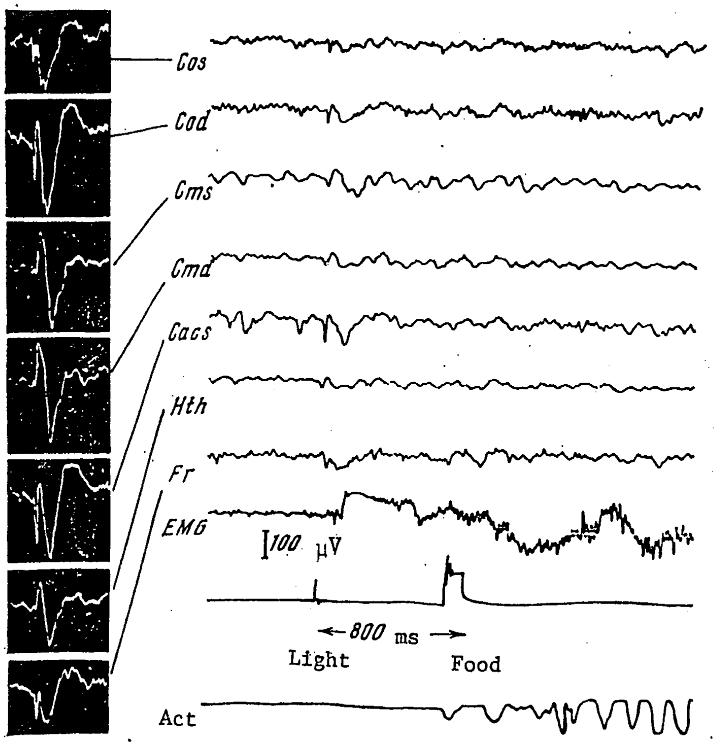


Figure 4. Rabbit EEG during elementary behavioral act: In response to the flash of light, the rabbit heads for the feeder, in which carrots appear after 800 ms. Top to bottom, leads: left and right visual cortex, left and right motor, left auditory cortex, hypothalamus, reticular formation of the mesencephalon, EMG of cervical muscles, stimulation marks, actogram (shows rabbit nearing the feeder)

Analysis of these tracings revealed that when the flash of light triggered food-obtaining behavior, AEP are synchronous and similar in configuration in several structures of the brain; for example, in Figure 5b, there are very similar AEP in the sensorimotor and auditory cortex, and in Figure 6b, this applies to the right visual and sensorimotor cortex, as well as reticular formation and hippocampus. If the similarity is assessed solely according to time organization of processes without consideration of amplitude of different elements and the initial level of constant potential, we can consider AEP to be similar in all leads, with the exception of the hippocampus, in rabbit No 2 (Figure 5b), and in all leads with the exception of the hypothalamus and left visual cortex in rabbit No 4 (Figure 6b). The difference in amplitude of different AEP components could be related to the location of electrodes in relation to active tissular elements and different conditions of derivation of electrical activity for differently localized electrodes.

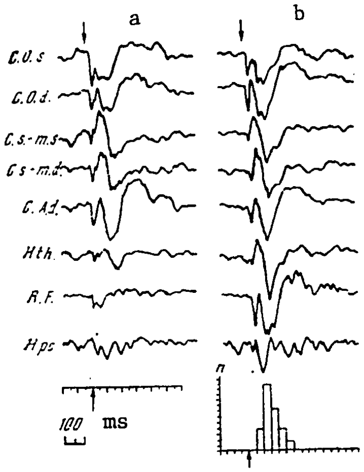


Figure 5.
Averaged evoked potentials in response to flash of light triggering orienting behavior (a) and running toward feeder (b) in rabbit No 2.

The time of the flash is shown by the arrow. Leads, top to bottom: left and right visual cortex, left and right sensorimotor cortex, right auditory cortex, hypothalamus, reticular formation, hippocampus. At the bottom of (b): histogram of distribution of latency periods of EMG of cervical muscles in 25 averaged combinations.

In some structures, AEP have opposite polarity of all or some components. This renders the AEP in such structures as the hippocampus in rabbit No2 and hypothalamus in rabbit No 4 dissimilar to AEP of other derivations; but if we judge only the dynamics of processes and consider that the amplitude and sign of components in each given structure are related to the location of electrodes in relation to active elements of brain tissue, on the basis of AEP configuration, we can conclude that in these structures also the dynamics of the processes have similar organization in time.

Thus, during a behavioral act, the processes in some functionally and morphologically different brain structures are synchronous and present similar time organization.

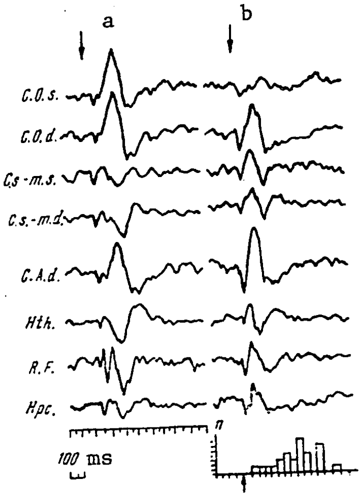


Figure 6.
Averaged evoked potentials for rabbit No 4. Designations are the same as in Figure 5.

Getting somewhat ahead of our presentation, let us mention that we obtained the same results in experiments with defense behavior, and with recording of activity of individual neurons in different parts of the brain during behavior.

We believe that the same time organization of processes in functionally and morphologically different structures, such as, for example, the visual and sensorimotor cortex, precludes interpretation of AEP as correlates of coding of some specific information, in this case visual. Since physiological functions of different structures evidently remain different in behavior, it must be accepted that common features of organization of activity are created by processes that are common to many structures, and they occur only during behavior, but not under anesthesia, when EP are recorded in limited points. The synchronism and similarity of organization of processes in different structures also rules out the possibility of "conduction of oscillations" from one structure to another, and description of processes whose correlates are EP in terms of "conduction pathways" is generally inadequate.

If we were to compile a general nomenclature of all EP components demonstrable in at least one lead and "synthesize" an artificial "common" EP from them, indicating only the time intervals taken up by specific components, regardless of their sign and amplitude, we could gain an idea about the time organization of processes in all derivations. A comparison of EP in each specific lead to the "common" EP would show us the form of involvement of a specific structure in general processes. And we learn that some structures have a complete set of components: primary positive oscillation followed by great negativity, then positivity and slow negative deviation. In other structures, there is not a complete set of components, but the existing oscillations are synchronous with some components of the "general" [common] EP. This shows that the EP of a separate structure, even if dissimilar in general configuration to EP of other derivations, may reflect involvement of this structure in some phases of the general process.

A comparison of EP in two different behavioral situations, orienting and food-obtaining behavior (Figure 5a and b; Figure 6a and b), indicates that although the configuration of EP in the same structures varies widely, the "general" EP consists of the same main components, each of which spreads differently in structures and is complicated by various subcomponents in different behavioral acts.

The same phenomenon was demonstrated when a comparison was made of EP of different rabbits with the same behavior (Figures 5 and 6): the distribution, configuration and even polarity of different components could be quite different; however, the four-component structure of the "general" EP is apparently mandatory. We observed this four-component EP structure in virtually all of our experiments, and we shall adhere to the following nomenclature of these components hereafter: primary, negativity and late positivity, which may be followed by a slow negative deviation under certain conditions.

Link Between EP and Time of Behavioral Act

In the same experiments, we measured the latency periods of electrical activation of cervical muscles, and plotted histograms of distribution of these latency periods. The earliest EMG reactions appeared with a latency period of about 50 ms; mean latency time ranged from 100 to 400 ms in different rabbits. A comparison of histograms of distribution of these latency periods to time of development of EP revealed that only primary and negative components of EP develop in the latency period of the EMG reaction, whereas late positivity corresponded already to the start of muscular contraction and, consequently, start of function of actuating mechanisms of the behavioral act (Figures 5 and 6).

Many studies have been devoted to EP changes related to different reaction times (Donchin, Lindsley, 1966; Bostock, Jarvin, 1970, and others). However, researchers concentrated mainly on the correlation between reaction time and amplitude of different EP components. The question of correlation between time characteristics of EP and time of behavioral act was not posed, probably because of the prevailing view that EP are related to "afferent processes." Still, R. Eason et al. (1967) demonstrated a link between reaction time and latency of various EP components.

If we compare the literature, according to which human reaction time to different stimuli constitutes 100-300 ms (Shoshol', 1966), while EP in response to the same stimuli constitute 300-400 ms (Rutman, 1974), it is easy to see that EP correspond to all processes in the behavioral act, rather than only "analysis of the stimulus."

In recent times, direct evidence has also appeared of the fact that the start of motor activity coincides in time with the rear front of negativity or anterior front of the positive component (Peymer, 1971; Ikeda, 1973). A correlation was demonstrated: in all cases of increase in reaction time, regardless of the cause of this increase, there is increase and even doubling of the negative component (Peymer, 1971; Ikeda, 1973; Ritter et al., 1972).

The fact that EP conform with processes of the entire behavioral act makes it unjustified to classify potentials as sensory and motor, since they only differ in means of isolation from the general, overall EEG. Indeed, if we average the electrical activity of some structure due to a stimulus, we obtain a sensory EP, whereas if we "reverse average" the same activity from the start of the EMG, we obtain a motor potential. In view of the variability of the latency period of the EMG reaction, the configuration of motor potentials may differ somewhat from the configuration of the evoked potential; however, the general composition of components remains the same.

Tracings of the motor potential related to voluntary movement of the foot, submitted, for example, in the work of L. Gilden et al. (1966), conform entirely with the late components observed in the behavioral act and triggered by some stimulus: first a small positive component, then negativity, which reaches a maximum about 100 ms after its start, followed by strong positivity. EMG activity begins together with the posterior front of negativity.

L. Decke et al. (1969) described a very similar sequence of components, associated with finger movement: against the background of "potential readiness" 86 ms before the EMG or 117 ms before deviations on the mechanogram, "premotor positivity" was recorded, which changed 56 ms before the start of EMG activity into a "negative motor potential," the posterior front of which corresponded to the start of EMG activity. The maximum level of this activity coincided with the next positive component. The same sequence of processes has been described with other forms of motion and eye movement (Becker et al., 1972).

All these facts convince us that in all cases the summated potentials associated with a behavioral act correspond to all processes of organization of this act.

Nevertheless, EP recorded in response to a sensory stimulus are usually analyzed as correlates of only sensory processes, whereas the potentials isolated by "reverse averaging" are analyzed as correlates of only motor processes. If we agree that both analysis of the environment and organization of actuating mechanisms are required to perform a behavioral act in any case and, as we have tried to demonstrate in the preceding section, that processes in sensory and motor structures have the same time organization, it becomes apparent that EP reflect very unique and qualitatively specific processes that occur during performance of integral behavior. The use of anatomical and physiological categories of "afferent--efferent," or "sensory--motor," is not adequate for evaluation of processes, the correlates of which are EP.

"Endogeny" of EP in Behavior

Evoked potentials were used in an enormous amount of studies of the most diverse problems.

These studies made it possible to accumulate some very important facts dealing with the dependence of diverse EP characteristics, such as configuration, latency periods, amplitude and polarity of components, on the most varied experimental conditions. Particularly many works dealt with determination of the dependence of EP on intensity of stimulation. Some authors found a link between intensity of stimulus and primary EP component (Schmidt, 1968); however, most studies demonstrated that later components depend on intensity of stimulation (Beck, Rosner, 1968; Wicke et al., 1964). EP were also found to be related to the content of stimuli, such as slides or words (Lifshitz, 1966; John et al., 1967), as well as information contained in the stimulus (Sutton et al., 1967; Buchsbaum, Fedio, 1969) and meaning of the stimulus for the subject (Kostandov, 1977; Jennes, 1972).

Many studies dealt with dependence of EP on level of attention (Garcia-Austt et al., 1964; Mackworth, 1969), and it was found that relevant, or meaningful, stimuli that the subject had to count or to which he had to respond always induced more marked EP than irrelevant ones. Here, the link between EP and the entire behavioral act is particularly distinct. In extreme cases of distraction of attention, EP are not recorded at all, as had already been demonstrated by R. Hernandez-Peon (1960, 1961).

In our experiments, in response to presentation of rhythmic flashes of light as a conditioned signal reinforced by electrocutaneous stimulation (ECS), a complete EP developed only to the first flash in a series, after which defense behavior began and the next flashes were "unmeaningful" (Figure 7) (Shvyrkov, Velichkina, 1970). We obtained similar data with regard to food-related behavior (Shvyrkov, Grinchenko, 1972), and they have also been described by many other authors. A correlation was also demonstrated between EP and nature of future motor response (Spinelli, Pribram, 1970), time and probability structure of presentation of stimuli (Jenness, 1972a, b; Boddy, 1973; Poon et al., 1976), etc., in other words, all factors determining integral behavior.

At the same time, correlations were demonstrated between EP and physiological parameters: the configuration of EP changed when stimuli were delivered at different phases of respiration or the cardiac cycle (Callaway, M. Buchsbaum, 1965), with change in state of the thyroid (Shagass, 1975), with administration of pharmaceutical agents, etc.

Interpretations of these facts are just as diverse as the data themselves; however, they can be divided into three groups. Some authors prefer to interpret EP changes in psychological terms, such as "perception," "attention," "recognition," etc. The second group of explanations refers to physiological discussion of the sources and pathways of conduction of a given component. The third group uses the terminology of information processes: "evaluation of signals," "information processing," etc., etc.

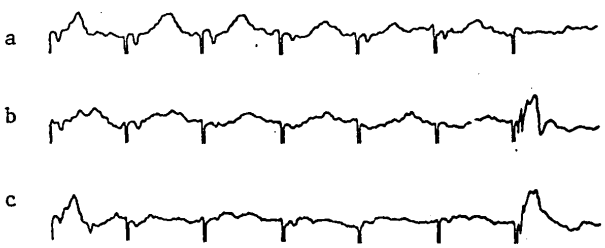


Figure 7. Evoked potentials in response to rhythmic flashes of light, in somatosensory cortex of the rabbit with development of conditioned reflex

a) before development of reflex
b) 1st to 20th combinations, delivery of electrocutaneous stimulation 500 ms after the 6th flash
c) 21st-40th combinations

All these interpretations make some use or other of the link between EP and parameters of the stimulus that induces them, while changes in EP configuration are related to the modulating influence of either attention, emotions, etc., or nonspecific structures, or informational meaning. A. M. Ivanitskiy believes that "the possibility of recording a response in the absence of stimulus is an objection to conceptions of the exclusively modulating action of nonspecific influences on late waves of the response (1976, p 73), and he cites extensive facts to support this possibility. However, A. M. Ivanitskiy believes that this is the only objection.

We believe that the list of objections must also include the results of experiments involving recording of "motor" potentials, as well as data that there are no EP in the presence of the stimuli described in the preceding section. But the decisive objections which, we believe, compel us to abandon these conceptions, were obtained from systematic experiments in the laboratory of E. R. John, which demonstrated the "endogeny" of all EP components after 40 ms (John, 1972) or even 25 ms (John, Morgades, 1969). The main experiment of E. R. John consists of delivery of flashes at a frequency of 3 Hz to cats trained to depress one lever in response to flashes at a frequency of 2 Hz and another lever, in response to flashes at 4 Hz. This was associated with "generalization," and the cats sometimes went to one lever and sometimes to the other. The EP configuration in response to such a "generalizing" signal corresponded expressly to the light that was a "signal" for the lever to which the cat went.

The conditions of these experiments were changed in all sorts of ways. The "generalizing" flash was replaced with a sound or electric stimulation of brain structures; depression of the lever was reinforced with either food or elimination of a possible nociceptive stimulus. In addition to EP, activity of neuronal "ensembles" was also recorded, and a computer was used to define the configuration of EP and "population activity" corresponding to specific behavioral acts.

All these modifications revealed that in response to any stimulus there was reproduction of the EP configuration corresponding to specific behavior, and it was unrelated to the parameters of the stimulus. In order to stress the independence of EP configuration from the parameters of exogenous stimulation, E. R. John called the components "endogenous" after 25 ms or 40 ms, i.e., reflecting internal activity of the brain read out of memory (John, 1973).

The fact that the early components were present with any form of behavior served as grounds to consider these components (up to 25 or 40 ms) "exogenous," related to input in the brain of "external information."

The fact that EP reflect the "memory of prior experience" (John, 1973, p 209), i.e., activity retrieved from the organism's memory, makes it possible to explain the dependence of EP on all factors in the exogenous and endogenous environment. According to functional system theory, retrieval of a given behavioral act from memory depends on both endogenous factors (motivation) and exogenous ones (situation). This shows that a stimulus is exclusively an impetus, or trigger factor, which does not determine endogenous brain processes, but only triggers them.

This is also confirmed by experiments, in which an exogenous acoustic stimulus was replaced with electrical stimulation of the auditory cortex (Miller et al., 1969) or photic stimulus was replaced by stimulation of the external geniculate body or visual cortex (M. I. Glickstein, 1972). The latency period of the motor response diminished with electrical stimuli by exactly the magnitude of the interval occupied by the primary component. These utterly artificial electrical stimuli apparently replace entirely the exogenous trigger signal, although, of course, it is unlikely that they carry "information about the physical properties of the stimulus."

Since, according to our hypothesis, EP reflect processes of coordination of elements of different structures into a single system, "endogeny" of EP signifies that the trigger stimulus reproduces processes of concordance of the elements that previously formed a functional system of the corresponding behavioral act.

Link Between EP and Future Events

According to functional system theory, the activity of different brain structures in the behavioral act is not only "endogenous," i.e., retrieved from memory, but goal-directed. In other words, the choice of a specific activity from memory is determined by hierarchically organized goals or anticipated future events.

The link between EP configuration in response to any trigger stimulus and future events can already be seen in the fact that EP to a conditioned stimulus followed by reinforcement is significantly different from the EP in response to an "indifferent" stimulus, as has been demonstrated in a vast number of studies.

The experiments of A. I. Shumilina (1965) revealed that the configuration of EP to a conditioned stimulus depends on the quality of reinforcement. EP in response to the same flash of light, with respect to its physical parameters, present different configurations when the flash serves as a conditioned signal of future food or defense reinforcement. The above-cited data of E. R. John can be interpreted as confirmation of another aspect of dependence of EP on future events. While in the experiments of A. I. Shumilina the same stimulus served as a signal of different future events, in the experiments of E. R. John different stimuli, which triggered the same behavioral act, were signals about the same future event.

There was direct demonstration of the possibility of purposeful transformation of EP when a specific EP configuration leads to reinforcement in the experiments of S. Fox, A. Ruddel (1970) and J. Rosenfeld, R. Owen (1972).

All these data warrant the assumption that the configuration of EP reflects organization of processes that leads to a specific future event. Of course, event is not a purely physiological concept. We have already stated that, as an organized aggregate of elements in the environment, it can be compared only to a specific organization of physiological processes. For this reason, the link between configuration of EP in response to some triggering stimulus and a future event can be demonstrated only by comparing the configuration of EP corresponding to two consistently successive events.

We found that with recording of EP in response to light and ECS in the somatosensory cortex, in the conditoned defense reflex, that these EP become amazingly similar (Shvyrkov, Velichkina, 1970). At that time we evaluated this phenomenon as the correlate of "anticipatory reflection" and manifestation of the model of future ECS, according to conditioned signal in expressly the somatosensory cortex. However, this conclusion was derived without considering the fact that EP reflect general cerebral systemic processes, rather than special functions of the somatosensory cortex.

The objective of the next series of experiments was to compare the EP configuration with conditioned and unconditioned stimuli in several structures of the brain performing different special functions. It is generally believed that the visual and somatosensory cortex perform different functions in the conditioned defense reflex to light, reinforced by electrocutaneous noxious stimulation: the conditioned stimulus is analyzed in the former and the unconditioned, in the latter.*

It was assumed that comparison of EP configuration in response to light and ECS would yield information about the extent of dependence of configuration of EP on light and configuration of EP to ECS, and thereby about reflection in EP configuration to light of the future event--electrocutaneous stimulation. A comparison of EP configuration in the visual and somatosensory regions would permit differentiation of components related to general cerebral, systemic processes from components related only to special functions of one structure.

Although there is no analogue in nature of constant combinations of light and electrocutaneous stimulation, this experimental model is methodologically very convenient for the study of elementary behavior. One can arbitrarily consider reduction of the deleterious effect of electrocutaneous stimulation as the goal of this behavior (Laptev, 1949; Ivanova, 1970).

We conducted our experiments on nine adult rabbits whose paws were immobilized on a stand. The conditioned defense reflex and differentiation were developed in one session, during which the rabbit received about 300 combined and separate stimuli. Three flashes of light, synchronized with clicks delivered at 700-ms intervals, served as the conditioned stimulus; 700 ms after the last flash we delivered reinforcing ECS, square-wave pulse lasting 1-500 ms, with amplitude of 40-120 W, and intersignal intervals of 30-90 s.

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*In using the terms "conditioned reflex," "conditioned stimulus," etc., we are merely following the physiological tradition of their referring to certain experimental procedures, but by no means do we impart in these terms their original conceptual meaning. In this book, we shall not specially discuss the problem of formation of new behavioral acts; let us merely indicate that, with the systemic approach to analysis of the mechanism of learning, the very formulation of the problem changes: if conditioned and unconditioned behavioral acts are not organized like "arcs" of corresponding reflexes, but as functional systems, there is no physiological meaning to the question of bridging of a connection between them. The organism does indeed detect a link between two events and organizes a conditioned behavioral act, with due consideration of future reinforcement, as established by I. P. Pavlov. However, the conditioned behavioral act is not a copy of an unconditioned reflex, but new integration, a new functional system organized to achieve a certain result, which plays the part of a system-forming factor.

Light flashes attenuated with a yellow filter, also synchronized with clicks, served as the differentiation signal. Since the rabbit retina contains only rods, differentiation apparently occurred according to brightness. Conditioned (reinforced) and differentiation stimuli were delivered in series of 25, which was motivated by the convenience of subsequent processing of evoked potentials.

The electrical activity derived from the muscles of the front leg served as a criterion of development of the conditioned reflex. Electrical activity of the visual and somatosensory cortex was derived with needle electrodes inserted in the cranial bone and immobilized with dental cement. After amplification by means of a Biophase universal unit, along with recoridng on an ink recorder, the EP and EMG were recorded on tape on a multichannel recorder ["magnettor"], using frequency modulation, and then they were averaged on a Mnemograph accumulator unit. The bandwidth of all of the equipment constituted 1.2-500 Hz. Time of analysis of evoked potentials constituted 400 or 800 ms, and averaging of 25 runs was performed. We analyzed the responses to electrical stimuli and the first in a series of flashes, since preceding experiments convinced us that, under such conditions, the EMG reaction appears already after the first conditioned signal flash, and the responses to expressly the first flash undergo the main changes related to developed of the conditioned reflex; the responses to other flashes are depressed, and they contain only the primary complex, as illustrated in Figure 7.

Our objective made it necessary to analyze expressly the configuration, i.e., the time parameters and component composition of an evoked potential, rather than amplitude.

Before combining the flashes with ECS, the responses to the former varied significantly in the visual cortex of different animals, and they contained a dissimilar number of components (compare Figures 8 and 11). The responses to white (future conditioned) and yellow (future differentiation) light presented the same configuration, but the latency period of the response to yellow light was usually several milliseconds longer. It is a known fact that there is a correlation between latency period of EP and brightness of flashes (Shevelev, 1971).

Light also induced some response or other in the somatosensory region, and such responses were virtually absent in only three rabbits (Figure 8). In the other three rabbits, the evoked potentials even contained the early negative components first described by K. M. Kullanda (1964), with a latency period of 15-20 ms (Figure 11).

As can be seen in Figures 8 and 11, before development of the conditioned reflex, the responses to light could vary, not only in the visual and somatosensory regions, but even in the left and right visual areas (Figure 8), which we had already observed in freely behaving rabbits.

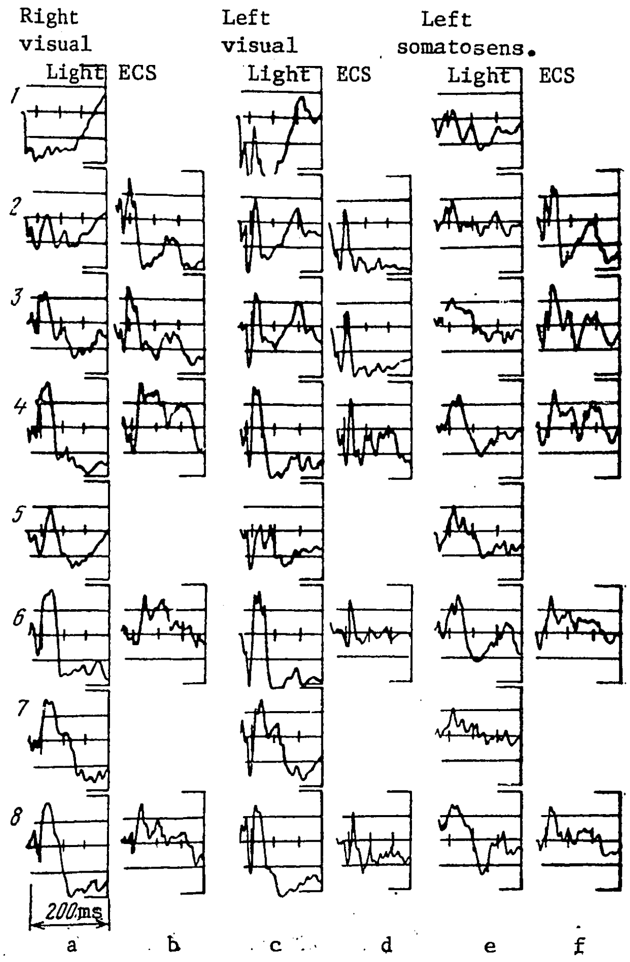

Figure 8. EP to light and ECS in right and left visual and left somatosensory cortex during development of conditioned reflex

Averaging of 25 runs at a time:

1) before combinations
2) 1st—25th combinations
3) 26th—50th combinations
4) 51st—75 combinations
5) 1st—25th delivery of differentiated yellow light
6) continuation, 76th—100th combinations
7) 51st—75th delivery of differentiated light
8) former differentiation yellow light reinforced by ECS, 1st—25th combinations

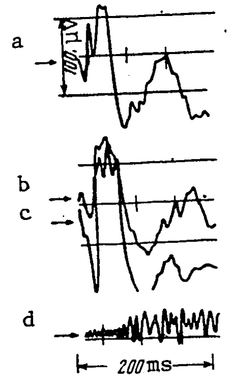

Figure 9.
Comparison of evoked potentials to one another and to averaged EMG reaction.

Same experiment as in Figure 8:

a) response to ECS in somatosensory cortex after development of reflex (frame "f" in Figure 8)
b) response to light in somatosensory cortex after development (frame e-6)
c) response to light in left visual cortex (frame c-6)
d) averaged conditioned EMG reaction, 76th-100th combinations

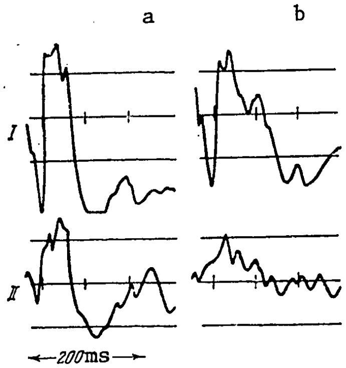

Figure 10.
Comparison of responses to conditioned (a) and differentiated (b) light in visual (I) (frames c-6 and c-7 in Figure 8) and somatosensory (II) (frames e-6 and e-7) cortex. Same experiment as in Figure 8.

The responses to ECS were also individual. They differed only in the first combinations in the somatosensory and visual cortex. Already after 25 combinations, the early components of responses to ECS in the somatosensory and visual cortex were the same and had a latency period of 10-20 ms (Figure 11). The responses usually presented initial positivity, but the main typical component of the response to ECS was negativity in all areas, with a latency period of 20-40 ms. Its duration was very individual, ranging from 40 to 200 ms in different animals. Negativity was followed by a late positive component.

The dynamics of responses to ECS during development of conditioned reflexes consisted of simplification of configuration, and they were similar in all of the examined parts of the cortex (Figure 8).

Responses to light, which had become a conditioned signal, were completely transformed in both the visual and somatosensory regions after 25-50 combinations; at the same time, a stable conditioned EMG reaction appeared. A comparison of configurations of EP to conditioned light in the visual and somatosensory cortex showed them to be very similar (Figures 8, 9 and

11); there was coincidence of latency periods and duration of phases, particularly the negative one, and often subcomponents as well.

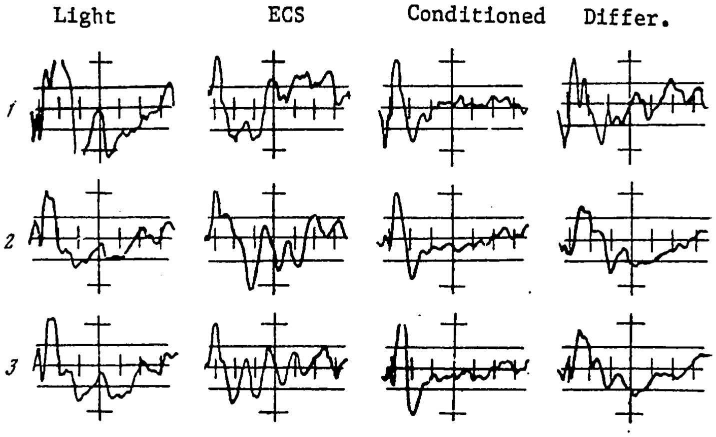

Figure 11. Comparison of responses in left visual (1) and somatosensory left (2) and right (3) cortex to light before development of reflex, to ECS, conditioned light (25th-50th combinations) and to differentiation yellow light (25th-50th deliveries). Averages for 25 runs, 400 ms frames

In other words, in defense behavior induced by a conditioned or unconditioned stimulus, the evoked potentials in different parts of the cortex were also synchronous and similar in configuration, as in the previously discussed food-related behavior. It is very important to note that, in our experiments, the responses to conditioned light in the somatosensory cortex always contained a short, early component, which was usually positive (Figures 8 and 10). In two experiments and before development of the conditioned reflex, light induced an early negative component in the somatosensory cortex, which persisted even after it was developed (Figure 11). The early components had a latency period of 15-20 ms, which was the same as the latency period of responses in the visual cortex (Figures 9 and 11). Appearance of such early oscillations of potential in response to a conditioned signal, at the "point of reinforcement" had already been reported in the literature (Artem'yev, 1959). The early component was followed by negativity, which lasted 40 to 200 ms in different rabbits and was complicated by a different number of subcomponents, and late positive oscillation.

A comparison of the responses to conditioned light and ECS in somatosensory regions confirmed our previous data (Shvyrkov, Velichkina, 1970) indicating the similarity of their configurations. The responses to light and ECS in the visual cortex after development of reflexes were also similar (Figure 11). If the response to ECS changed, similarity was observed between the response a given rabbit presented before the conditioned reflex, rather than the one that was transformed as a result of development thereof (Figures 8 and 9). This transformation of EP in response to ECS was studied by us in separate experiments (Shvyrkov, 1969), and we shall not discuss it specially here. The similarity of configurations of responses to conditioned light and ECS was graphically demonstrable with any individual configuration of EP (Figures 10 and 11).

The responses to differentiated light in the visual cortex differed in most experiments from the conditioned evoked potential, in that they contained an additional negative oscillation and had no late positivity, or else the latter was shifted in time (Figures 10 and 11). In the somatosensory cortex, the responses to differentiation light were always less marked than before the combinations; they did not resemble the response to ECS or conditioned signal and, what is important to note, they contained no early components (Figures 8, 10 and 11). With the reinforcement of differentiation light, the responses immediately acquired all of the features of a conditioned one, in both the visual and somatosensory regions (Figure 8).

The conditioned EMG reaction appeared after 25-50 combinations, and it had a relatively stable latency period for each rabbit, from 50 to 300 ms. The EMG reaction began at the time of the posterior front of negativity and late positive oscillation (Figure 9). According to the EMG reaction, differentiation reached a 70-80% level after 25-75 separate presentations of differentiation light.

These data indicate that the phenomenon that accompanies development of a conditioned reflex does not consist merely of generalization or transformation of the evoked potential to light, but the responses to conditioned signals in the visual and somatosensory cortex become synchronous and identical in configuration; and the responses to reinforcing ECS were also the same as before the combinations. This pattern was demonstrable in all animals, with any individual configuration of EP.

The fact that, before and after development of the conditioned reflex, the same stimulus could induce responses of utterly different configuration, while different stimuli, light and current, could evoke the same responses after development (in different regions) demonstrates, once more, that the mechanisms that determined EP configuration in behavior are qualitatively different from the mechanisms that determined EP configuration in anesthetized animals, in which case there is a distinct link between configuration and distribution of EP, on the one hand, and anatomical porjections of receptor surfaces, on the other hand. This serves as additional confirmation of the "endogeny" of processes, the correlates of which are EP.

Our data indicate that the primary response, at least in the somatosensory cortex, is also "endogenous," since presence or absence thereof are directly related to reinforcement and, consequently, like the later components, the primary response also corresponds to prior experience stored in memory.

The link between configuration of EP in response to light and to current also indicates that retrieval of a certain organization of physiological processes from memory takes place in accordance with a future event. The order of processes may be as follows. According to functional system theory, any stimulus that appears in the environment finds preliminary integration of elements prepared, and determined by the future event, the appearance of which is predicted by motivation and situation.

In our case, this event, which generated preliminary [pretrigger] integration, was ECS. The result, i.e., attenuation of the deleterious effect of ECS, was achieved by means of a functional system that contained specific elements in different structures, including the visual and somatosensory cortex. Coordination of activity of expressly these elements was reflected in a specific EP configuration in response to ECS. Since motivation (defense) and situation (constant) do not predict any future event other than ECS, the preliminary integration in our experiments corresponds mainly to one future event and one goal: to reduce the injurious effect of ECS. The similarity of EP in response to light and ECS can be explained by the fact that the light flashed in the presence of preliminary integration created by ECS, and after it there was coordination of activity of mainly the same elements that were involved in the functional system of the unconditioned behavioral act.

We tested this hypothesis in special experiments, where we recorded neuronal impulsation activity, which is discussed in Chapter 4. Here, let us merely mention that, since EP in response to differentiation flashes differ from EP to both conditioned and indifferent flashes, it is imperative to assume that development of differentiation consists of formation of a separate behavioral act, the functional system of which is formed of different elements than the functional system of the other acts studied.

Although delivery of combinations and differentiation flashes in our experiments was performed in blocks of 25 presentations which, of course, led to a change in preliminary integrations already after the first flashes in a successive block, we can still assume that both preliminary integrations exist from the time of introduction of differentiation light in any intersignal intervals.

Triggering of a given integration is determined by the parameters of delivered light. Since, in our experiments, the EP to a conditioned light differed from EP to differentiation light in that there was already a primary response with a latency period of 15-20 ms in the somatosensory cortex, it should have been assumed that not only "identification of physical properties," but "determination of signal meaning" of the light occur within the latency period of cortical EP. This conclusion seems paradoxical. However, one should apparently seek the cause of the paradox in the conceptions of identification of physical properties and determination of signal meaning of a stimulus as real processes.

EP Components--Correlates of Systemic Processes of the Behavioral Act

It appears to us that the EP distinctions demonstrated in behavioral experiments compel us to change the view of EP as a physiological phenomenon. Synchronism and similarity of EP configurations in different structures do not offer grounds to maintain that there are some unidirectional "afferent messages" or "flows of excitation" spreading from one structure to another. Rather, we can conceive of multilateral exchange of influences between elements of many structures, which occurs at each phase of an evoked potential.

This hypothesis can also be extended to EP demonstrable under anesthesia, the only difference being that elements involved in interaction processes under anesthesia are limited to constant "narcotic" preliminary integration, which could refer to the correlation between intact functional links between structures and links impaired by a specific anesthetic. As we know, with the use of different types of anesthesia, stimulation of the same nerve elicits an evoked potential with different localization and configuration (Nabil', 1969).

Thus, the possibility of recording EP under anesthesia, without integral behavior, is not in contradiction with the conception that EP are linked with systemic processes of organization of the integral behavioral act: EP is a phenomenon that reflects processes of any interaction of many elements. In behavior, this interaction is determined by the goal and goal-directed organization of preliminary integration; under anesthesia, this interaction is due to the stable state created by anesthesia.

The distinctions of EP in integral behavior are an expression of these differences: synchronism and similarity in functionally different structures; dependence of configuration on future events and relative independence of parameters, modality and even presence of a trigger stimulus; distinct link with time intervals of the behavioral act.

In the continuum of behavior, a single behavioral act--single organization of activity of elements--replaces another behavioral act--another organization. Transitional processes triggered by a stimulus, the result of a prior act, are reflected in EP.

According to functional system theory, there must be processes of afferent synthesis and decision making in an elementary behavioral act, between the stimulus and start of action: start of muscular contraction already indicates implementation of the acceptor of action results and program of action.

The rather stable correlation between EP components in different behavioral acts and start of the EMG reaction warrants the assumption that the primary response and negativity of EP correspond to processes of afferent synthesis and decision making; late positivity already coincides with the start of actuating mechanisms of the behavioral act, which are integrated in processes of the acceptor of action results and program of action.

In order to determine more precisely the meaning of different EP components as correlates of processes in the functional system of behavior, we conducted several series of experiments.

In the first series, we studied a behavioral act contained in the continuum of behavior in order to track the dynamics of processes corresponding to the moment of transition from one behavioral act to another.

According to functional system theory, motivation and situation retrieve preliminary integration from memory, which corresponds to the goal of entire behavior. This goal is hierarchically organized, and preliminary integration includes all elements of future behavior. Performance of the first behavioral act and achievement of the first result out of the entire hierarchy, which leads to achievement of the ultimate goal, must be associated with the following successive processes: comparison of parameters of achieved result to the acceptor of results of action of this act, afferent synthesis and decision making of the second act; then there is formation of the acceptor of action results and program of action for the second act, which determine action until the results of the second act are reached, etc.

We simulated this segment of the continuum of behavior in the model of instrumental behavior, in which rabbits turned on a flash of light and headed for a feeder by pulling a ring with their teeth over a specific distance. Both behavioral acts monitored by the experimenter (pulling the ring and approaching the feeder) are contained in the general functional system of food-obtaining behavior, but each of them is a functional system with its own interim result. We can describe this segment of the behavioral continuum schematically (Figure 12).

The first objective of our experiments was to have expressly the flash of light serve as an interim result, i.e., the goal of tugging and trigger stimulus to run toward the feeder. Experiments were conducted on 16 rabbits in a specially outfitted cage. Flashes of light were delivered from the top at a distance of 70 cm from the floor of the cage (flash energy 0.3 J and duration 50 μs) from a Soneclat stimulator lamp. In experiments on 8 rabbits, we used a series of six flashes at 600-ms intervals; in the experiments on the other 8 rabbits, we delivered series of 3 flashes at 700-ms intervals.

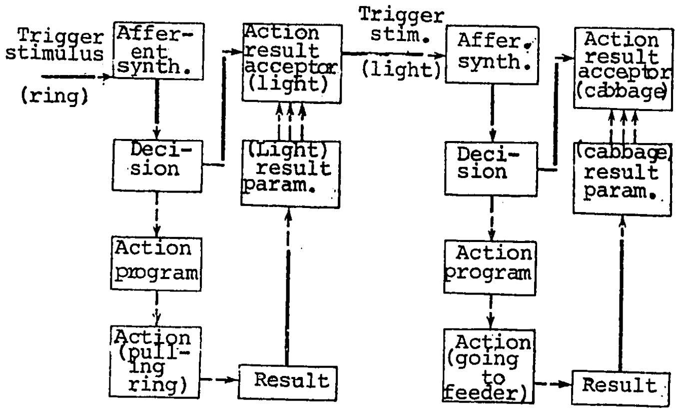

Figure 12. Schematic rendition of segment of behavioral continuum

In all of the experiments, activity of the visual and sensorimotor cortex was derived monopolarly using implanted electrodes. The silent electrode was over the frontal sinuses. We used special stainless steel pins to derive electrical activity of cervical muscles, which were inserted in the skin on both sides of the neck; the EEG and EMG were recorded on a Polygraph XVII electroencephalograph; in addition, a tape recording was made of the experiments on the 8 rabbits to whom three flashes of light were presented.

In these experiments, electrical activity of the cortex and EMG were recorded, after amplification on a universal Biophase unit, on magnetic tape. For reproduction from the tape, electrical activity was averaged using a Mnemograph accumulator unit.

In the first experiments, the animals developed a classical conditioned reflex: the flash was reinforced by automatic presentation of a feeder with 10-20 g cabbage. The control pulse for presentation of the feeder as 500 ms away from the last flash. Thus, the first flash was more than 2 s ahead of presentation of the feeder. The conditioned reaction was recorded as electrical activity of cervical muscles (Figure 14). Already after 3-5 combinations, the rabbits turned their head and went toward the feeder in response to the conditioned signal. After 10-30 combinations, running to the feeder was triggered by a flash in almost 100% of the cases. During the second to fourth experiments, i.e., after 100-150 combinations, we began to develop the instrumental behavior of tugging the ring, in which we put a cabbage leaf for the first 3-5 times. A string connected the ring to three contacts, which were so located that to bridge the first one the ring had to be pulled over 3 cm, for the second 8 cm and the third 14 cm (Figure 13). By tugging at the ring, the rabbit could successively bridge all contacts; however, the flash and then the feeder were presented only after bridging of the contact that the experimenter connected to the stimulator.

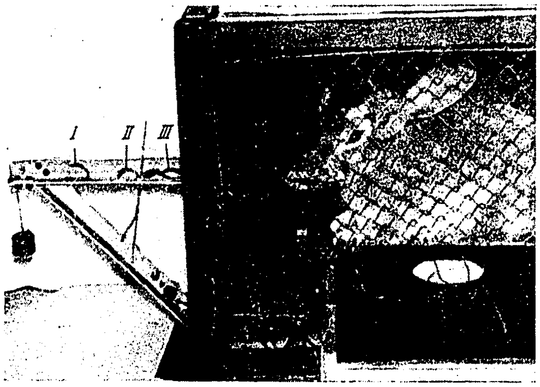

Figure 13. Experimental cage. By tugging the ring with its teeth, the rabbit moves a lever and bridges contacts I, II, III, one of which turns the light on

Interestingly enough, already in the first tests many rabbits, after reaching for the cabbage leaf in the ring and unintentionally making contact, dropped the leaf when the flash appeared and headed for the feeder, which did not yet contain any cabbage.

At first, the first contact was effectively produced. But when the rabbits learned to tug the empty ring and this skill became fixed (usually after 50-70 times), each of the 3 contacts became alternately effective. We tried to change contacts in random order; the procedure for this change consisted of silent movement of the switch on a console 3 m from the cage. Thus, the rabbit did not receive a signal that the contact was changed, let alone which contact would be effective when it next pulled the ring.

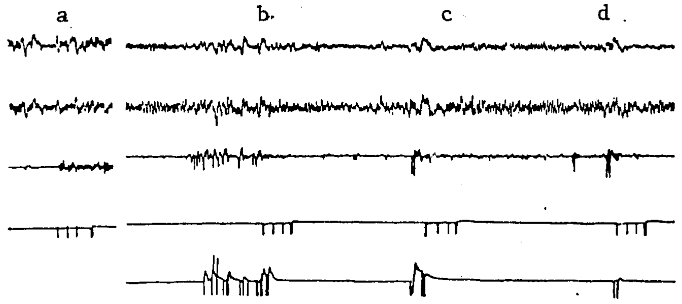

Figure 14. Classical conditioned reflex (a) and instrumental behavior (b, c, d) of rabbit.
Top to bottom: EEG of sensorimotor and visual cortex; EMG of cervical muscles; marks for 3 flashes and presentation of feeder; marks for making contact--in b, c, d, a--conditioned EMG activation, corresponding to the rabbit's turning toward the feeder, begins after the first flash.

Nevertheless, the experiments showed that all rabbits related quite accurately pulling the ring to appearance of light: if they saw the light after pulling the ring over 3 cm (Figure 14d), they immediately released the ring and headed for the empty feeder; if, however, the experimenter rendered the third contact effective, the rabbits pulled the ring to the maximum distance. They did not always succeed in so doing at the first try; however, the rabbits did not stop trying and did not head toward the feeder until the light was flashed (Figure 14b). When they failed, they often "stood up" and sniffed the lamp. One of the rabbits, who could not pull the ring over a distance of 14 cm by moving only its head, had to first tug the ring down with its paws, then grab the string from the contacts in its teeth and additionally pull it out by moving the head. As soon as the light appeared, the rabbit dropped the string and ring, and headed for the feeder.

Since no signal was delivered as to the distance over which the ring had to be pulled and the rabbits pulled it out each time over a different distance, it must be conceded that, in our experiments, the scope and discontinuation of pulling were not determined by the conditioned signal, but by the goal.

The cage itself or the ring may be considered the signal to trigger pulling; however, these factors were constant, while the rabbits pulled the ring over different distances each time, for which purpose they performed different actions, including some to which they were not specially trained. Since the volume of movements varied and could not be determined by any stimulus prior to the start of movement, the event that stopped pulling the ring had to appear as a result of movement. Evidently, merely the position could not be such an event, since the rabbits pulled the ring over different distances, and kinesthetic afferentation arising when the ring was pulled out for 3 cm was associated with termination of action in some cases and continuation in others. Evidently, the result of action could not be the feeder itself, since the rabbits released the ring with appearance of the first flash.

The light was expressly the result that stopped pulling at the ring and it was necessary to stop pulling, whatever the mode of action. By altering the effective contacts, the experimenter could always predict which action would be performed and when it would stop.

Thus, our experiments showed once more that it is expressly the model of the result, rather than any conditioned signal, that determines the range and mode of action performed to achieve it.

Whenever the ring was pulled there were many consequences: appearance of the sound of movement of the lever, change in position of the ring, position of the rabbit, etc. However, only the light had the property of stopping the pulling. The distinction of light from the other consequences is expressly that it emerges as a foreseeable and necessary event, i.e., as the goal of pulling.

Of course, light acquired this property as a result of prior development of signal-related link with the feeder, which was the more distant goal of the entire food-obtaining behavioral cycle: approaching the ring--pulling--obtaining light--approaching feeder--receiving cabbage. Thus, we added light to the general hierarchy of results of food-obtaining behavior and, consequently, it merely served as an interim, but immediate goal, which was reached by pulling the light, and it was contained in the hierarchically organized goal of the entire food-obtaining behavior.

We observed a rather interesting form of behavior in some experiments. After becoming satiated by the end of an experimental session, a rabbit began to tug the ring often and regularly, relating the pulling distance to appearance of light. It did not pay attention to the automatically presented feeder with cabbage, and could tug the ring even at the moment the feeder was presented (Figure 15). After pulling the ring over the required distance, it waited for the end of the series of flashes, then pulled the ring again.

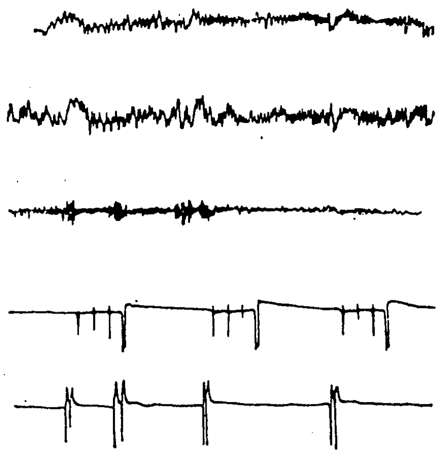

Figure 15.
Satiated rabbit regularly pulls ring and obtains light, but ignores the feeder completely. Top to bottom: EEG of sensorimotor and visual cortex; EMG of cervical muscles; marks of 3 flashes and presentation of feeder; marks of closing contacts

Thus, light added to the hierarchy of goals acquires independent meaning as reinforcement, although the feeder, of which it is a signal, temporarily loses this meaning due to elimination of the motivation of hunger.

In our opinion, these findings also corroborate the conclusion that the flash of light is the immediate goal of pulling the ring. Evidently, achievement of this goal elicits some positive emotional state, similar to the state of satisfaction that appears when the ultimate, biologically useful effect is reached. It may be assumed that, in this instance, behavior is no longer guided by hunger, but by newly acquired, secondary (Miller, 1960) motivation that causes game behavior.

The results indicate that the first objective of this series was reached, that we developed a method, with which any stimulus can be made the goal of a behavioral act, or method of "enrichment" of the acceptor of action results with additional events.

The proposed modification of instrumental behavior does not differ essentially from methods that are already known (Skinner, 1938; Beritov, 1961; Konorski, 1970, and others). However, addition of the procedure of "variable action controlled by the result" enabled us to become convinced that pulling the ring was indeed performed to obtain expressly the light.

In the same experiments, we tried to demonstrate the electrographic correlates of systemic processes and, particularly, formation of the interim acceptor of action results, i.e., prediction of light. For this purpose, we analyzed the electrical activity of the visual cortex at the time preceding pulling the ring and appearance of light. According to data in the literature concerning the possibility of reproduction of the rhythm of "marked" unconditioned reactions to a conditioned signal (John, 1966; Ruchkin, John, 1966), we could have expected appearance at this time of oscillations in the rhythm of future light in the visual cortex.

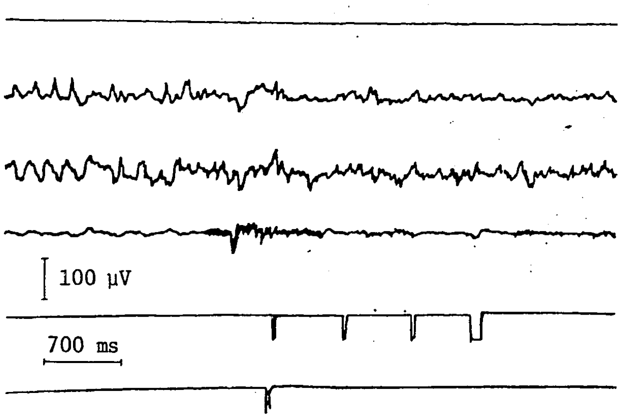

Figure 16. 158th pull of the ring. No EEG oscillations in flash rhythm either before pulling or during the action of light. Top to bottom: EEG of somatosensory and visual cortex; EMG of cervical muscles; marks of flashes and presentation of feeder; mark of making contact

In addition to visual appraisal of the ink tracings (Figure 16), we performed reverse averaging using a mnemograph in the series of experiments on the 8 rabbits exposed to three flashes of light. This procedure consists of reproducing the tape by moving it in the reverse direction. We averaged 25 runs at a time; the mark of the first flash served as the trigger signal, and analysis time was 2 s. Our analysis revealed that, when the rabbit pulls the ring, there is development of negative oscillation in the visual cortex, which precedes appearance of the first flash (Figure 17a, *2*, *3*, *4*). During the first pulls, it starts 1100 ms before appearance of the light (Figure 17a, *2*) and upon fixing of instrumental behavior it starts 850 ms before (Figure 17a, *4*). A comparison of this negativity to the start of pulling at the ring was, unfortunately, not feasible, since the moment of movement toward the ring was not fixed in our experiments, and pulling itself lasted a different period of time in each instance. However, it is apparent that this oscillation also existed during pulling, since the latter stopped after the flash.

The fact that the described negative oscillation increases with strengthening of the skill renders it similar to an anticipatory wave or conditioned negativity (G. Walter, 1965). In our experiments, light served as the expected stimulus, and therefore it may be assumed that the dynamics of negative oscillation reflect the dynamics of formation of the interim acceptor of action. Perhaps, the so-called readiness potentials that precede voluntary movements of man (Deecke et al., 1969), which are similar to the above-described negativity in the rabbit, also reflect formation of the parameters of the result of voluntary movement. The schemes of the experiments are very similar, since in most studies the subjects were instructed to achieve a "good" movement, monitoring their own EMG on the oscillograph screen. At the same time, this slow negative oscillation must also conform with performance of the program of action, since it develops while the rabbit is pulling and stops when it stops pulling.

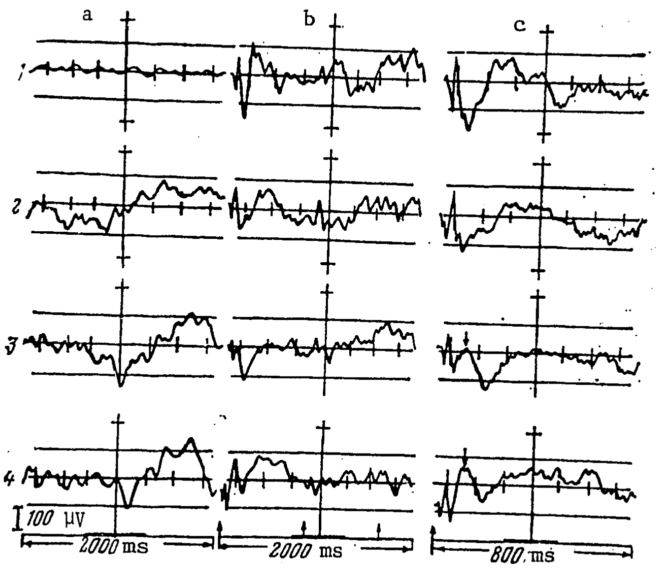

Figure 17. Averaged activity of rabbit's visual cortex during classical conditioned reflex (1) and at different stages of instrumental behavior (2, 3, 4)

a) activity preceding presentation of light
b) evoked potentials in response to all 3 flashes; time of flashes is marked by arrows at the bottom
c) response to first flash in the same combinations but a different time scale; in each case, 25 runs are averaged
1) classical conditioned reflex
2) instrumental behavior, 14th to 39th pull of the ring
3) 76th to 100th pull; in (c), the arrow shows additional negativity
4) 151st to 176th pull; additional negativity also shown by arrow

It must be noted that we failed to demonstrate oscillations of rhythm of future light in the visual cortex, either in averaging or analysis of each separate tracing in the period before pulling the ring and during the latter. Moreover, already upon formation of the classical conditioned food reflex, we found that evoked potentials to the first and subsequent flashes differed in amplitude and configuration, as in defense behavior, in accordance with previously described findings. The conditioned EMG reaction started in our experiments after the first flash (see Figure 14a), and cortical responses to the first flash were always the most marked (Figure 17c, *1*), whereas responses to subsequent flashes were deformed and disappeared. The structure of EP to the first flash before addition of tugs did not differ from that described before.

In the situation of instrumental behavior, the rabbits stopped pulling right after the first flash. The response to the first flash remained the most marked, although its configuration changed (Figure 17, *2*, *3*, *4*).

The changes in configuration consisted chiefly of appearance of an additional late negative oscillation with amplitude of about 100 μV, which appeared at the site of the former late positive peak. Figure 17, *3*, *4*, where this negative oscillation is shown by arrows, indicates that late positivity does not disappear, but is shifted in time by about 100 ms. Appearance of additional negativity did not cause an increase in latency period of the late positive oscillation in any of the rabbits, since this negativity lasted only 30 ms.

As the skill in pulling the ring became more fixed, the additional negative oscillation increased in amplitude. Figure 17 shows that the increase in additional negativity of EP is concurrent with increase in negativity preceding the flash. At first, we assumed that the additional negative oscillation could be somehow related to comparison processes (Shvyrkov, Grinchenko, 1972). However, the fact that similar additional negativity appears in response to differentiation light in defense behavior, as well as that comparison processes occur also when the flash is delivered without pulling, compelled us to reject this hypothesis.

Since "light-goal" differs from "trigger light," not only in that the former coincides with a specific moment in the rabbit's behavior, but also in that it stops active pulling, whereas the triggering light stops only passive anticipation, the hypothesis was expounded that the additional negativity is related to processes of discontinuing active pulling (Trofimov, Grinchenko, 1975). However, control experiments proved this to be wrong.

In the control experiments, which were conducted on 2 rabbits, only one flash was delivered, and a lag of 200 ms was produced between closing contact and delivery of the flash. This resulted in a change in rabbit behavior: after pulling the ring over some distance, the rabbit waited for the light either after dropping the ring or holding it in its teeth.

In this case, when we compared the EP in response to "triggering" light and "light-goal," we also observed additional negativity (Figure 18). On the basis of these experiments it was concluded that appearance of additional negativity was not related to the preceding acti, i.e., pulling, but to the one for which the flash was a trigger, i.e., the act of heading for the feeder.

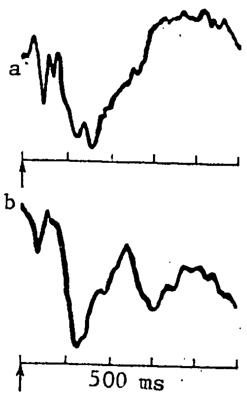

Figure 18.
Doubling of negative oscillation and appearance of P-300 in EP to light 200 ms after making contact; arrow indicates time of appearance of flash; n = 25

a) potential in response to trigger flash
b) evoked potential to flash of light--result of pulling

Such doubling of negative oscillation has been described in experiments on man with increase in number of alternatives, out of which the subject must choose one. For example, in the experiments of Ya. A. Peymer (1971), additional oscillations appeared when the subject had to determine one out of several possible positions of a pointer on a briefly displayed dial or in response to a flash which was a signal for the reaction of choice among four alternatives. The possibility of alternatives means that elements are involved in "pretrigger integration" in activity required to perform all possible behavioral acts; the decision making mechanism, which is triggered after the stimulus, chooses only one of them, i.e., it reduces the superfluous degrees of freedom.

It may be assumed that, in our experiments, "trigger light" coincided with only one formed pretrigger integration in the simple conditioned reflex, corresponding to the run toward the feeder. Implementation thereof corresponds to EP with one negativity. When pulling on the ring, the "light-goal" always was associated with at least two mutually exclusive integrations corresponding to continuation and repetition of pulls, as well as running to the feeder. This made decision making difficult, i.e., processes of implementing the one integration that corresponded to running to the feeder. Probably, doubling of negativity was a reflection of this increase in superfluous degrees of freedom and more difficult decision making.

It appears to us that this hypothesis can be extended to other instances of doubling of EP negativity. In experiments involving a choice among several alternatives, there was apparently no doubt as to the presence of pretrigger integrations corresponding to several acts (Chuprikov, 1978). Addition of a differentiation stimulus in our experiments should also have been associated with expansion of pretrigger integration.

Thus, double negativity can be interpreted as a reflection of "two-cycle" reduction of superfluous degrees of freedom, i.e., a reflection of processes of afferent synthesis and decision making that occurred twice. Assuming that EP negativity corresponds, in any case, to concurrent systemic processes of afferent synthesis and decision making, we can observe that there remain only the latency period and primary response for processes of comparison of parameters of the result to acceptor of results.

Since we had demonstrated in preceding experiments that appearance of a primary response in the somatosensory cortex can be induced by a conditioned signal and not by a differentiation one, one must assume that the appearance of the primary EP component in nonspecific regions is attributable already to the result of comparison and coincidence of parameters of the light with some model thereof or other. This again leads us to the assumption that such comparison is made during the latency period of cortical EP.

The constancy of the primary EP component in projection regions, in relation to the modality of the stimulus, in different experimental situations led many authors to the conclusion that it is related to a reflection of the "physical properties of the stimulus" (Ivanitskiy, 1976). However, the "endogeny" of the primary component in nonprojection regions warrants the assumption that it already reflects processes of implementation of pretrigger integration, i.e., retrieval of activity of specific elements from memory.

Thus, the primary component can be interpreted as the correlate of processes of comparison of the real result--trigger stimulus and its model--acceptor of action results.

We thus have some arguments for identifying the "anticipation wave," latency period, primary component and negativity of EP with specific systemic mechanisms of the elementary behavioral act.

The late positive component of EP, which may have different latency periods under different experimental conditions and in different rabbits, coincides with the start of EMG activity and changes to a slow negative oscillation, which we related to the function of the acceptor of action results and program of action. Consequently, it is contained between processes of decision making and function of actuating mechanisms of the behavioral act.

The correspondence of this potential to the start of EMG activity led us to analyze these correlations. As we have already mentioned, according to functional system theory, the behavioral act is implemented as organized activity of many elements, and any muscle could be involved in the actuating mechanisms only to the extent of its contribution to achieving the result. The coordinated involvement of muscles is implemented by the "program of action" or "effector integral," which can be determined from the order of involvement of different muscle groups in actuating mechanisms.

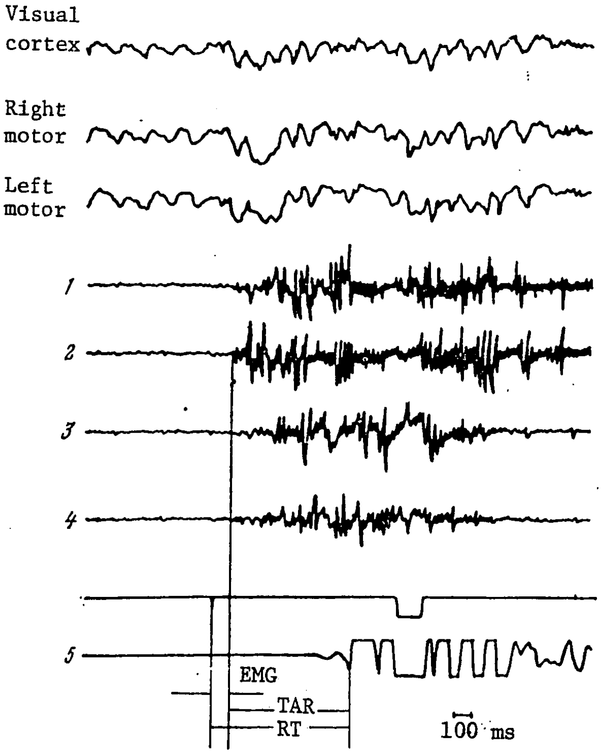

Figure 19. Correlation between EEG activity, latency periods (LP) of EMG activation of different muscle groups, time of achievement of result (TAR) in one act of approaching feeder; RT--reaction time. Top to bottom: EEG activity of right visual, right and left motor cortex; 1, 2, 3, 4--EMG activation of right and left groups of cervical muscles and posterior groups of brachial muscles of the right and left front legs, respectively. Below this, mark for delivery of flash and feeder; 5--actogram

In experiments conducted with A. Kh. Pashina on five rabbits involving the simple conditioned reflex, where the light triggered going to the feeder, we recorded activity of cervical muscles on the right and left, and activity of posterior muscle groups of the front legs, also on the right and left. This activity was compared to the parameters of the late positive component of EP recorded in the visual and sensorimotor cortex (Figure 19).

The experiments revealed that the order of involvement of different muscle groups is not constant, even after 500 runs to the feeder. One muscle group, then another was first to be active (Figure 20), and the latency period of the very first EMG reaction constituted a mean of about 100 ms (Figure 20).

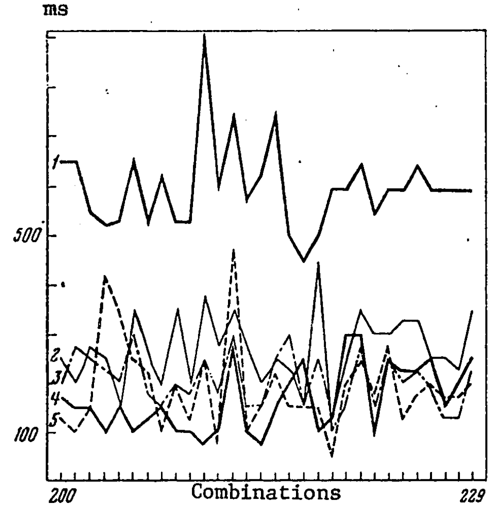

Figure 20.
Correlation between latency periods of activation of different muscle groups; x-axis, sequential number of behavioral act; y-axis, latency period, ms

1) time of achieving result
2) latency period of activation of right front leg muscles
3) left front leg
4) right cervical muscles
5) left cervical muscles

In general, the distribution of latency periods of involvement of different muscle groups coincided. When we compared EP to histograms of latency periods of EMG reactions of any muscle, we only found that the earliest EMG reaction corresponded to the posterior front of negativity and anterior front of late positivity, as was also demonstrable when recording the activity of one muscle.

A comparison of late positivity to latency periods of EMG activation of all muscles studied revealed that all EMG activations begin within the range of the late positive component.

Figure 21 illustrates the AEP in the visual cortex, as compared to time of involvement of all muscles in these 25 acts. A comparison of the top and bottom parts of this figure indicates that the form of the late positive component of AEP corresponds to the composition of the time segments between involvement of the first and last muscles in acts that were "averaged." It is therefore possible that the variability of configuration of late positivity in unaveraged EP is correlated with the instability of time of involvement of various somatic and autonomic components in actuating mechanisms of single behavioral acts.

By measuring the time between triggering of the first and last EMG reaction, we can obtain information about the time of existing of the initial "efferent integral." Subsequently, in the course of performing action, the constantly

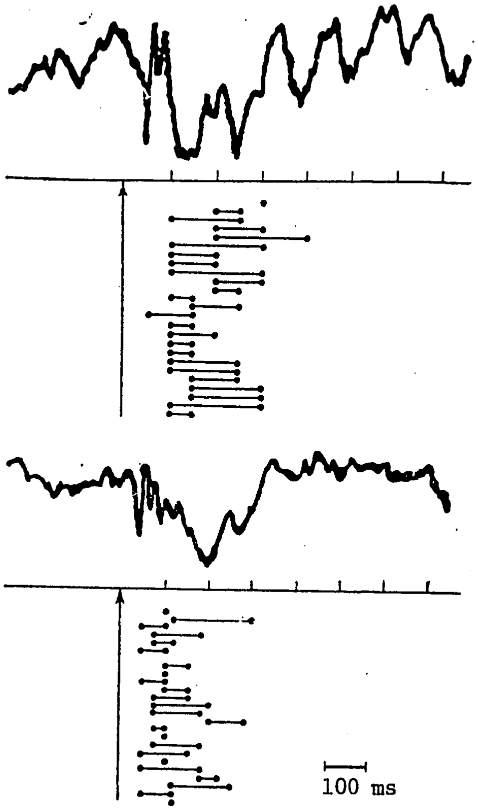

Figure 21. Correlation between late positivity of averaged evoked potential (in visual cortex) and time of involvement of all recorded muscles in actuating mechanisms of the behavioral act. Averaged EP in 26th-50th acts (top) and 101st-125th acts (bottom). Under them are the time segments in which all muscles became involved.

The starting point on a line segment corresponds to the time of involvement of the first muscle and the last point, to that of the last muscle recorded. The top segment of the line corrresponds'to the first run to the feeder and the bottom segment to the 25th. The dot refers to combinations when all muscles were involved simultaneously and the arrow shows time of delivery of flash.

incoming feedback, of course, corrects significantly and readjusts the initial program of action within the framework of the precoordinated subsystems on the physiological level.

According to functional system theory, the program of action is formed concurrently with the acceptor of action results which actually determines the entire possible set of mechanisms included in the program. Consequently, it is more correct to interpret the late positive component as a correlate of the process of mobilization of actuating mechanisms of the behavioral act, which trigger both the acceptor of action results and program of action.

The latency period of late positivity of AEP [averaged EP] in our experiments could constitute only 100 ms (according to maximum), but could also increase significantly, particularly in the experiments involving tugging at the ring. For example, in Figure 17 this late positivity has a latency period of about 300 ms.

As we know, late positivity with a latency period of 300 ms, or so-called P-300, has attracted the special attention of psychologists, since this component appears in human EP in situations of "elimination of uncertainty" (Sutton et al., 1965, 1967; Debecher, Desmedt, 1974; Ruchkin et al., 1975).

Evidently, the latency period of the late positive component depends on the duration of prior EP components. As we have already mentioned, the number of prior negative oscillations is related to the number of "cycles" of afferent synthesis and decision making which, in turn, are determined by the number of competing behavioral acts represented in general pre-triggering integration.

Thus, late positivity does indeed appear at the time when excessive degrees of freedom, present in preliminary integration, are eliminated, but this "elimination of uncertainty" apparently occurs earlier, during the negative component.

From the point of view we are developing, P-300 does not differ in meaning from the late positive component, which has a shorter latency period in simple situations. In both instances, the late positive component corresponds to the process of mobilization of actuating mechanisms of the behavioral act. The presence of P-300 only in response to "relevant" stimuli is probably related to the fact that it is only after such stimuli that the corresponding actuating mechanisms become involved. The link between P-300 and complexity of the situation can be explained by the fact that it is only in such situations that additional negative oscillations appear, which defer late positivity to a later interval; in simple situations, the actuating mechanisms of the behavioral act become active sooner, and one observes earlier positivity, and not P-300.

Thus, the general scheme of conformity of EP components with systemic mechanisms of the behavioral act acquires the following appearance: in the latency period and at the time of the primary response there is comparison of parameters of the stimulus to its model; the negative component corresponds to simultaneous processes of afferent synthesis and decision making; late positivity is a correlate of simultaneous processes of formation of the acceptor of action results and program of action; "conditioned negativity" serves as the correlate of actuating mechanisms of the behavioral act--acceptor of results of action and program of action; the "stimulus-result" of a given behavioral act triggers the next cycle, starting with the comparison process, etc. (Figure 80).

All of the above-listed systemic processes are processes that relate the organism to external events, both those existing before action and those appearing during and after action.

It is convenient to begin our discussion of the entire cycle, in terms characterizing organization of elements of the organism itself, with the preceding behavioral act, when organization of real activity of elements is related expressly to this prior behavioral act. At this time, preliminary integration, which corresponds to a possible subsequent behavioral act, without being realized, increasingly loses "excessive degrees of freedom" as the preceding act is performed. Upon achieving the result of the preceding behavioral act, the "stimulus-result" initiates, like a trigger, processes of reorganization of the activity of many elements; EP are a reflection of this transitional process.

A change in organization probably does not occur during the latency period of the primary component, and in this sense it is indeed a "latent" period. The primary response corresponds to processes of partial realization of preliminary integration, i.e., establishment of interaction between only the elements whose "degrees of freedom" were coordinated at the time of appearance of the "stimulus-result."

Negativity is a correlate of a complete change from one form of organization of elements to another. During negativity, integration corresponding to preceding behavior "falls apart," there is elimination of "excessive degrees of freedom" of all elements contained in pretrigger integration, and only one form of organization of elements is left. In the case of competing organizations corresponding to different behavioral acts, within the framework of a single preliminary integration, this process may be repeated several times.

Late positivity corresponds to the process of involvement of all necessary elements, i.e., implementation of a single integration, formed during negativity, and start of "maturation" of organization of a future behavioral act.

Finally, slow negativity, referred to as "conditioned negativity," "wave of anticipation," "potential of readiness," etc., corresponds to processes of implementation of actuating mechanisms of a current behavioral act and "maturation" of preliminary integration for the next one, i.e., it corresponds to processes of organized function of physiological functional systems contained in the hierarchy of the functional system of a given integral behavioral act.

The characteristics of systemic processes from the standpoint of physiological mechanisms are characteristics of processes of organizing the activity of various elements into a single whole; for this reason, none of the EP components, according to the view presented, reflects only afferent or only efferent processes, and it is not related to stimulation of some individual morphological, isolated pathways or structures. EP are related to reorganization of activity of elements and relations within the entire brain.

Of course, the above-presented conceptions concerning the correlation between EP and systemic processes are speculative to a significant extent, because of the complexity of the link between summated activity and that of single elements. In order to define the actual mechanisms involved in processes of organization, it is necessary to study the activity of elements, i.e., impulsation activity of single neurons.

CHAPTER 3. SYSTEMIC ORGANIZATION OF NEURONAL ACTIVITY IN BEHAVIOR

Link Between Overall Activity and Neuronal Impulsation

For a long time, impulsation of single neurons, like overall electrical activity, was studied in accordance with reflex conceptions and related conceptions of localization of functions. Neuronal activity appeared to be a very obvious reaction to a stimulus, which came to the neuron under study over specific pathways. According to the reflex conception, excitation appearing in receptors activates chains of neurons situated in successively connected structures, which serve their own special functions up to the effectors.

These conceptions appeared to be so obvious and firm that the question of mechanisms of the behavioral act was simply not posed in studies of neuronal impulsation. All efforts were concentrated on two different and unrelated directions; one consisted of examining neuronal impulsation in different structures in order to determine the mechanisms of "sight," "hearing," "movement," etc.; the other concentrated on determination of the neuronal mechanisms of learning, which was interpreted as formation of a new "conditioned reflex," i.e., as "bridging of a new arc" between receptors and other effectors than before.

From the standpoint of functional system theory, the main question that should have been posed in studies of neuronal impulsation related to behavior is the question of mechanisms of organization of activity of single neurons into a single whole, into the functional system of the behavioral act. Since the researcher usually deals with the activity of only one neuron in his experiments, the question of organization of activity of many neurons can be technically divided into two: first to determine organization of activity of single neurons in time and then, after comparing the time organization of discharges of different neurons, to obtain information about organization of neuronal activity in different structures for the behavioral act. It could be of substantial help to compare impulsation discharges of single neurons to the activity recorded with a macroelectrode, since overall activity reflects processes of interaction of many elements.

There is a long history to the problem of correlation between impulsation of single neurons and overall potentials (see, for example, V. I. Gusel'nikov, 1975), and it is closely linked with the problem of electrogenesis of summated activity.

The link between impulsation discharges and "spontaneous" summated potentials turned out to be quite complex (Frost, A. Gol, 1966; Livanov, 1972; Lebedev, Lutskiy, 1972; Elul, 1972). At the same time, it was shown that the oscillations of membrane potentials of single neurons recorded intracellularly correlated with macroactivity (Klee et al., 1965; Jasper, Stefanis, 1965; Elul, 1964, 1972). Since changes in membrane potential are related to entrance of synaptic influences in neurons, macroactivity can be used to evaluate overall organization of synaptic influx in a given structure as a function of time.

The reactions of single neurons to some stimulus or other were evaluated in early studies only on the basis of impulse frequency, and they were described as excitation and inhibition without consideration of organization of impulsation in time. A more comprehensive analysis revealed that neuronal reactions usually consist of alternating phases of activation and inhibition, which made it necessary to search for new criteria to classify the entire neuronal reaction, reserving excitation and inhibition only for evaluation of different phases.

A comparison of impulsation to evoked potentials opened up some utterly new opportunities for analysis of the time and space organization of processes in the nervous system. It was found that the phases of neuronal excitation and inhibtion often coincided with specific phases of EP (Polyanskiy, 1965; Kondrat'yeva, 1967). At the present time, the link between single neuronal discharges and some components or other of EP has been demonstrated in virtually all parts of the brain, for example, the retina (Fokin, Fomin, 1969), visual (Creutzfeldt et al., 1969), sensorimotor (Vasilevskiy, Soroko, 1970; Storozhuk, 1970) and other parts of the cortex (Thompson et al., 1969), in the cerebellum (Bratus' et al., 1971), hippocampus (Dubrovinskaya, 1971), activating structures (Shevchenko, 1975a), etc.

Since, as we strived to demonstrate in the preceding section, EP serves as a correlate of general cerebral processes of organization of activity of different elements into the functional system of the behavioral act, the correlation between EP and impulsation of different neurons is of special interest to us. For this reason, we shall discuss in detail the relationship between EP and neuronal discharges.

Link Between Neuronal Activity and EP

When using anesthetized preparations, discharges of single neurons in projection regions, in relation to the stimulus, were demonstrable chiefly during the period of superficially positive EP oscillations. However,

G. Fromm and G. Glass (1970) demonstrated that the form of correlation with some EP component or other could be related to the constant cortical potential, which changes with different doses of anesthetic.

In experiments on waking animals, with the use of neutral stimuli, neuronal discharges also appeared chiefly during superficially positive EP components, which served as grounds to assume that there was inhibition of neurons during negative EP waves. The few cells (2-3%) that presented a discharge during negativity were interpreted as special inhibitory neurons. S. N. Khayutin demonstrated that, in the presence of natural, increased food motivation and stimulation of the "hunger center" of the hypothalamus, the number of neurons responding to neutral flashes of light with a discharge in negativity of the evoked potential increased to 22% (1971, 1973). He critized the conception of inhibitory pause and inhibitory neurons, and he concluded that the form of link between the neuronal response and EP components was not fixed (Khayutin, 1973; Loseva et al., 1970).

Neuronal discharges are observed in all EP phases, in response to stimuli that trigger a given form of behavior (John, 1972; Shvyrkov, 1974 and others), and the quantitative correlations between neurons presenting discharges in the presence of different components of EP vary in different behavioral acts and different structures (Aleksandrov, 1975; Shevchenko, 1975; Shevchenko, Aleksandrov, 1978).

We shall discuss the forms of correlations between impulsation and EP on the example of neurons of the somatosensory cortex with the use of electrocutaneous stimulation (ECS), which induces integral defensive behavior. In our experiments, we examined the activity of 182 neurons of the somatosensory cortex on waking rabbits, stereotactically immobilized, with the use of novocain alone. We used glass microelectrodes with tip diameter of about a micron, which were filled with 3 molar solution of KCl. EP were derived from the surface of the somatosensory cortex with a silver electrode immersed in agar, with which the trephination opening was filled. ECS which consisted of square-wave pulses varying in duration and intensity and delivered from a Physiovar stimulator by means of needle electrodes, inserced subcutaneously in the assumed receptive field of the neuron under study, which was found in advance by testing different parts of the body.

We recorded impulsation and EP on tape, using the Ampex recorder, and processed it on an AI4096 analyzer.

Under these experimental conditions, we observed the most diverse forms of relations between neuronal discharges and EP components (figure 22); and the same neuron could present discharges that coincided with several or even all EP components. In other cases, a discharge appeared only during the anterior or posterior front of one of the components (Figure 22). The phases of activation of single neurons could be more "divided" than the EP components, but in general the pattern of activity of a single neuron could be described by the EP components, which coincide with the phases of its activation. The discharges of only some neurons correspond to specific EP components. In our experiments, 84 (46.4%) out of 182 neurons presented discharges corresponding to some phase or other of EP, and we succeeded in demonstrating a primary response in 29 neurons (16%), discharges during negativity in 45 units (24.8%) and late activation, which began during the late positive EP component or later, in 31 units (17.2%).

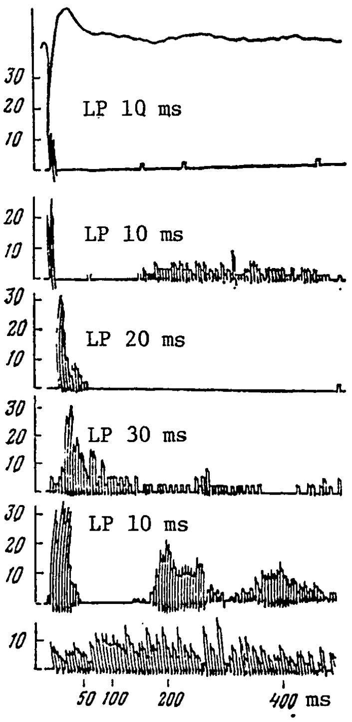

Figure 22.
Poststimulus histograms of 6 neurons of the somatosensory cortex as related to averaged evoked potential (top)

In these and all subsequent histograms the x-axis shows time in ms and y-axis the number of impulses in the channel; n = 25, channel width 5 ms. Averaging was done from the time of delivery of ECS; LP--latency period of the first phase of activation

In these same experiments, we examined the correlation between the pattern of neuronal responses and ECS parameters, and we found that the neuronal pattern could change entirely with different intensity and localization of stimulation. For this reason, the figures cited above characterize only the number of neurons that served as the material of our study, and they do not characterize activity of neurons of the somatosensory cortex in any single behavioral act or ECS of specific parameters.

Synchronism and Similarity of Neuronal Discharge Patterns in Various Brain Structures

The link between pattern components in a single neuron and EP components leads us to pose the question of correlation between time organization of neuronal discharges in different brain structures. This is a critical question to reflex conceptions of the behavioral act. Indeed, according to reflex theory, the latency period of a behavioral reaction is defined as the time of conduction of excitation over the arc of the corresponding reflex. This conception is based chiefly on the idea of localization of functions and the common sense of the temptingly understandable reflex scheme of stimulus--reaction. For example, processing of visual information is viewed as the function of the visual analyzer, "from receptors to the cortex," and the "output" of the visual analyzer then proceeds to motor structures that issue a "command" to actuating organs.

Thus, under the influence of a given conditioned or unconditioned stimulus, excitation travels over a specific route, forcing some structures or other to perform their inherent functions. In this case, different structures should discharge successively, and the time structure of neuronal discharges in each structure should be related to the specific function of this structure.

According to functional system theory, in the interval between stimulus and action there are processes of coordination of activity of different elements into a single system. Of course, the coordination processes must be similar and simultaneous in structures to be coordinated.

Quite a long time ago it was demonstrated that neurons of the same structure could response to stimuli of different modalities. At first, this property was believed to be specific for neurons of the reticular formation and other activating structures on which the collaterals of specific or classical afferent pathways converge (Rossi, Zanchetti, 1960; Magoun, 1960). Soon, however, "convergent properties" were also found in the neurons of cortical projection regions (Jung et al., 1963; Buser, Imbert, 1964; Murata et al., 1965) and in all brain structures in general (Dubner, 1967; Baklavadzhan et al., 1971; Kazakov, Izmest'yev, 1972).

These data indicate that, after a stimulus, neurons situated in many parts of the brain are activated somehow or other. A mere comparison of latency periods of neuronal responses recorded in different structure after afferent stimuli shows that neurons of different structures can be stimulated simultaneously. For example, a click in an interval of up to 30 ms elicits responses or alters activity not only of the auditory analyzer, but neurons in other parts of the cortex (Voronin, Ezrokhi, 1971), hypothalamus (Baklavadzhan et al., 1971), hippocampus (Dubrovinskaya, 1971; Lidsky et al., 1974), cerebellum (Khanbabyan, 1971), α- and γ-motoneurons of the spinal cord (Buchwald et al., 1961), primary cutaneous afferents (Banno et al., 1972), optic nerve fibers (Spinelli, M. Weingarten, 1966), etc.

J. Olds et al. (1972) obtained direct data on time of activation of neurons of different structures in the same behavioral act with the use of numerous implanted electrodes. In these experiments, a click caused rats to run to the feeder. A total of 64 different brain structures was examined. The experiments revealed that there are neurons that fire in the interval of 0-20 ms. An interval of 20 ms is the maximum resolution capacity of the method.

Continuing these studies, J. Disterhoft and J. Olds (1972) demonstrated that neurons that present discharges with the same latency period are present in different structures in a different percentile ratio. In all of these experiments, thick microelectrodes were used, the tip of which was 62.5 μm in diameter, which made it possible to describe the activity of expressly neuronal ensembles, although one could also isolate the activity of single cells using a computer.

As we have already mentioned, in all structures the time organization of discharges of single neurons corresponds to some components or other of EP derived from this structure. Since the EP in different structures become synchronous in response to stimuli that trigger a given form of behavior, it is understandable that neuronal discharges with the same latency period are demonstrable in many regions of the brain. E. R. John et al. (1969, 1972, 1974) also used the technique of recording activity of neuronal ensembles, and they demonstrated that the activity of ensembles is synchronous and similar in different structures.

The objective of our studies was to compare the discharge patterns of expressly single neurons of different structures in the same behavioral act. Experiments were conducted using the same method: rabbits immobilized stereotactically, with anesthetization of the sites of fixation, developed conditioned reflexes to a flash of light reinforced by ECS after 600 ms. We analyzed the evoked potentials and responses of neurons in the visual and somatosensory regions of the cortex and reticular formation of the mesencephalon. Unlike the experiments of J. Olds and E. John, in ours we used glass microelectrodes filled with 3 M KCl, with tip diameter of about one micron, which enabled us to reliably isolate the activity of expressly a single neuron.

Since our objective was to demonstrate the possible patterns of neuronal discharges in the structures under study, ECS was delivered to different points of the body surface so that we could assess the discharge patterns in the course of various pretrigger integrations.

Impulsation, EP and electrical activity of cervical muscles, which served as a control of development of the conditioned reflex, were recorded on tape and processed on AI-256 and NTA-512 analyzers. The results, i.e., averaged EP and poststimulus histograms of neuronal discharges, were recorded on a two-coordinate automatic recorder, or photographed from the analyzer oscilloscope.

We recorded 35 neurons in the visual cortex; 7 of them remained "areactive" to light whatever the ECS parameters; 1 was always inhibited and 27 showed some pattern or other corresponding to EP. Since the pattern of the response to light could change with changes in ECS parameters and the discharges could correspond to several different EP components, we shall classify the phases of neuronal activation independently of the number of phases for a single neuron.

We observed a discharge during the first EP component in response to light with various ECS parameters in seven neurons. In this phase, there were usually only 1-3 impulses, which appeared with a latency period of 18 to 26 ms. During the negative EP component, 5 neurons presented activation with a latency period of 28 to 88 ms, and 26 neurons presented late activation with latency period of 100 to 500 ms.

Late activation was observed both in neurons that did not response or were inhibited during preceding phases (15 cells) and neurons that were activated in preceding phases.

In response to ECS, 3 out of 35 neurons showed a primary response; discharges in negativity were observed in 13 cells; late activation was found in 19 neurons, both among those that fired discharges in the preceding EP phases (8 neurons) and those inhibited or that did not respond during the early phases (11 neurons).

Data for the somatosensory cortex were obtained in experiments conducted under the very same conditions also on 12 rabbits. We analyzed the activity of 83 neurons. Of this number, 33 cells responded to the conditioned signal in accordance with the EP phases: we succeeded in demonstrating a primary response with latency period of 21-30 ms in 10 neurons, discharges in negativity (latency period of 30-86 ms) in 17 and late activation in 19, 6 of which did not present early phases.

Phasic activity was observed in 49 neurons out of 83 in response to ECS: a primary response in 12, discharges in negativity in 29 and late activation in 21, 8 of which did not present discharges in the early phases.

In analyzing the activity of neurons of the reticular formation, we compared the phases of activation to EP derived from the surface of the visual cortex, rather than reticular formation. Although we also recorded EP from the reticular formation in these experiments, as the microelectrode was introduced its position in relation to different tissular elements of the reticular formation changed, and this led to a change in configuration and even inversion of polarity of different EP components.

The studies of A. Ramos et al. (1975, 1976) revealed that there could be independent change in "focal EP" and impulsation derived with the same microelectrode. This is probably related to the plastic geometric localization of microelectrodes in tissue. When recording EP from the cortical surface with a macroelectrode, the derivation conditions remain constant, which enables us to compare the phases of activation of different neurons, demonstrated even during different "passages" of the microelectrode, to the same components.

We observed phasic reactions in response to a conditioned stimulus in 31 out of 68 neurons of the reticular formation. A total of 20 cells fired discharges during the primary response, 11 did so during EP negativity, and late activation was demonstrated in 24 neurons, 8 of which did not have early phases of activation. Phasic reactions to ECS were observed in 41 neurons: primary response in 25, discharges in negativity in 7 and late activation in 26, 9 of the latter presenting only late activation.

A comparison of all these data leads us to conclude that, in all of the structures examined, the time organization of neuronal discharges is similar and that each of them contained neurons that presented identical discharge patterns in response to a conditioned signal or ECS.

Figure 23 illustrates poststimulus histograms of responses of neurons of different structures to a conditioned signal, which contained the main components of the pattern.

The responses to ECS were also similar and had components corresponding to the phases of synchronous EP in different parts of the brain. For the sake of comparison, Figure 24 illustrates the poststimulus histogram of a reticular formation neuron, and Figure 25 illustrates poststimulus histograms of a neuron of the somatosensory cortex, which show discharges during the negative EP component, both in the conditioned and unconditioned responses.

For direct comparison of time characteristics of neuronal activity in the visual and somatosensory cortex, we (with Yu. I. Aleksandrov) conducted special experiments, in which we recorded neuronal activity in both regions using two microelectrodes at the same time. The rest of the experimental conditions were analogous to the preceding ones.

We recorded 61 pairs of neurons: 48 neurons of the visual cortex and 53 of the somatosensory. These proportions are attributable to the fact that we sometimes were able to record the activity of one neuron in one region "in a pair," with two or three successively demonstrable neurons in another region.

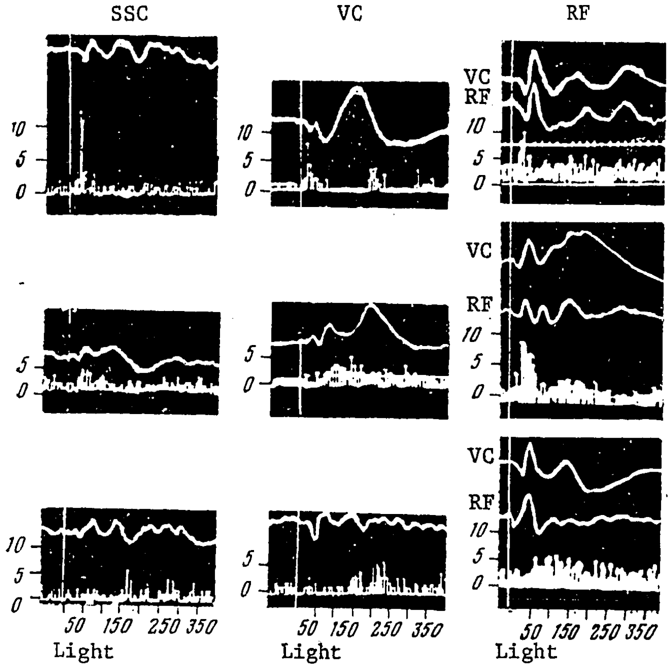

Figure 23. Identical types of neuronal responses to flash of light, in somatosensory (SSC) and visual (VC) cortex, and in mesencephalic reticular formation (RF). Photograph of NTA-512B screen, n = 25; channel width 4 ms. Averaged potentials in corresponding regions shown above the histograms. The top row of histograms refers to neurons firing discharges at the time of the primary EP response; the middle row is at the time of negativity and the bottom row, late activation

In some cases, we were able to directly observe neuronal discharges in both regions that were synchronous and coincided with the same EP components. Figure 26 illustrates a vivid example of discharges of two neurons coinciding with the primary components of EP, in response to both the conditioned stimulus and ECS.

In this series, we tried to assess the order of involvement in activation of neurons in different cortical regions after delivery of conditioned signal. For this purpose, poststimulus histograms were plotted with channel width of 2 and 4 ms. The latency period of the neuronal response was defined as the time between the stimulus and first maximum on the

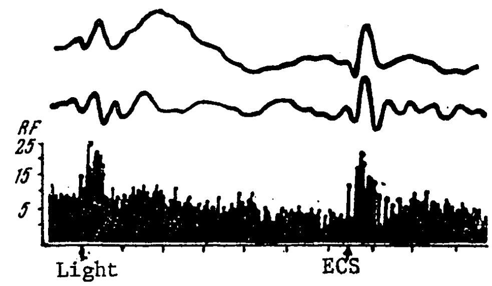

Figure 24.
Responses of reticular formation neuron to conditioned stimulus (light) and electrocutaneous stimulation (ECS). Top: averaged EP of visual cortex and reticular formation; bottom: poststimulus histogram of reticular formation neuron responses. Channel width 3 ms; n = 25 (51st to 75th combinations); 650-ms interval between light and ECS

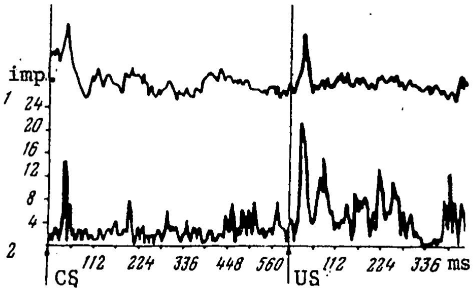

Figure 25.
Poststimulus histogram of somatosensory cortical neuron firing discharges in EP negativity. Bottom: histogram; channel width 4 ms; n = 25; photograph from X=Y recorder. Arrows show time of stimulation

histogram. We analyzed neurons with maximums within 100 ms after the stimulus. We found 24 such neurons in the visual cortex and 28 in the somatosensory cortex.

Figure 27 illustrates histograms of distribution of neurons of the visual and somatosensory cortex according to latency periods. In both regions, neurons become active simultaneously and the maximums of probability of their responses are in the range of 20 to 40 ms. These probabilities constitute 0.58 for the visual cortex and 0.57 for the somatosensory cortex.

In order to compare the dynamics of processes in these regions according to the parameter of number of activated neurons, we calculated the latency periods not only for the first, but all phases of activation of each neuron. From these data we plotted histograms of distribution of activation phases of 34 neurons of the visual cortex and 40 of the somatosensory cortex (the rest of the neurons presented no phasic activation). These "activity profiles" are illustrated in Figure 28. Although they differ somewhat from one another, due to the difference in number of neurons in different regions that are active within a given interval, it is obvious that there is no question of any successive [systematic] involvement of these regions.

Thus, after a stimulus that triggers a behavioral act, the neurons of each region fire discharges throughout all phases of EP. There are neurons that fire discharges synchronously in different structures at any given time.

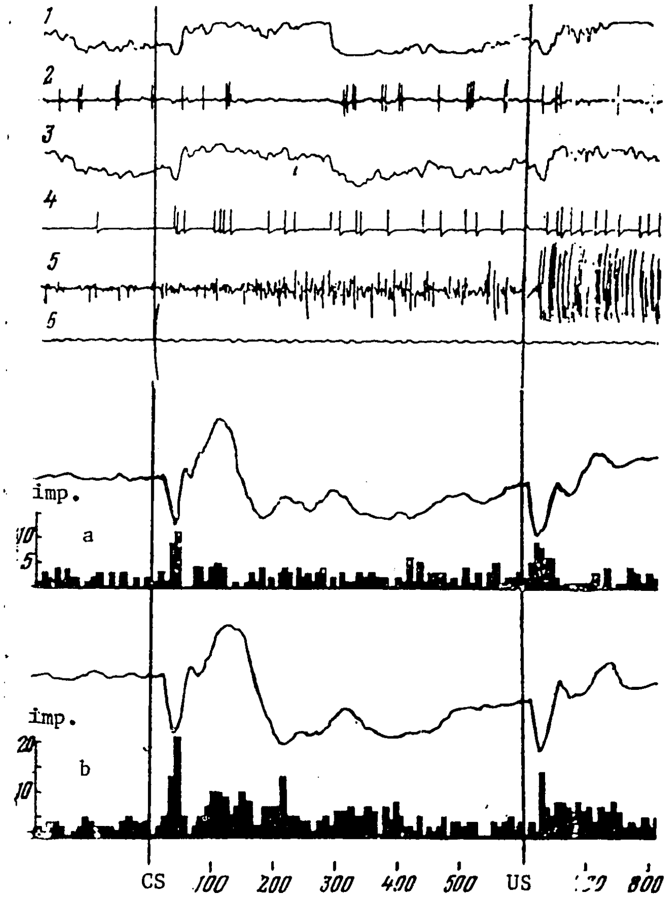

Figure 26. Synchronism of neuronal discharges in visual and somatosensory cortex in response to conditioned light flash (CS) and electrocutaneous reinforcement (US [unconditioned stimulus]). Bottom: averaged EP and peristimulus histogram of neurons of visual cortex (a) and somatosensory cortex (b). Channel width 8 ms; n = 25

1, 3) EEG of visual and somatosensory cortex, respectively
2, 4) impulsation activity of neurons
5) EMG
6) marks of stimulation

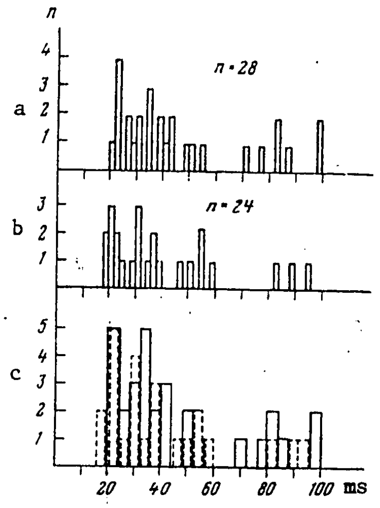

Figure 27.
Histograms of neuronal distribution according to latency periods of reactions to conditioned light stimulus. X-axis, latency period, ms; y-axis, number of neurons
a) somatosensory cortex
b) visual cortex
c) somatosensory (solid line) and visual (dash line) cortex

It is not always the same neurons that fire synchronous discharges, since the latency periods of activation phases of the same neuron vary significantly. Figure 29, for example, illustrates the dynamics of latency periods of two simultaneously recorded neurons in the visual and somatosensory cortex in response to a conditioned signal. When the stimulating electrodes were moved from the front leg to the contralateral hind leg, the response patterns of these neurons to the conditioned signal changed significantly, although the physical properties of the conditioned stimulus remained constant. This change in patterns was reflected in the change in dynamics of latency periods of responses.

Since there are neurons that are stimulated during any EP component in all regions, it is obvious that the discharges of some neuron in some part of the cortex are synchronous with discharges of some neurons or other in other brain structures.

It appears to us that all of the above data warrant the conclusion that there are simultaneously functioning neurons in all structures in the behavioral act. Although a different number of neurons is activated in each structure during different phases of EP, the overall time structure of processes in different regions is identical, and it corresponds to the time structure of "synchronous" or "general" EP.

We believe that synchronism and identical nature of time organization of both EP and neuronal discharges in different structures rule out successive performance of any functions by separate structures, and cannot conform with conceptions of "conduction of stimulation" over the "reflex arc." The neurons in each structure do not become active for a specific time as excitation advances from receptors to effectors, but they are involved in all processes that participate in formation and implementation of the behavioral act.

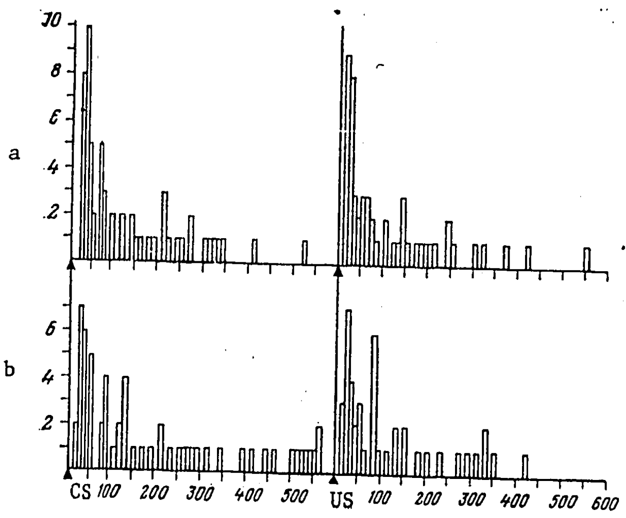

Figure 28. Histograms of distribution of activation phases for neurons of somatosensory and visual cortex, according to latency periods of responses to conditioned light flash (CS) and electrocutaneous stimulation (US). X-axis, latency period, ms; y-axis, number of activation phases with the indicated latency period

a) in somatosensory cortex b) in visual cortex

It is also apparent that the similarity of EP configuration and neuronal discharge patterns in different structures precludes consideration of EP configuration and neuronal discharge pattern as the expression of only some specific function of a structure; the question of time pattern as a means of coding expressly specific information is also eliminated.

All of the submitted facts indicate, in our opinion, that processes in different structures of the brain acquire common features of organization in performance of a behavioral act and only during this act.

Since EP and neuronal discharge patterns corresponding to EP phases are demonstrable locally, they reflect local physiological processes; but since they are synchronous and common to different structures, it must be agreed that the same processes develop in many structures. Since both physiological functions and links between various structures are different, only processes of interaction between elements of different structures can have the same dynamics. In other words, in the course of a behavioral act, organization of physiological processes in time is the same for different brain structures, and it is determined by the time structure of systemic processes of the behavioral act that are common to the entire brain and organism, specific processes of organization of an integral functional system out of special physiological mechanisms, rather than the function of specific, for example, "visual," mechanisms in the visual analyzer.

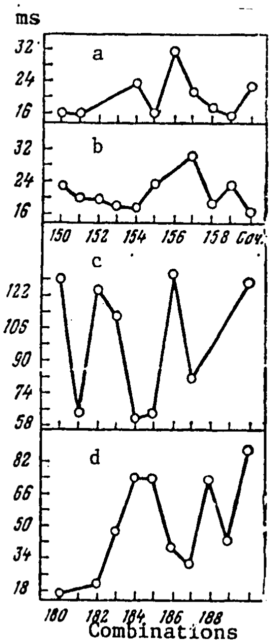

Figure 29.

Dynamics of latency periods of reactions of two simultaneously recorded neurons. X-axis, sequential number of combinations; y-axis, latency periods of responses to light, ms. Reinforcement ECS of 45 V was delivered to the front (a, b) or hind (c, d) leg

a, c) latency periods of responses of somatosensory cortical neurons to flash
b, d) same for neurons of visual cortex

It is difficult to reconcile the fact that there is synchronism and similarity of pattern configurations in the responses of neurons of different structures to the same stimulus, as well as the possibility of obtaining similar responses by the same neuron to different stimuli, with the analytical data obtained on preparations as to determination of the latency period of a given discharge by a fixed number of synaptic arrests on the way from a receptor to the recorded neuron.

Indeed, the specific and constant anatomical organization of links in different parts of the brain cannot explain the similar configuration of responses to the conditioned stimulus and ECS in, for example, the somatosensory cortex, where this has been described by many authors (Shul'gina, 1967, 1969; Vasilevskiy et al., 1972), or similar patterns in response to the same conditioned stimulus by neurons of the visual and somatosensory cortex. Evidently, morphological links remain constant and implement all types of time organization of processes in all regions and with all stimuli. However, the link between the discharge of some neuron and arrival of excitation over any specific pathways can be established only on anesthetized preparations, in which behavior is impossible.

Even the earliest neuronal responses, with a latency period of 10-20 ms, could be related to delivery to it of simultaneous influences from many sources. The very possibility of such influences (for example, on neurons of the somatosensory cortex) was demonstrated through stimulation of various brain structures in anesthetized preparations (Storozhuk, 1974). Some of these influences may be subliminal, with the use of anesthesia, for onset of a spike response, while others may be so strong that they induce EPSP [excitatory postsynaptic potentials] and spikes.

For example, stimulation of the amygdaloid complex of cats given nembutal elicited a response in 11 out of 194 neurons of the somatosensory cortex, in 5 of which an impulse appeared with a latency period of 1-2.2 ms, and in another the "latency period of the response to stimulation of the amygdaloid complex was even shorter than in response to stimulation of VPL [expansion not known]: 2.2±0.2 and 2.4±0.17 ms, respectively, although in both cases the response consisted of one impulse, and the probability of a response was the same, P = 1" [Storozhuk, 1974, p 149). In response to stimulation of the posterior hypothalamus, 15 out of 132 neurons responded, 4 of which had a latency period of 1.9-3.9 ms (p 150). Upon stimulation of the pyramidal tract, orthodromal spikes appeared in 13 out of 21 neurons, with latency periods of 2.6 to 7.5 ms.

The collateral influences from pyramidal cell axons could be addressed to different neurons. In the opinion of V. M. Storozhuk, "in the case of spontaneous activity this could cause a distinctive chain reaction of dissemination of excitation in the somatic cortex" (p 151).

If we consider that fibers from the most diverse regions of the brain come to the somatosensory cortex and that these structures have a "tonic" effect on neurons of the somatosensory cortex (Li, 1956; Tori et al., 1965), even if stimulation thereof does not induce spikes in somatosensory neurons, we arrive at the somewhat trite conclusion that the neurons of the somatosensory cortex are under the inlfuence of all structures of the brain.

As we have already mentioned, a stimulus in the behavioral act induces neuronal responses in many structures with short latency period and, in particular, ECS induces responses with short latency periods by elements of the optic nerve (Spinelli, Weingarten, 1966), reticular formation (Shevchenko, 1975a), hypothalamus (Baklavadzhan et al., 1971), hippocampus (Dubrovinskaya, 1971), etc. For this reason there are no grounds to question the fact that, even with delivery of ECS that is "specific" for the somatic analyzer, even the early responses of the projection neurons of the somatosensory cortex may be due to synchronous convergence of many influences, rather than afferentiation over lemniscal pathways alone.

A. S. Batuyev et al. arrived at the same conclusion earlier, with reference to the primary evoked potential: "The experiments convinced us that the primary response has a rather complex structure and contains components that differ, not only in source in subcortical structures, but in distinctions of their expression on the cortical level.... The main debatable question is whether the primary response is the result of one afferent volley in a specific thalamocortical system or whether it is the product of integration on cortical neurons of many afferent messages from various subcortical structures, and we uphold the latter view" (1971, p 29).

These considerations are even more valid with regard to the early responses of nonprojection regions and all late activations.

The presence of simultaneously discharging neurons in many structures and the unquestionable links between them invalidate the question of how expressly one structure affected another. From the point of view that we are developing, all processes in all structures reflect interaction of neurons in all structures, in accordance with the morphological links between them. For example, while we know from morphological studies that the somatosensory cortex has direct communication with VPL, nonspecific thalamic nuclei, reticular formation, other cortical regions, etc., it is obvious that the discharges of neurons in the somatosensory cortex are caused by influences that are carried over a certain number of fibers from all these structures.

At the same time, the question of which exact fibers deliver influences to the somatosensory cortex, for example, from VPL or visual cortex, can be answered on the level of VPL neurons or neurons of the visual cortex, the activity of which, in turn, depends on all influences converging on the VPL or visual cortex neurons. Ultimately, each spike of each neuron is caused by the integrative activity of the entire brain.

Thus, as applied to a waking organism, the explanation that any phase of neuronal activation occurs by conduction of excitation over some isolated pathways or chains of neurons is unjustifiably simple, since these chains, by virtue of the specificity of morphological communications of each neuron, must be specific and show quite diverse phases of activation in different neurons. It is only organization of processes in the entire network of neurons that can cause similar patterns for different neurons that have a different place in this network. Consequently, it is only organization of all processes that causes appearance of each spike.

It is known that quite a large number of synaptic influences should reach a neuron simultaneously for at least one spike to appear (Kostyuk, 1971). The time and space organization of influences on a specific neuron should, in turn, be a function of coordination of integrative processes occurring in many neurons. The appearance of phases of neuronal reactions can apparently be attributed to the presence of statistical maximums and minimums in the dynamics of number of selectively related and mutually coordinated elements. Expressly such dynamics of processes of coordination of activity of different elements must probably be the same and common to different parts of the brain involved in the functional system of the behavioral act.

The fact that both neuronal discharges and EP, which are a reflection of membrane potentials of many neurons, has the same time organization in different structures indicates that different structures receive and send influences simultaneously in the behavioral act. If we consider the synaptic influx from different sources into each individual structure, by virtue of synchronism of discharges in the other structures this influx will have the same time organization as everywhere else, and it will determine neuronal discharges also in accordance with the general time structure of processes in all other parts of the brain. In this sense, we can refer to systemic general cerebral time organization of synaptic influx to any neuron. The similar EP in different structures are a reflection of this general cerebral synaptic influx.

The identical time organization of processes in various structures indicates that it is only the specificity of afferent and efferent communications that determines the difference in significance of spikes appearing simultaneously in two different neurons in two different parts of the brain. According to functional system theory, any exogenous stimulus finds pretrigger integration ready, i.e., a dynamic system of interrelations of elements prepared in advance, which is what determines the "spatial" composition of synaptic influx to each element.

Determination of Neuronal Discharge Pattern by Pretrigger Integration

When the activity of neurons was compared to EP in response to an insignificant stimulus, it was already found that the patterns of activity of different neurons could change (Kogan, Klepach, 1967). Moreover, in some cases, the poststimulus histogram summated for many responses did indeed reflect different patterns present in different responses, as illustrated in Figure 30, taken from the work of T. N. Loseva, S. N. Khayutin and V. B. Shvyrkov (1970).

E. John (1972, 1974) even expounded the view that neuronal responses are always extremely variable, and that it is only the pattern of activity of neuronal ensembles that does indeed have a constant correlation with EP. However, the experiments of Ramos et al. (1976a, b, c) and Schwartz et al. (1976) in the laboratory of E. John revealed that the response pattern of the same neuron may even be more constant than the EP configuration with the same behavior, and that it is demonstrable for several days. The same neuron yielded different patterns in response to the same stimulus that triggered different behavior. The stability of neuronal responses with stability of stimulus of behavior was also observed in the studies of other authors (Olds, Hirano, 1969; Hirano et al., 1970; Phillips, Olds, 1969).

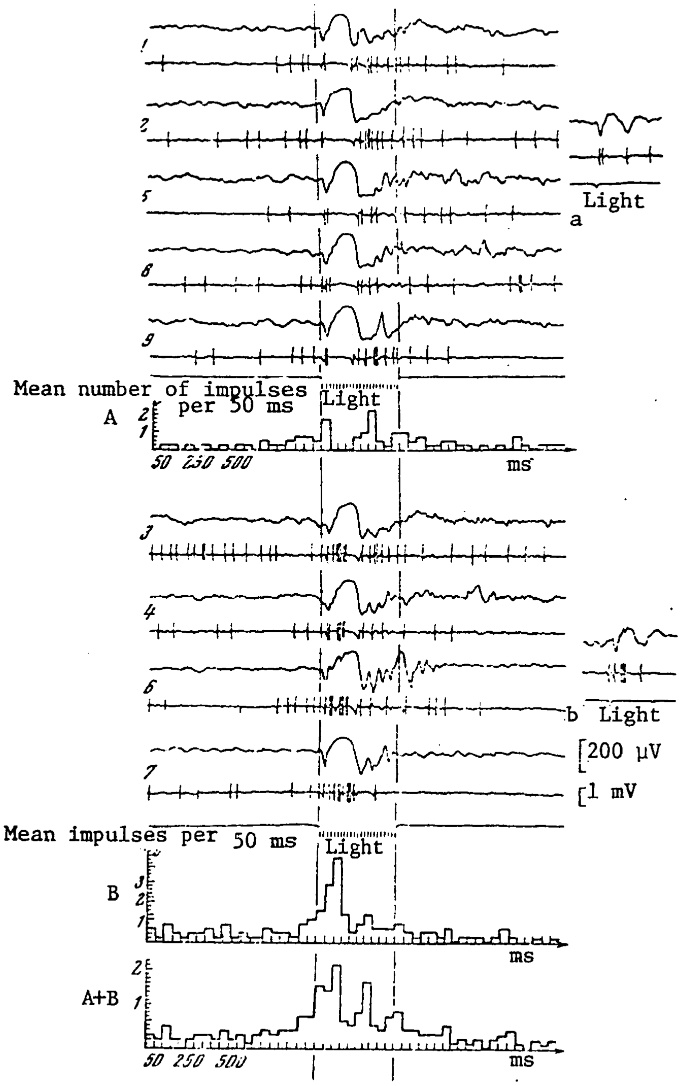

Figure 30. Reaction of one neuron of the visual cortex to exposure of the retina to 9 successive 500-ms flashes. On each strip: top line is superficial ECC [electrocorticogram]; the numbers on the left are sequential flash numbers.

A) average of 5 neuronal responses, including a primary response and late activation; inhibitory pause corresponds to slow negative oscill.
B) average of 4 responses of same neuron, where activation phase corresponds to slow negative oscillation
A+B) averaging of all reactions of same neuron

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SYSTEMIC MECHANISMS OF BEHAVIOR

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BY V. B. SHUYRKOV

2 OF 3

Thus, the phases of activation of single neurons under different experimental conditions may be related to diverse ways to EP components. However, these relations are not formed at random, and they depend on the behavior triggered by the stimulus. As validly observed by M. N. Livanov, "one should probably think about participation of each neuron in the formed system of integration, rather than initially inherent capacity of neurons to react only to a given stimulus and only in a specific way. It seems correct to refer to nature of reaction of cortical neurons, rahter than to types of such neurons" (1971, p 7).

Just like EP, the discharge pattern of a single neuron is "endogenous" in behavior, i.e., it can be quite different in response to the same stimulus that triggers different behavior. This has already been demonstrated in numerous experiments involving development of conditioned reflexes, which showed that the responses of neurons in different parts of the brain to a light flash, which became a conditioned stimulus, changed in configuration (Kondrat'yeva et al., 1970; Sviderskaya, 1971; Vasilevskiy, 1971, and others).

At the same time, different stimuli that trigger similar behavioral acts can trigger similar discharge patterns in the same neuron, and this was demonstrated in a comparison of patterns of conditioned and unconditioned responses of neurons in defense behavior (Vasilevskiy, 1973; Shul'gina, 1968; Shvyrkov, Aleksandrov, 1973, and others). Many authors have reported that, with change in behavior, there is change mainly in the late phases of the pattern of neuronal responses (Travis, Sparks, 1967; Ramos et al., 1976, and others). On the basis of analysis of activity of neuronal ensembles, E. R. John and Morgades (1969) also believe that the early components of the pattern are "exogenous," unlike the "endogenous" late ones.

According to our point of view about the conformity of EP with systemic processes, the greater dependence of late phases on behavior could be attributed to the fact that the late phases correspond to processes of implementation of one specific behavioral act, which changes with the slightest change in exogenous conditions. The early EP components reflect the transition to actuating mechanisms of one act from pretrigger integration, corresponding to all possible behavioral acts in a given situation; for this reason, the early phases are less related to one specific behavioral act, and they should change with change in all pretriggering integration.

We tested this hypothesis in special experiments, which Yu. I. Aleksandrov (1975) conducted on rabbits with developed conditioned defense reflex. The ECS parameters were changed to alter pretrigger integration, since ECS differing in duration and force induce, of course, different degrees of defensive motivation (Leander, 1973). ECS of different localization also has different ecological and behavioral significance (Rozhanskiy, 1953; Menitskiy, Trubachev, 1974).

Experiments were conducted on 12 stereotactically immobilized rabbits, with anesthetization of fixation sites. The conditioned stimulus, a flash of light synchronized with a click delivered from a Soneclat stimulator (0.3 J, 50 μs), remained unchanged throughout the experiment; ECS delivered through needle electrodes from a Physiovar stimulator was altered after every 25-75 combinations. The light was 600 ms away from ECS, and interstimulus intervals ranged from 10 to 2 min. We recorded impulsation of neurons of the visual cortex, EP and EMG, which served as a control of development of the conditioned reflex, on magnetic tape, and the data were processed on AI-256 and NTA-512-B analyzers. The results (averaged EP and poststimulus histograms of neuronal discharges) were recorded on a two-coordinate recorder or photographed from the analyzer oscilloscope.

Of the 30 neurons of the visual cortex that presented phasic responses to the light or ECS, we succeeded at least once in altering the parameters of reinforcement in 15 neurons. In 9 of the latter, there was a change in pattern of responses to a light flash that was unchanged in physical parameters. In one neuron, a change in pattern was observed when the stimulating electrodes were moved over just a few centimeters. In others, we succeeded in inducing such change only by changing significantly the intensity of ECS or moving the electrodes to another leg. The changes in pattern could consist of either disappearance of one of the phases, or appearance of new components, and they were observed in neurons that had different "base patterns."

These data are listed in Table 1, which also shows that, even in neurons whose activation phases did not change the response to change in ECS parameters changed quantitatively, i.e., it contained more or fewer spikes in the same phases.

Table 1. Modification of reactions of visual cortex neurons to conditioned flash of light with change in ECS parameters

Type of response	Number of neurons	Qualitative and quantitative changes in reactions	Changes in pattern
Primary activation	6	6	4
Negative activation	3	3	1
Late activation	5	5	4

It must be noted that even the primary phases of the pattern were related to ECS parameters. In three cases, the primary response present with the initial parameters disappeared and in another it appeared (Figure 31). The responses of neurons of the visual cortex to ECS itself also changed with change in its parameters (Figure 32). These changes were less marked, but they also involved all phases of the pattern, as can be seen in Table 2.

Table 2. Modification of reactions of neurons of visual cortex to ECS with change in its parameters

Type of response	Number of neurons	Qualitative and quantitative changes in reactions	Changes in pattern
Primary activation	1	1	1
Negative activation	9	4	1
Late activation	1	1	1

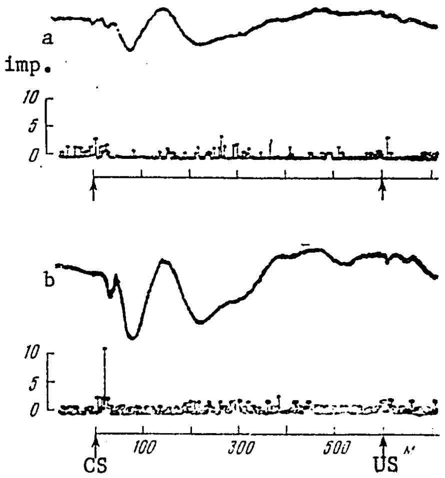


Figure 31.
Appearance of primary response by neuron of visual cortex to conditioned light flash with increase in intensity of ECS

a) inhibition of neuronal activity in response to flash, reinforced by ECS of contralateral front paw, 30 V
b) appearance of primary response to conditioned flash with increase in ECS to 60 V.

Above (a) and (b): averaged EP; below: peristimulus histogram of impulsation activity. Channel width 4 ms, n = 25

CS--conditioned stimulus
US--unconditioned stimulus

These data indicate that all phases of the pattern can change with a change in pretrigger integration. Since primary discharges appear in different neurons in response to the same conditioned signal that triggers different preliminary integrations, it may be assumed that even in regions that are projections in relation to the stimulus the response is "endogenous," i.e., it corresponds to activity of expressly the elements that were included in advance in pretriggering integration. Of course, "endogeny" of the primary response in projection regions could not be demonstrated when recording only macroactivity.

Comparable results were also obtained for neurons of the somatosensory cortex (Shvyrkov, 1974) and reticular formation (Shevchenko, 1976a).

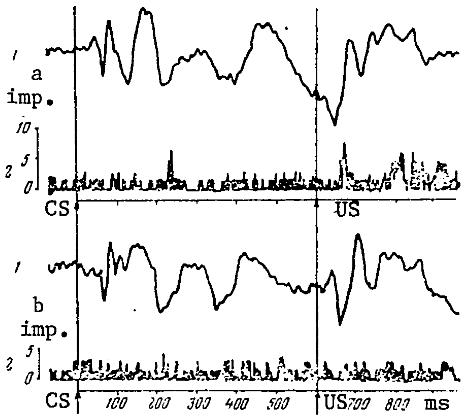


Figure 32.
Disappearance of visual neuron response to conditioned light and ECS with change in localization of stimulating electrodes.

1) averaged EP
2) peristimulus histogram; channel width 2 ms, n = 25

a) late activation in response to light and activation in negativity with afterdischarges in response to ECS of contralateral hind paw, 30 V
b) disappearance of reactions with stimulation of ipsilateral front paw with same intensity of current

There was equally graphic demonstration of the dependence of pattern of activity of visual neurons in response to light on pretrigger integration in experiments where a change in preliminary integration was produced by changing reinforcement from food to defensive (Shvyrkova and Shvyrkov, 1974; Shevchenko, 1976). We shall consider these findings in connection with other questions.

Involvement of Neurons in Systemic Mechanisms of the Behavioral Act

Cortical neurons: For a long time, the activity of neurons of different structures of the brain was traditionally analyzed solely as a parameter of the specific function of a given structure. It appeared quite logical to relate all types of activity (for example, of neurons of the visual cortex) to the parameters of a visual stimulus and processing of information about this stimulus. However, the very first data obtained on waking animals in learning studies revealed that the activity of visual cortex neurons changes in relation to change in behavior (Ricci et al., 1957; Jasper et al., 1962). The same experiments revealed that neuronal activity in other structures, in particular, somatosensory, motor and frontal cortex, depended on behavior.

Subsequently, all researchers concerned with development of conditioned reflexes observed a change in neuronal activity in response to a stimulus that had become conditioned (Vasilevskiy, 1968; Shul'gina, 1967, 1968; Rabinovich, 1975, 1976, and others).

At the present time, because of development of techniques for recording neuronal activity of freely behaving animals, an increasing number of works is being published demonstrating a direct link between activity of neurons of all brain structures and specific stages of integral behavior, rather than a given stimulus. For example, V. Mountcastle et al. (1975), who studied neuronal activity of the associative cortex demonstrated a link between the discharges of these neurons and situational distinctions that cannot be formulated in other than terms of and objectives of behavior.

An entire series of studies conducted by H. Niki (1974a, b) demonstrated a relationship between neuronal activity in the prefrontal cortex and specific stages of behavior.

I. Ranck (1973), who studied hippocampal neurons, found that it was possible, in general, to compare their activity to only specific behavioral acts. He calls this approach "microphrenology." However, we believe that the term "microethology" would be more suitable, since we are dealing here with the link between activity of specific neurons and specific behavior, rather than specific behavior and activity of a localized region of the brain.

The experiments of J. Olds et al. (1969a, b; 1972) and E. R. John (1969, 1972, 1974) showed that a link with specific behavior is observed for neuronal activity in many structures of the brain.

A link with expressly behavior was noted by many authors for neurons of the reticular formation (Sparks, Travis, 1968; Travis, Sparks, 1967), as well as neurons of cortical projection regions (Shvyrkova, Shvyrkov, 1975; Andrianov, Fadeyev, 1976; Miller et al., 1972, 1974). J. Miller et al. (1972) maintain that "cellular activity in sensory systems is strictly determined by the behavioral situation and objective" (1972).

All of the cited data, as well as our experiments that demonstrated a correlation between neuronal activity and parameters of future reinforcement, confirm the validity of the thesis of functional system theory, to the effect that "elements referable to some anatomical system or other are involved in the system of a behavioral act only to the extent that they aid in achieving a preplanned result" (Anokhin, 1973a, p 35).

Indeed, each neuron participates in the behavioral act in the form of impulses which, as they spread over axonal collaterals, have a specific influence on all elements linked with this neuron and, ultimately, the entire system. The presence of "superfluous" impulses, as well as absence of "necessary" ones would create a discordance in the system and make it difficult to achieve the useful adaptive result. In this sense, any impulses have actuating output functions.

According to functional system theory, impulses can only appear in neurons whose past activity led to achievement of a specific result; in this sense, we can speak of goal-directed activity of each element in the functional system of the behavioral act. The link with behavior can be explained, from the point of view we are developing, by the fact that neuronal activity is not a "reaction" to a "stimulus," but is retrieved from memory, as it is necessary to achieve the result of the entire behavioral act.

Of course, this is possible only when the model of the result is already represented in pretriggering integration.

The link between activity of single neurons and the entire behavioral act enables us to raise the question of involvement of neurons in specific systemic mechanisms of the behavioral act. At the same time, this is a question of how pretriggering integration is implemented in the goal-directed activity of many different neurons.

Since, as we tried to prove in Chapter 2, EP components serve as correlates of specific systemic processes in the behavioral act, and the discharges of single neurons coincide in time with some EP components or other and have the same properties, the next hypothesis logically arises. Neuronal discharges corresponding to the primary EP component reflect processes of implementation of the part of preliminary integration that is the most "prepared" for the triggering stimulus; the discharges during EP negativity must correspond to processes of afferent synthesis and decision making, i.e., total replacement of prior organized activity of the integral organism by coordinated activity corresponding to the next behavioral act. The discharges during the positive EP component must correspond to processes of mobilization of organized actuating mechanisms and, finally, late activation should correspond to actual implementation of the acceptor of action results and program of action, i.e., coordinated purposeful activity of elements that were united in prior processes into a single functional system of the behavioral act. At the same time, there must be "further maturation" of pretrigger integration of the next behavioral act directed toward achievement of the next goal in the entire hierarchy of behavioral acts that ultimately result in survival of the organism.

Since the same neuron can be activated in different EP phases, it must be assumed that the same element can participate in several or even all systemic processes of the behavioral act. The fact that a neuron can present phasic activation in different behavioral acts suggests that the same neuron may be involved in different integrations. Since neuronal function, i.e., its possible contribution to achievement of the result of a behavioral act, is determined exclusively by the topography of its axonal collaterals, diverse integrations can be related only to the diversity of sets of neurons included in a given integration.

We tested all these hypotheses in collaboration with Yu. V. Grinchenko by means of special experiments. We used the same method as for the study of evoked potentials in the continuum of behavior. The modification was that the rabbit was trained to pull on a ring upon delivery of the conditioned signal of a click. The click triggered approach to the ring and pulling on it; the light flash stopped the pulling and triggered movement to the feeder.

In these experiments, in addition to recording of EP in the visual cortex by means of a silver electrode immersed in agar, which filled a trephination opening, we recorded the impulsations of 68 neurons of the visual cortex. These recordings were made using a method developed in our laboratory (Grinchenko, Shvyrkov, 1974). We used a micromanipulator attached to the rabbit's skull; a field transistor operating in the mode of a source follower and connected in the circuit (Rosetto, Vandercar, 1972) was also placed on the skull. This technique enabled us to record, with virtually no artefacts, the activity of single neurons in the course of several behavioral cycles and, occasionally, several hours.

After amplification with a UBP 1-02 and Biophase, the EEG of the visual cortex, impulsations, EMG of cervical muscles and marks for sound, pulling, light and presentation of feeder were recorded on magnetic tape of a 14-channel magnettor. These tapes were then reproduced on paper using an automatic ink recorder, with reduction of feed rate to one-eighth.

Impulsation was processed by the histogram method, and 50% deviations from the background were considered as a change in activity. We selected 39 of the 68 neurons of the visual cortex under observation in these experiments for comprehensive analysis, among those demonstrated in at least five behavioral cycles. Of these 39, 7 neurons did not change their activity in any of the phases of the behavioral cycle. The change in activity of the other 32 neurons coincided with some behavioral act which, in accordance with functional system theory, we singled out as a segment of the behavioral continuum from one result to another: from the click to appearance of light, and from the light to the feeder. In the first behavioral act, we observed a change in activity of 20 neurons, 7 of which contained activation phases in their response and 13 only inhibition. In the second behavioral act, activation was demonstrated in the responses of 18 neurons and 12 cells were inhibited; in all 30 neurons showed a change in activity in the second act.

As in the preceding experiments, we found that neuronal activity in the visual cortex is observed in all time intervals of the behavioral act (Figure 33). The early (up to 200 ms) phases of activation were clearly related in time to the prior stimulus--result (Figure 34), whereas the late ones appeared with a variable latency period. This "late" activation was observed in 4 neurons in the first behavioral act and 6 in the second. They were demonstrable much better by the method of "reverse" averaging, i.e., by plotting the "preresult histograms" (Figure 35).

Expressly these activations are related to the actuating mechanisms of the behavioral act directed toward achievement of a specific result. Appearance of "stimulus--result" stops these activations (Figure 35).

In our rabbits, we occasionally observed intersignal tugging at the ring, i.e., tugging that started without the click and, of course, did not lead to appearance of the flash. In such cases, the link between late activations and a specific behavior was also manifested in the absence of a stimulus (Figure 35), which does not warrant consideration of these activations as reactions to some factor. Actually, expressly these late activations reflect the coordinated purposeful activity of elements of the integral organism in a specific behavioral act.

A comparison of late activation of neurons of the visual cortex in two successive behavioral acts revealed that two neurons participated in both behavioral acts and the remaining eight in only one of them. Five neurons that showed late activation only in the second act were not reactive or inhibited in the first (Figure 36), while three cells, which showed late activation in the first act were areactive or inhibited in the second, but two of them presented a primary response to light (Figure 34).

Thus, various neurons of the visual cortex are involved in various behavioral acts, and with a change from one behavior to another one can observe a "change in integration" in the visual cortex. Figure 36 illustrates examples of different activations of 12 neurons in two acts. In these transitional processes between the first act and the second, 14 neurons were consistently involved, 10 of which showed only a primary response, 2 only discharges in negativity and 2 both early phases of activation, while 8 neurons were consistently inhibited in the early phases also.

A comparison of the set of neurons showing late activation to neurons showing a primary response indicates that these groups do not coincide: in response to the light flash, 4 neurons presented both of the analyzed phases (Figure 36), 6 presented a primary response and no late phase, or even inhibition during the late phases (Figure 34), 2 presented late activation and were inhibited during the early phases (Figure 36).

In our opinion, these findings signify that at first the light flash generally triggers a different set of activations from the one that is needed to achieve the future result, i.e., reach the feeder. This, in turn, indicates that the primary responses are due to all of the pretrigger integration that is formed by the time the flash is used, rather than the only integration that corresponds to a single act. This single integration is formed only during the later phases.

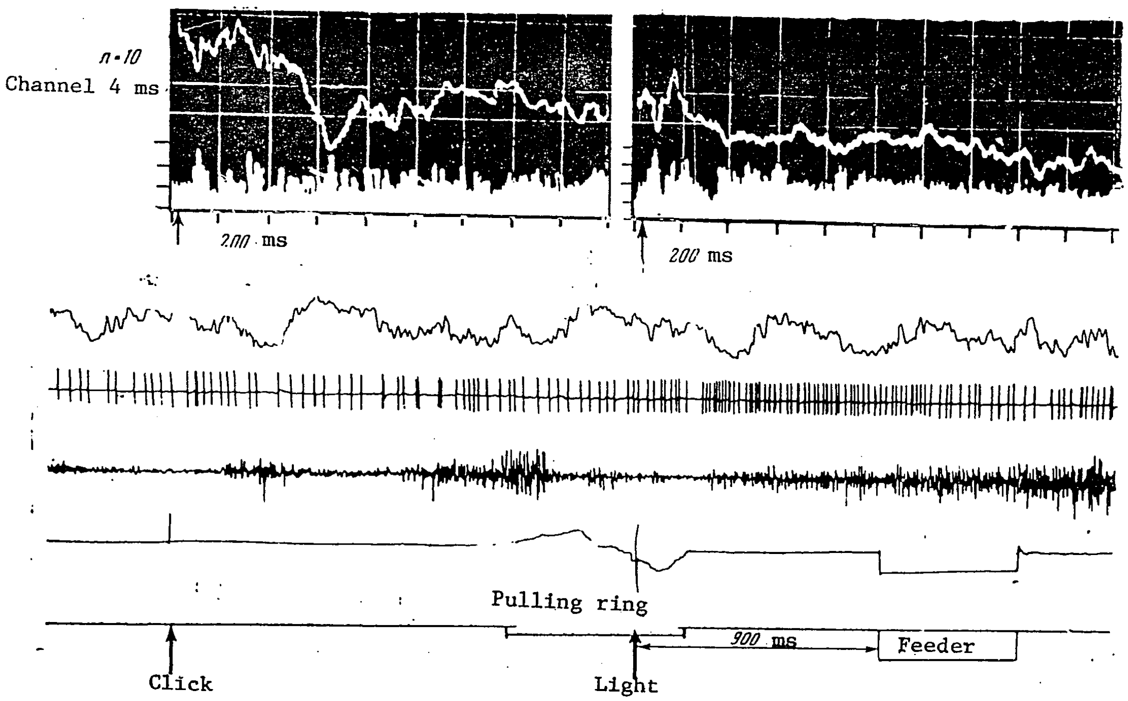


Figure 33. Activity of visual cortex neuron in all phases of the food-obtaining cycle. Top: averaged EP and histograms of neuronal activity. Photographed from the screen of an NTA-512B, 4-ms channel. Top to bottom on the single tracings: EEG of visual cortex, neuronogram, EMG of cervical muscles, sound, ring pulling, flash and feeder marks

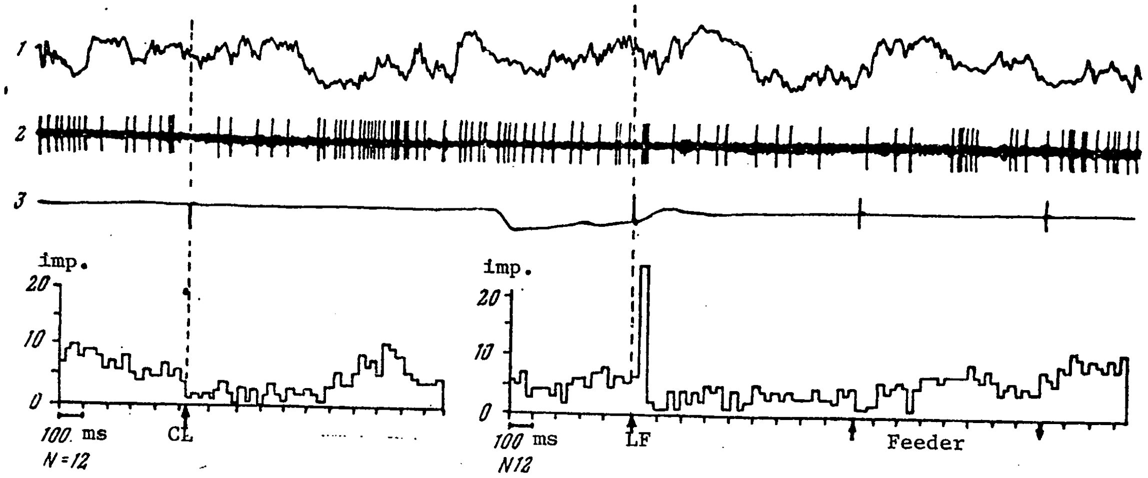


Figure 34. Primary response of visual cortex neuron demonstrated by plotting histogram from time of appearance of light flash.

Top to bottom: 1) EEG of visual cortex
2) neuronogram
3) behavior marks

Bottom: histogram of neuronal activity in 12 cycles plotted from time of delivery of click (CL) and light flash (LF)

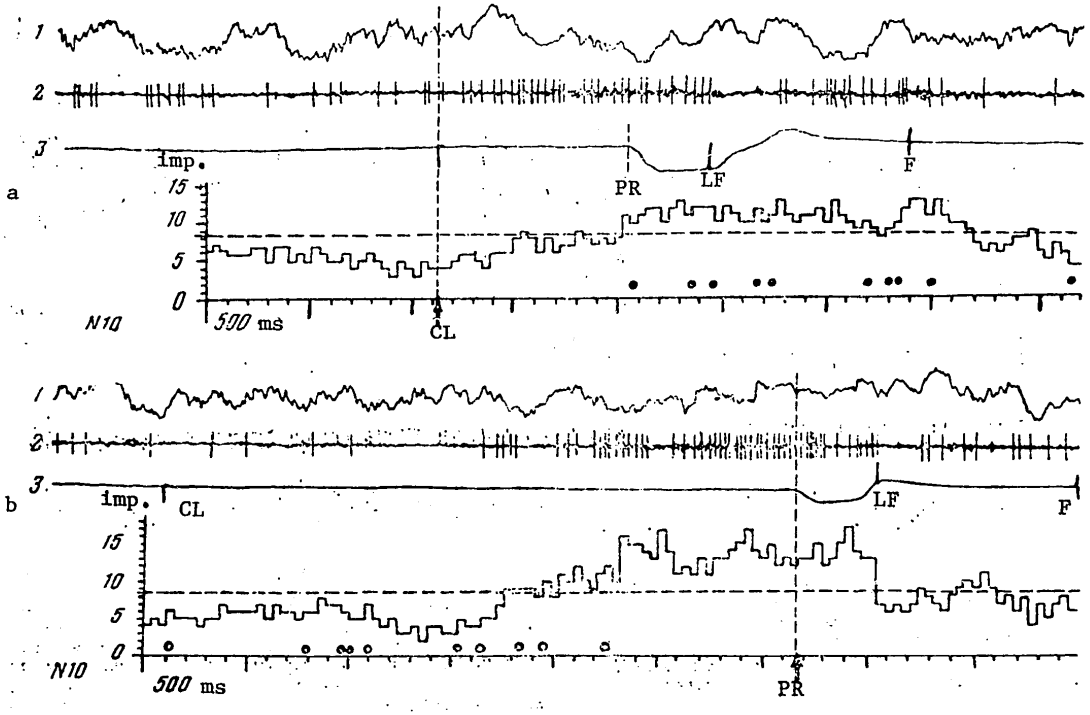


Figure 35. [caption furnished on the next page]

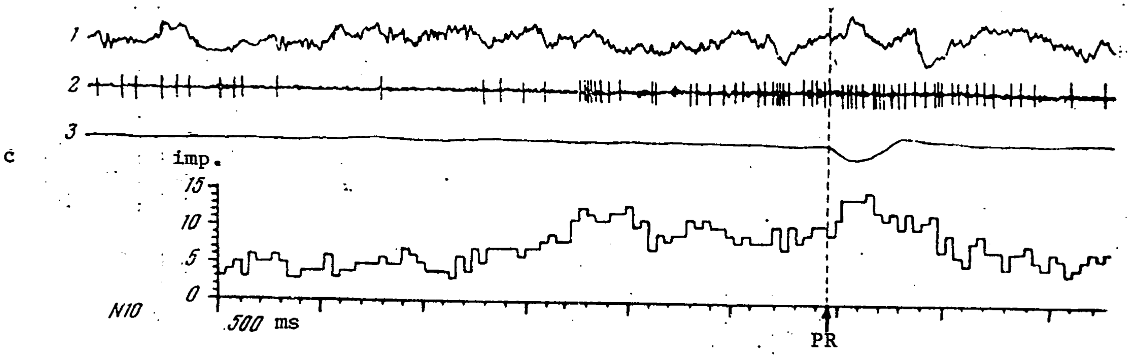


Figure 35. Demonstration of activity preceding result by the method of reverse averaging

In a, b, c: single tracings at the top:
1) EEG of visual cortex
2) neuronogram
3) behavior marks (PR--pulling ring, CL--click, LF--light flash, F--delivery of feeder)

Bottom: histograms of neuronal activity in 10 behavioral cycles

a) histogram plotted from time of click (black circles show start of ring pulling)
b) when histogram is plotted from the time the ring is pulled, activation is considerably more marked (white circles refer to time of delivery of click)
c) neuronal activity during intersignal ring pulling

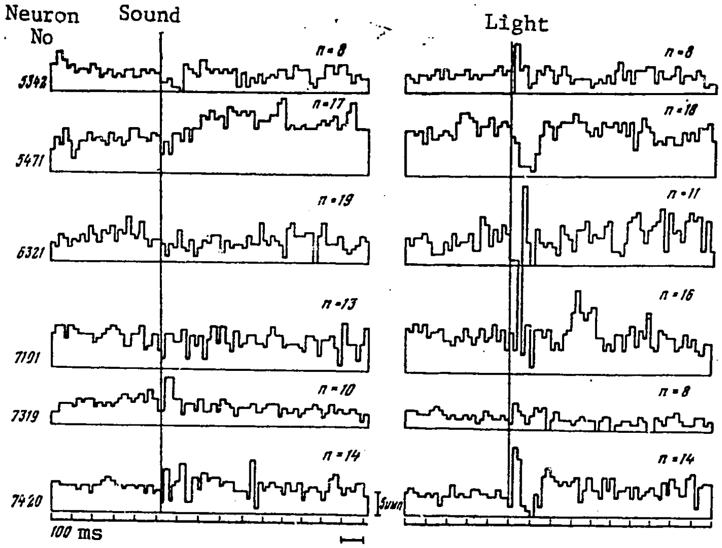


Figure 36. Different types of neuronal activation in rabbit's visual cortex during food-obtaining behavioral acts triggered by click and light flash
Time of triggering click and light flash is shown by vertical arrows. Number of runs is shown on histograms, 20-ms channel

The fact that late activation appeared in neurons that presented no primary response indicates that pretrigger integration is not complete at the moment of the flash, so that it is necessary for additional activation and coordination of activity of different elements, which takes place in the interval between the primary response and late activation, i.e., during EP negativity.

We observed discharges during EP negativity after the flash in four cases, in two of which the neuron also presented a primary response, one presented late activation and one fired discharges in all phases.

Thus, coordination of activity of neurons inlcuded in actuating integration and providing for performance of action and achievement of the result occurs during EP negativity by means of both discharges of these neurons and of elements that will not be subsequently used in the behavioral act. A comparison of forms of activity of different neurons in the first and second behavioral acts revealed that the discharge patterns are generally independent. For example, out of the 10 cells that presented a primary response to light, 2 also had a primary response to sound, 1 fired discharges in negativity (Figure 37), 2 showed late activation, 3 were inhibited and 2 did not change their activity.

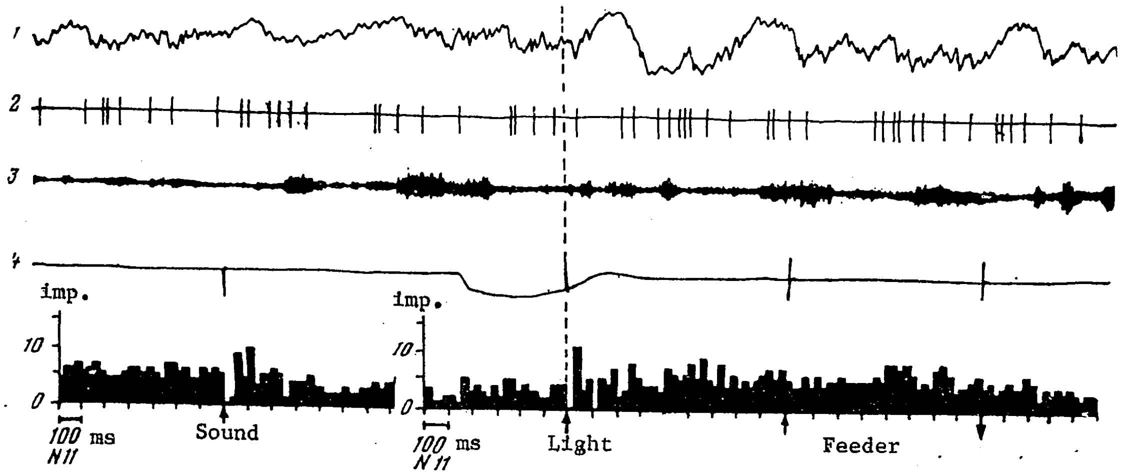


Figure 37. Early activation of visual cortex neuron appearing in connection with click and light flash.

Bottom: histograms of neuronal activity in 11 runs, primary response and discharge during EP negativity to sound and primary response to light with late activation

1) EEG of visual cortex
2) neuronogram
3) EMG
4) behavior marks for a single act

Thus, processes of coordination of activity of elements in different behavioral acts occur in the general case as discharges of different sets of neurons. These data are in striking contrast to those of many authors, including ourselves (Shvyrkov, Aleksandrov, 1973) concerning a similarity of patterns of neuronal responses to conditioned and unconditioned stimuli in the case of combining light and ECS. This difference is probably due to the difference between the two behavioral acts analyzed in the experiments we have described.

In some cases, we observed neuronal impulsation during incorrect rabbit behavior: the click did not trigger movement to the ring and pulling it, but triggered movement toward the feeder, which should have been done by the flash. In such cases, the patterns of neuronal activity after the click could be very similar to those induced by light with correct behavior. Figure 38 illustrates one of the 15 neurons whose activity could be observed not only with mistakes, but "in the absence of behavior": the rabbit that became satiated in the course of the experiment took a "break" and did not even change its position in response to the click; in this case, 14 neurons out of 15 were areactive, although in the presence of behavior 8 of them were inhibited in some phase or other, while 6 were activated, and 2 of the latter presented a primary response.

These facts confirm once more both determination of all types of activity by pretrigger integration and the link between any impulses and achievement of a specific result through specific behavior.

In addition to cells involved in actuating mechanisms of either behavioral act, we observed two neurons that were diffusely activated throughout the behavior cycle, from the click to the start of chewing, and six cells that were inhibited throughout this behavior. Perhaps, their activity was related to implementation of actuating mechanisms of the functional system of the entire food-obtaining cycle.

Pretriggering integration, which occurs prior to delivery of the click, must include both elements whose activity is required to reach the light and those whose activity ultimately leads to the feeder. Although, as we mentioned in our study of EP, light could acquire independent positive meaning, it is merely an interim result, and its model is included in the hierarchy of goals, achievement of which leads to the feeder and, ultimately, to satisfaction of food motivation.

The fact that different behavioral acts are related in pretrigger integration by the hierarchic rather than time principle indicates that, already at the time of the first act in a sequence there can be coordination of functions of all elements, the activity of which will lead to the ultimate result, i.e., activity of all elements of the first, second, etc., acts on the way to achievement of the end result. This can explain the mistakes in behavior observed in our experiments, for example, when the rabbit moved directly toward the feeder instead of the ring in response to a click, i.e., performed the last act immediately, and not the first.

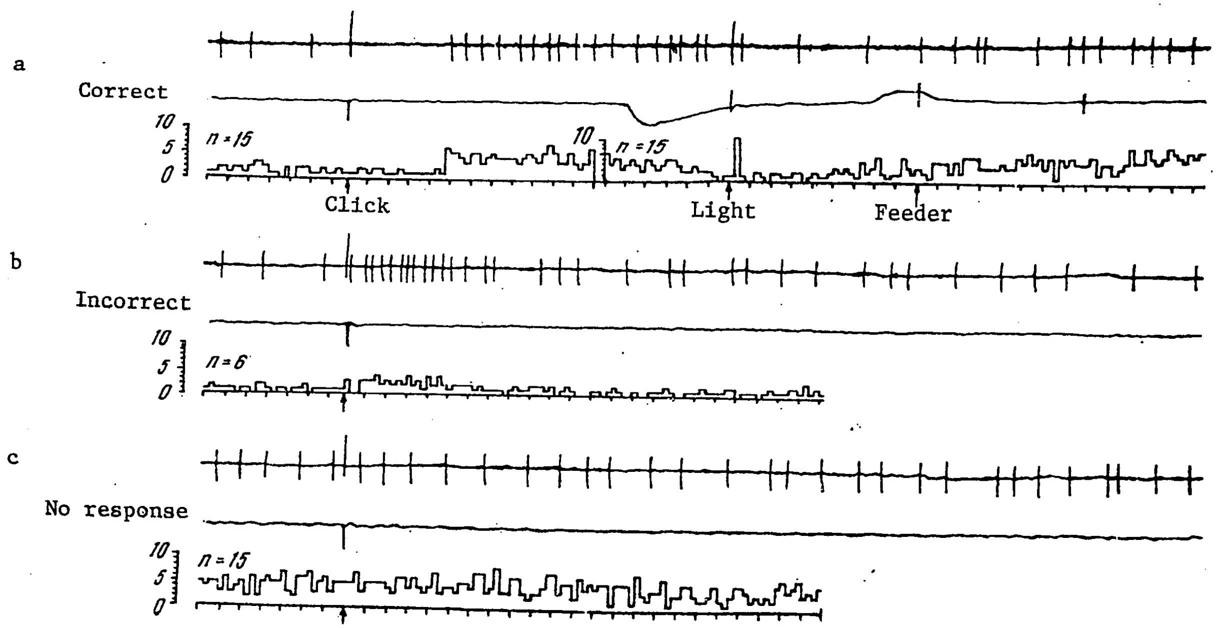


Figure 38. Link between activity of visual cortex neurons and behavior

a, b, c) top to bottom: neuronogram in a single act, behavior marks, histograms of activity in several acts (number of runs shown on histogram). We see the difference in neuronal activity after a click that triggers movement toward the ring (a), running to feeder (b) and absence of behavioral response (c)

For correct successive behavior, the part of pretrigger integration that corresponds, for example, to the last act in the hierarchy must be specially inhibited during the first act; in any case, the elements whose activity will hinder this act must be inhibited. The same reasoning can be applied to the situation when several alternative behavioral acts are contained in the pretrigger integration: the choice of one behavioral act makes it necessary to destroy the part of preliminary integration that corresponds to the other alternative.

The possibility of anticipatory excitation of elements that do not hinder current behavior was actually demonstrated already in the classical experiments of I. P. Pavlov with conditioned salivation reflexes. But in instrumental behavior, anticipatory salivation may hinder achievement of an interim result, and then it could also be inhibited (Ellison, Konorski, 1964; Konorski, 1970). Such inhibition of hindering elements is observed, for example, in experiments on dogs, when the dog has to lift a front leg to eliminate electrocutaneous stimulation of the hind one. Then a special activity develops in the muscles of the hind leg, which prevents it from bending so as not to impair equilibrium when the front leg is raised (Aslanova et al., 1963; Aslanova, 1971).

According to functional system theory, the choice of one act out of all those "provided by pretrigger integration" is made by means of the systemic mechanism of decision making, which provides for coordination of activity of all needed elements and inhibition of all those whose activity could prevent reaching the result.

Decision making occurs in the interval between the trigger stimulus and start of action. This process coincides with the time of development of the negative EP component and neuronal discharges that coincide with this component. Since the same neurons fire discharges in this interval that could do so during performance of the behavioral act, it may be assumed that decision making is a coordination of activity of the same elements whose activity would then be used or not used to reach the result.

Such a process does not require involvement of any special "deciding" neurons or structures, the existence of which was assumed by many authors. However, it is known that injury to some structures, particularly the frontal lobes (Shumilina, 1949b; Luriya, 1962) and hippocampus (Gambaryan, Koval', 1973; Vinogradova, 1975), causes difficulty in expressly the choice of adequate acts when organizing the entire successive behavior. For this reason it was very interesting for us to analyze the involvement of one of these structures, namely the hippocampus, in systemic mechanisms of the behavioral act.

Hippocampal neurons: Experiments involving injury of the hippocampus revealed that single behavioral acts are not affected, whereas any differentiation, as well as organization of successive behavior are indeed made more difficult or impossible (Penfield, Milner, 1958; Vavilova, 1971, 1974;

Voronin, Semenova, 1971; Gambaryan, 1973; Mering, Mukhin, 1971; Hsiao, Isaacson, 1971, and others). Experiments involving recording of summated electrical activity in free behavior showed that theta rhythm appears in a choice situation; this led some authors to conclude that the hippocampus is involved in decision making (Kamp et al., 1971).

The most recent studies of neuronal activity of the hippocampus in free behavior showed that hippocampal neurons not only participate in the situation of choice, but the most varied forms of behavior, both "voluntary" and "automatic, " as well as "appetent" and "consummatory" (Ranck, 1973; O'Keefe, 1976). Thus, according to I. Ranck (1973), analysis of unit activity confirmed that the role of the hippocampus is to organize combinations and sequences of automatic and nonautomatic behavioral acts in successive behavior.

In comparing cell activity to visually observed behavior, I. Ranck distinguishes "theta cells" involved chiefly in organizing voluntary behavioral acts and "complex spike" cells that fire discharges only during appetent behavior or only consummatory behavior. The cells of these two types differ in frequency of background activity: theta cells usually have a background activity that is higher than 8-10 impulses/s while complex spike cells have activity that is lower than this frequency.

The objective of our experiments, conducted in collaboration with K. Reyman and Yu. V. Grinchenko, was to determine the time intervals during which hippocampal neurons fire discharges in performance of successive food-obtaining behavior and, consequently, the systemic processes in which hippocampal neurons are involved during single behavioral acts and all successive behavior. Chronic experiments were conducted on three rabbits, each of which was involved in 3-4 experiments. The difference from preceding experiments was that, after the click delivered by the experiment, the rabbit turned toward a pedal, instead of a ring, and depressed it to such a level as to achieve an interim result in the form of a light flash. This flash was, as in the preceding series, also a trigger stimulus for the next behavioral act of going to the feeder. A photoelectric cell was used to record the moment the rabbit put its snout into the feeder as a result of this act. The feeder was presented automatically 1 second after the flash; therefore the feeder usually appeared after the rabbit dropped its snout in the opening, in which food appeared. After eating the feed, the rabbit returned to the pedal and waited for the next click.

In these experiments, we arbitrarily distinguished three successive acts: from the click to depression of the pedal and appearance of flash; from the flash to bending the head in the feeder; from bending the head to termination of chewing. Impulsation of hippocampal neurons was derived and amplified in the same manner as in preceding experiments. But, after amplification, this activity was fed into a standard impulse shaper and immediately recorded using an automatic ink recorder, together with the EEG of the visual cortex, EMG of cervical muscles and behavior marks.

In these experiments, we recorded the neurons of fields H_3 and H_4 of the dorsal hippocampus and dentate fascia. After the experiments, we made a morphological examination and reconstructed the microelectrode track.

In all, we recorded 65 hippocampal neurons. The activity of these cells was correlated with all successive behavioral acts. Some cells fired discharged or changed their spontaneous activity in only one behavioral act, while others did so in several (not necessarily consecutive) acts. We selected 31 neurons, whose activity was demonstrated in at least 5 runs of the entire successive behavior, for detailed analysis.

Figure 39 illustrates a tracing of a complete cycle of successive behavior from the time the rabbit removed its head from the feeder to the start of chewing, which can be seen from the typical activity on the summated EEG. This neuron always fired discharges after the snout was removed from the feeder, as shown by the histogram plotted from the time the snout was lifted (bottom left) and during the primary response to light (bottom right on the histogram). Of these 31 neurons, 12 presented early phases of activation in some behavioral act and 19 presented late activation. Their discharge patterns did not differ in any way from those recorded for the visual cortex. As in the visual cortex, late activation was related to actuating mechanisms of reaching the result of the behavioral act, while early activation coincided with the time of the "stimulus--result" of the preceding act.

Figure 40 illustrates a neuron that was activated during the behavioral act "from click to flash." A comparison of behavioral acts with different latency periods for depressing the pedal showed that activation always preceded the start of touching the pedal and occurred even during inter-signal behavioral acts in the absence of the click. In other neurons, we observed activation preceding another result, dropping the snout into the feeder, and such activation was also observed in cases of incorrect behavior, when the rabbit performed this act without depressing the pedal before it (Figure 41). The same neuron could present different phases of activation after reaching the result of one behavioral act and activation preceding the result, in another act.

Figure 42 illustrates the periresult histograms of activity of one neuron in the same behavioral acts, which were plotted in relation to a flash of light (b) and putting the snout in the feeder (c). The variable interval between the flash and turning toward the feeder (see marks on x-axis of histogram) resulted in absence of late activation in the poststimulus histogram in response to the flash, whereas on the histogram plotted in relation to the time of putting the snout in the feeder there was masking of early postflash activation.

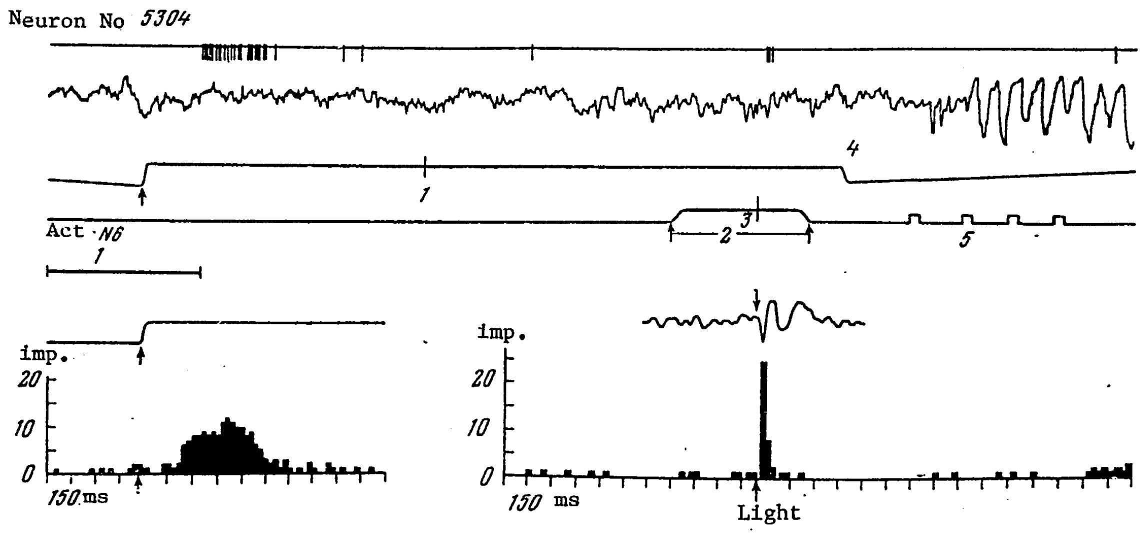


Figure 39. Involvement of hippocampal neuron in two behavioral acts out of the entire cycle of food-obtaining behavior.

Top to bottom: neuronogram, EEG; marks for one cylce: removing head from feeder (arrow), click (1), putting snout in feeder (4), depressing pedal (2), light flash (3) and delivery of feeder (5); n = 10; 30-ms channel

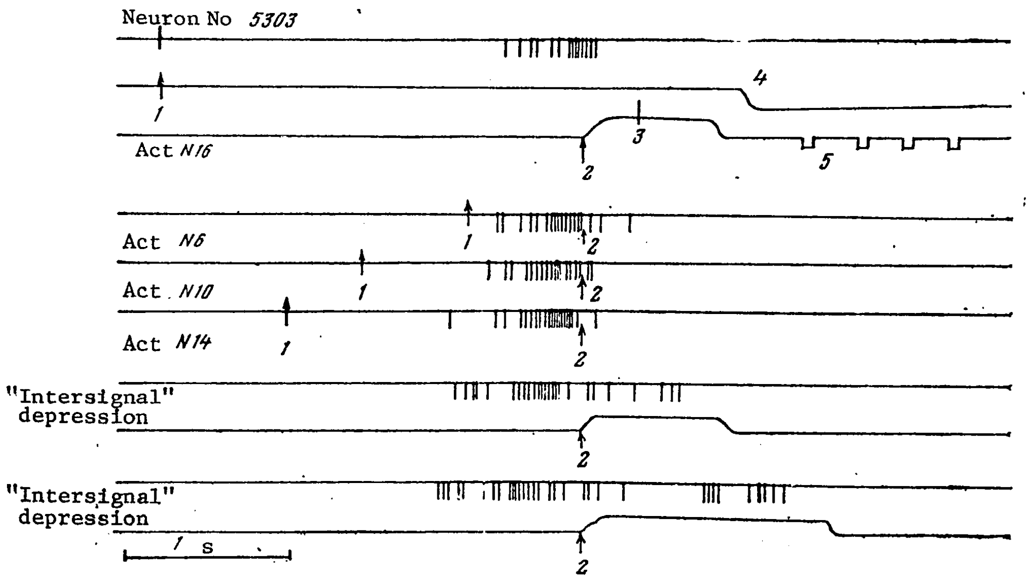


Figure 40. Activation of hippocampal neuron before depressing pedal. Sequential numbers of behavioral cycles shown on the left; all tracings compared in relation to time of depressing pedal

1) click 2) depressing pedal 3) light 4) snout in feeder 5) cabbage

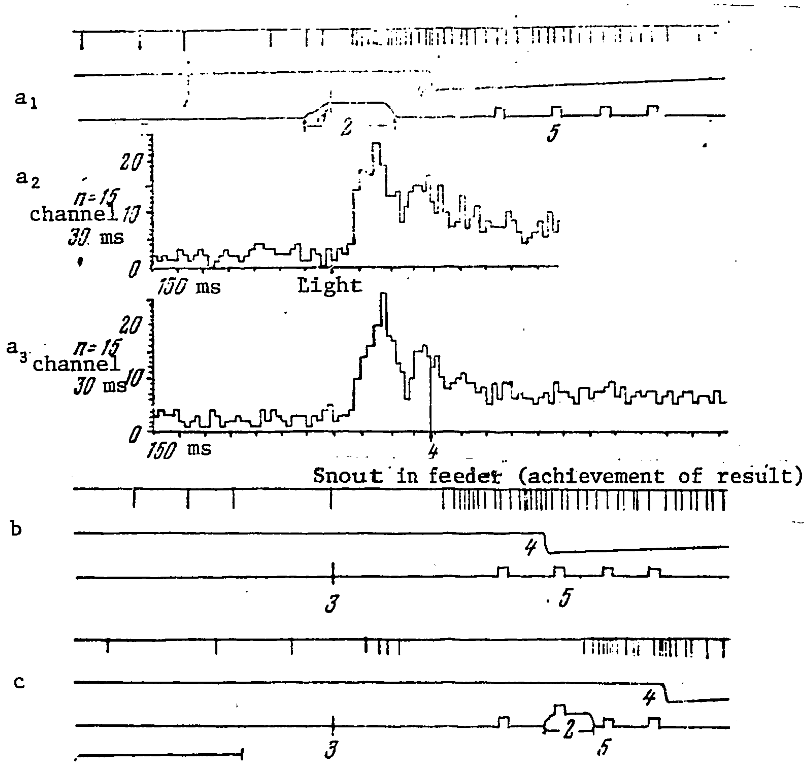


Figure 41. Activation of hippocampal neuron before putting snout in feeder

a₁) marks are the same as in Figure 39
a₂) histogram of neuronal activity in 15 acts, plotted from time of appearance of flash
a₃) histogram for the same 15 acts plotted from time that snout is put in feeder. The small variance of time between the flash and putting snout in feeder renders these histograms very similar
b) flash delivered immediately, without prior click or depression of pedal; the increased latency period in this case for putting snout in feeder permits demonstration of "preresult nature" of neuronal activity
c) flash triggers pedal depression, like the click; in this case, neuronal activity also precedes putting snout in feeder

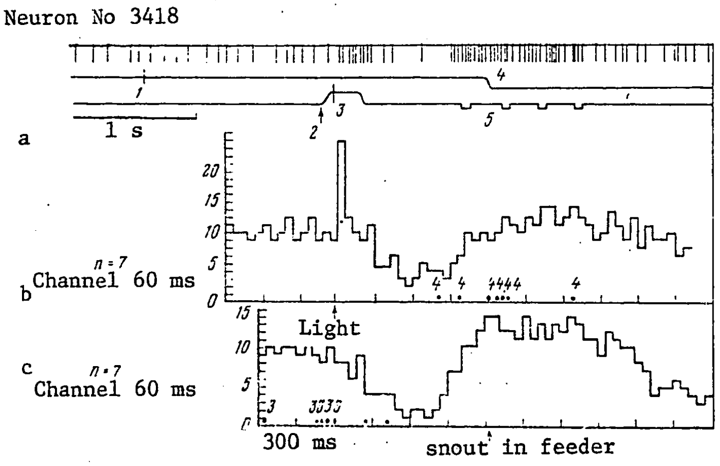


Figure 42. Activation of neuron in different time intervals within a single behavioral act

a) neuronogram during single behavioral act (marks are the same as in Figure 39)

b,c) histograms of neuronal activity in the same behavioral cycles; in plotting histograms in relation to flash (b), we demonstrate activation in the first 60 ms after the flash (putting snout in feeder in separate acts is shown on x-axis by dots); in plotting the histogram in relation to time of putting snout in feeder (c), there is demonstration of activation preceding this result (time of appearance of flashes is shown on x-axis by dots)

1) click
2) depressing pedal
3) flash
4) head in feeder
5) delivery of feeder

We also observed neurons that showed late activation in different acts. Figure 43 illustrates an example of a neuron activated in the "click--flash" interval and the longer "flash--feeder" interval. This figure is also furnished to show that the distinction of three interim results and three behavioral acts in this cycle is largely arbitrary. Indeed, depressing the lever is also an interim result, and the illustrated neuronal activity is more likely to be related to achievement of expressly this result, since it is the most marked just before this event.

At the same time, the activity of this neuron prior to tapping with the feeder, which did happen or did not in the case of intersignal behavior, is triggered most likely after releasing the lever, rather than after the flash, and the moment the snout is put in the feeder, which we singled out as an interim result in the rabbit's integral behavior, did not induce any reorganization of activity of a single neuron. Evidently, these correlations between activity of a hippocampal neuron and different events may be indicative of a rather close link between separate hippocampal neurons and separate forms of behavior, which confirms the views of I. O'Keefe (1976).

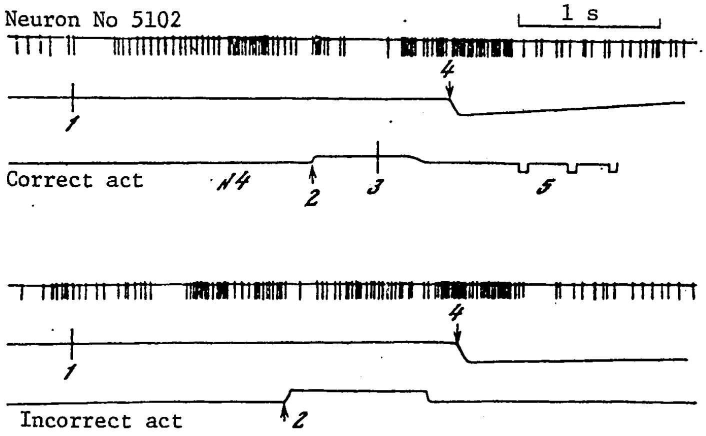


Figure 43. Activation of hippocampal neuron in two behavioral acts. Top: with "correct" behavior, activation precedes depression of pedal and taking food from feeder; bottom: activation corresponds to the same times in the behavioral cycle of "incorrect" behavior (the rabbit did not depress the pedal enough and, without seeing the flash, dropped its snout in the feeder). Marks are the same as in Figure 39

1) click
2) depressing pedal
3) flash
4) head in feeder
5) delivery of feeder

On the whole, hippocampal neuron activity turned out to be "endogenous" also, and it was determined by pretrigger integration, like the activity of other brain structures; the different elements whose activity was necessary only to the next behavioral act could be involved in the coordinated function of actuating mechanisms of behavior already during preceding behavioral acts.

Although the distinction of only three behavioral acts and three results is, of course, arbitrary, it enables us to assess the activity of hippocampal neurons in the entire continuum of behavior. In the bottom part of Figure 44, activation of all neurons analyzed in detail is compared to "click--pedal," "flash--feeder" and "eating" intervals. This figure shows that hypocampal neurons are activated in all behavioral acts, and the same neuron may be activated in different acts. In Figure 44, the neurons are arranged in accordance with their background activity, which was determined as the mean of 10 1-s intervals recorded before delivery of the click. At the top of Figure 44 is the number of neurons with the indicated background frequency.

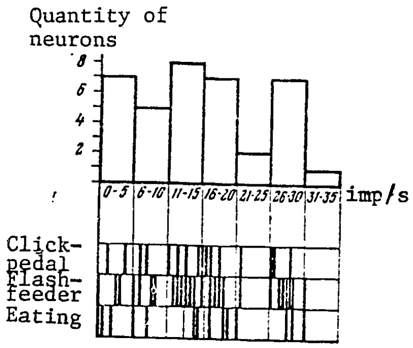


Figure 44.
Distribution according to frequency of background activity of hippocampal neurons involved in isolated behavioral acts.
Top: histogram of distribution of neurons according to background frequency; bottom: involvement of neurons with indicated background activity in 3 segments of behavioral continuum (black bands show involvement of a single neuron)

A comparison of the top and bottom parts of Figure 44 shows that neurons involved in one or several behavioral acts could have the most varied frequency of "background" discharges. Consequently, the activity of both theta cells and complex spike cells, which differ in background frequency (Ranck, 1973), could be related to either a single or several behavioral acts.

The differences between hippocampal neurons and those of, for example, the visual cortex are the link between their activity and usually only specific acts, and absence of changes in impulsation in other forms of behavior. This link is so obvious and constant that it is not even necessary to plot histograms in many cases, and this has also been noted by other researchers (Ranck, 1973; O'Keefe, 1976).

On the other hand, the neurons of the visual cortex undergo constant change in activity, and it is only by means of averaging that one can learn that the activity of a recorded neuron is also linked with the stage of behavior under study.

As for the time organization of discharges, in complex behavior hippocampal neurons do not show any special form of activity specifically related to the integrative function of the hippocampus. As in other brain structures, time organization of hippocampal neuron activity is related to specific time intervals within a behavioral act and, consequently, to specific processes within the functional system of a single behavioral act.

A link has also been demonstrated between hippocampal neuron discharges and EP (Shaban, 1969; Dubrovinskaya, 1971). Presence of EP has been demonstrated in the hippocampus in experiments we conducted, as well as those of other authors (John, 1972; John, Morgades, 1969). Thus, the integrative function of hippocampal neurons should be implemented by discharges occurring in the same time intervals as the discharges of neurons of other, specific and activating brain structures, the involvement of which in a single behavioral act is mandatory.

At the same time, destruction of the hippocampus leads to impairment of expressly successive behavior and behavior related to a choice between alternatives, and it does not change single behavioral acts. The involvement of hippocampal neurons in individual behavioral acts can be related to the lack of sensitivity of the latter to destruction of the hippocampus, if we assume that hippocampal neurons, which are specifically related to a specific behavioral act, have a coordinating influence on other neurons at all stages of formation and implementation of its functional system.

The discharges of a specific set of neurons related to only one act can additionally activate and increase the probability of responses by only the neurons whose activity was used in the past to reach a given result, and inhibit the neurons whose activity could hinder achievement of a concrete interim result, in spite of the fact that it was provided in pretrigger integration. This is a very real possibility because of the extensiveness of both afferent and efferent links between the hippocampus (Gambaryan, Koval', 1973; Vinogradova, 1975) and specific selective link between individual neurons and individual behavioral acts. There has been experimental demonstration of the inhibition of many neurons upon stimulation of the hippocampus (McKenzie, Gilbert, 1972).

This coordinating role of the hippocampus in organizing behavior would explain many behavioral disorders associated with injury thereof. Destruction of the hippocampus should not affect behavior, in which the trigger stimulus is delivered in the presence of one pretriggering integration. But in the presence of several acts in pretriggering integration, which is the case in a situation of complex successive behavior or situation of choice between alternative behavioral acts, absence of coordinating influences of hippocampal neurons would lead to excessive anticipatory excitation or simultaneous implementation of two alternative integrations.

CHAPTER 4. MECHANISMS OF TRANSFORMATION OF EXOGENOUS INFORMATION INTO ORGANIZATION OF PROCESSES IN THE FUNCTIONAL SYSTEM OF A BEHAVIORAL ACT

Relationship Between Prior Experience, Motivation and Information About the Current State of the Environment in Determination of Goal-Directed Behavior

We learned from the two preceding series of experiments that neuronal activity in a behavioral act is so organized that it leads to achievement of a result. This organization consists, first of all, of selection and inclusion in the functional system of a behavioral act of neurons with the "required" functions and exclusion of elements with "superfluous" functions.

The generally accepted view is that the topography of axonal collaterals is constant. For this reason, the physiological meaning of discharges of a given neuron is also constant. Regardless of the time of appearance of a spike or the specific synaptic points of entry through which the neuron is activated, these are always merely additional influences via specific synaptic points of entry for the "postsynaptic" cells.

"Homogenization" of all influences in a single axonal exit of a neuron (Anokhin, 1968, 1974a) alleviates significantly the task of purposeful organization of many neurons in behavior. The constancy of "addresses" to which the spike of a specific neuron is sent and, consequently, the constancy of its "efferent" function reduces this task to selection for the functional system of only a specific set of elements, and expressly those whose joint and coordinated function will lead to the goal in a given situation. This "screening" is performed through the interaction of memory, motivation and external information.

In the systemic interpretation, memory, motivation and situation are informational categories, and they characterize the relationship of the organism as a whole with the environment. All inborn or acquired forms of correlation between the organism and environment are stored in memory. Motivation is conceived as reproduction of the part of memory or information that was related in the past to satisfaction of one of the needs; situation is viewed as the part of memory that reproduces current information from the environment. The question arises: How is this information used to screen elements for the functional system of the behavioral act?

We explored this question in special experiments, where we examined impulsation of visual cortical neurons in food and defense behavioral acts by rabbits, where the trigger stimulus was a light flash that was the same in physical parameters. In food behavior, it was reinforced by carrot juice and in defense behavior, by ECS. By comparing the neuronal responses to light in two different behavioral acts, we hoped to gain information about the sets of neurons whose activity could be related to the parameters of real light, i.e., exogenous information in the presence of different motivations. By comparing the neuronal responses to a conditioned stimulus and reinforcement of specific behavior we expected to identify the set of neurons whose activity could be related to a specific motivation in the presence of some trigger stimulus or other.

Experiments (in collaboration with N. A. Shvyrkova) were conducted on 10 waking rabbits, who were loosely tied by the legs to a stand. The conditioned stimulus was a flash of light from the lamp of a Soneclat phonophotostimulator (0.3 J, 50 μs). Food reinforcement (carrot juice) was delivered automatically to the feeder in front of the animal's snout, from a rubber bulb, by means of an electrical relay which opened the valve for 500 ms to release 1-2 mℓ carrot juice. Electrocutaneous stimulation (30-60 V, 1 ms) was delivered from a Physiovar stimulator to the contralateral hind leg, in relation to the region of recording neurons, through needle electrodes inserted under the skin. The intensity was selected in such a manner as to induce marked EMG activation. The lag constituted 600 ms (1300 ms in some experiments). The interval between combinations ranged from 50 s to 2 min.

The experiment began with development of conditioned food-related behavior, which consisted of the fact that upon delivery of a conditioned flash the rabbit put its head in the feeder and sometimes licked it. Development of the reflex constituted 90-100% according to the EMG parameter after 30-60 combinations. Food reinforcement was then replaced with electrocutaneous, and a "modification" was made. The criterion of development of a conditioned defense behavioral act was appearance of conditioned EMG activation in 90% of the cases.

We recorded the activity of the same neuron of the visual cortex over a series of food behavioral acts and then defense acts, etc., for several "modifications." Each series consisted of 25-50 combinations. Sometimes there was a series of 30-60 presentations of a differentiation stimulus, which consisted of the same flash of light attenuated to one-fourth with a yellow filter. There were up to 5-10 "modifications" per neuron, the activity of one neuron was recorded for 2-3 h, and the experiment lasted up to 24 h. As a rule, the rabbit ingested the carrot juice just as well in the 10th series with food reinforcement as in the first. If it refused to eat, the experiment was interrupted for 4-6 h.

EEG of the visual cortex, neuronal activity derived by the above-described chronic method, EMG of cervical muscles and marks of stimuli were amplified on a 4-channel Biophase unit and recorded on an Ampex tape recorder, with subsequent reproduction on paper, with 8-fold reduction of feed rate. An NTA-512-B analyzer was used to average EP and plot poststimulus histograms.

In all, we examined 50 neurons of the visual cortex, 30 of which presented phasic activation after one or several stimuli (photic, electrocutaneous, presentation of food). A total of 21 neurons reacted in response to a light flash with some form of behavior or other. Analysis of reaction patterns revealed that none was equally activated in response to the differentiation stimulus and a stimulus with any signaling meaning.

The reactions differed in both latency periods and duration of different activation phases, and in sign. Only three neurons presented similar patterns in response to the same flash in defense and food behavior, but they did not response to differentiation light (Figure 45). The responses of 18 neurons to a light flash in two different behavioral acts were absolutely different (Figure 46).

Figure 46 illustrates the opposite reactions of a neuron to a flash that triggered different behavioral acts. Unlike differentiation light, to which the neuron did not react, with food reinforcement the conditioned flash induced distinct and prolonged (up to 700 ms) inhibition of neuronal activity. The neuron responded to a light flash with the same physical parameters, which triggered defense behavior, with a distinct phase of activation that coincided with the negative EP component. It must be noted that, with a change in reinforcement, the response changed after the very first delivery of the flash with a different signal meaning, whereas in the case of simply eliminating reinforcements there was very slow change in configuration of the response. Figure 46d illustrates the response of a neuron to 25 flashes after 200 separate presentations of light (after discontinuing ECS). We still see a tendency toward grouped impulses during EP negativity.

These data indicate once more that the pattern of neuronal activity and, consequently, involvement of a neuron's impulses in some systemic processes of the behavioral act are largely determined by pretriggering integration, as we already demonstrated in one of the preceding sections. The same findings were made in our laboratory by D. G. Shevchenko, who analyzed the neuronal activity of the reticular formation of the mesencephalon (1976). Figure 47 illustrates an example of absolutely different activity of the same neuron of the reticular formation with different behavior.

A comparison of neuronal activation in response to conditioned and unconditioned stimuli revealed that the neurons reacted to the flash in the same way as a reinforcement stimulus in only 50% of the cases, at least with regard to presence of phases; in the other 50% of the cases, these reactions were absolutely different (Figure 48).

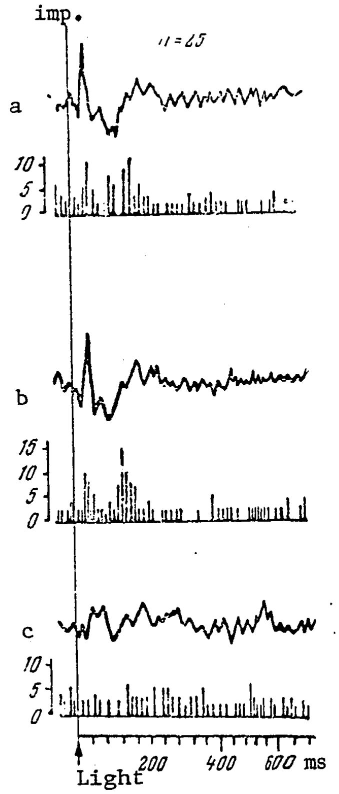


Figure 45.
Averaged evoked potentials similar in configuration and histograms of neuronal activity in visual cortex in response to conditioned flash in food (a) and defense (b) behavior. No neuronal response to differentiation flash (c). Vertical line is mark of light flash, channel width 10 ms

We also tried to determine how the parameters of the trigger stimulus and motivation are reflected by the number of reacting neurons in the visual cortex. Of the set of 30 neurons that reacted to any stimulus, 12 reacted to adequate photic stimulation in food behavior and 20 reacted to a flash with the same physical parameters in defense behavior ($p<0.05$). Evidently, it is not only the composition, but number of reactive neurons are not invariant in relation to the stimulus parameters.

Since it is known that increased motivation leads to expansion of receptive fields (Bandler, Flynn, 1972) and increased excitability of selective sets of neurons (Fadeyev, 1968; Sudakov, 1971; Khayutin, 1973), it may be that the number of active neurons reflects the "amount of motivation" related to "expansion" of receptive fields and inclusion in pretriggering integration of a larger number of possible behavioral acts to reach the same result with defense motivation than weaker food-obtaining motivation. This hypothesis is also supported by the fact that the same number of neurons, 20 and 20, reacted to different stimuli photic and electrocutaneous) in defense behavior, while 12 and 9 reacted to conditioned light and delivery of juice in food behavior.

Defense or food motivation, as hierarchies of the corresponding goals, creates the possibility for neurons to be activated in both the former (conditioned) and latter (unconditioned) behavioral acts. For this reason, the set of neurons whose reactivity corresponds to motivation can be determined by considering the neurons that respond in specific behavior to one or both stimuli ("conditioned and unconditioned"). Only 17 units responded in food behavior and 28 in defense behavior.

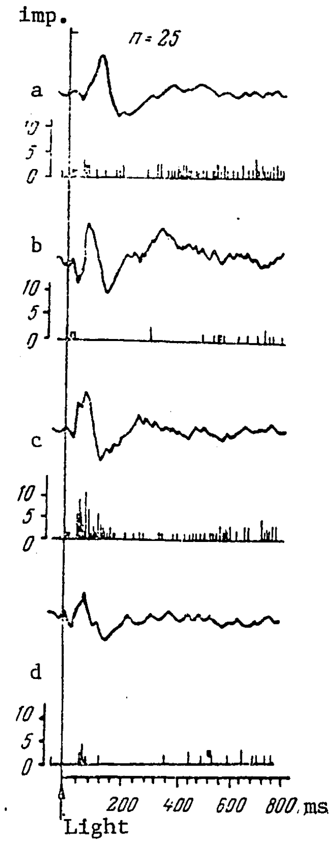


Figure 46.
EP and poststimulus histograms of neuronal activity in rabbit's visual cortex in response to flashes that trigger different behavioral acts

a) the neuron does not react to differentiation stimulus-flash attenuated with light filter
b) marked inhibition of neuronal activity in response to conditioned flash in a series with food reinforcement
c) distinct activation phase with latency period of 40 ms in response to conditioned flash in series with electrocutaneous reinforcement
d) reduced neuronal reaction to flash after 200 separate presentations of light

Top: averaged EP; bottom: poststimulus histograms. Channel width 10 ms

All these groups are compared in Figure 49. The diagram in Figure 49 shows that different sets of neurons are involved in the functional system of food-obtaining and defense acts, and they are potentially capable of reacting to the flash of light. In the case of defense motivation 20 neurons out of 21 respond and in the case of food motivation 12 respond.

Consequently, in either behavioral act, reactions arise only in neurons (potentially capable of reacting to light) whose activity could be related to satisfaction of a specific motivation.

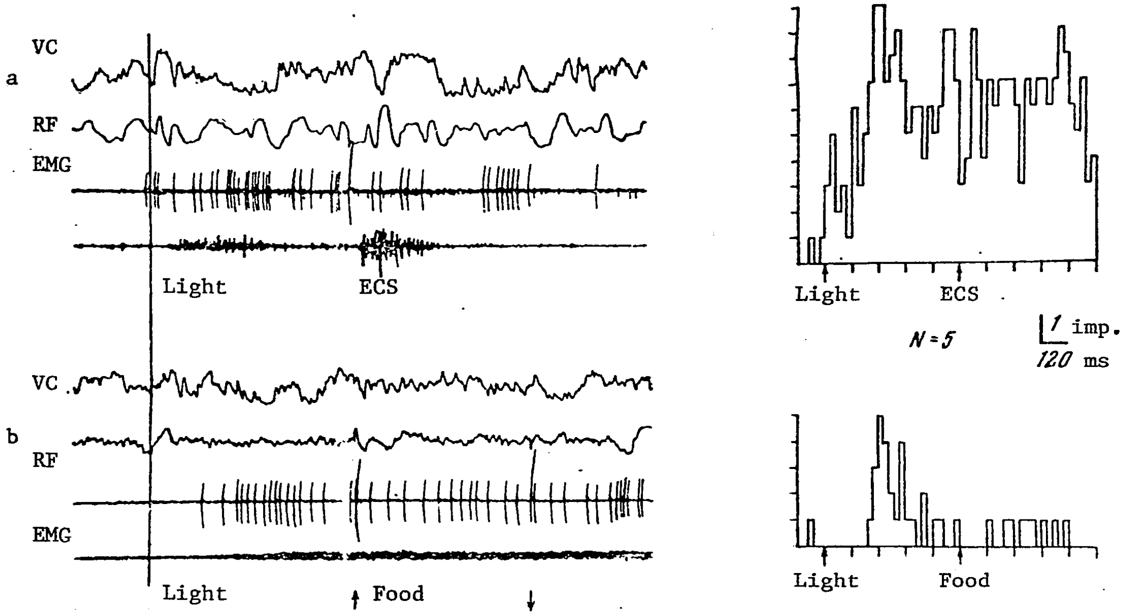


Figure 47. Different neuronal reactions in mesencephalic reticular formation to light triggering different behavioral acts

a) in defense behavior (flash reinforced by electrocutaneous stimulation)
b) with food reinforcement
In a and b, top to bottom, on the left: EEG of visual cortex (VC), reticulogram, activity of reticular formation neuron (RF), EMG; on the right: poststimulus histograms, channel width 20 ms. Arrows mark time of delivery of flash, ECS and juice

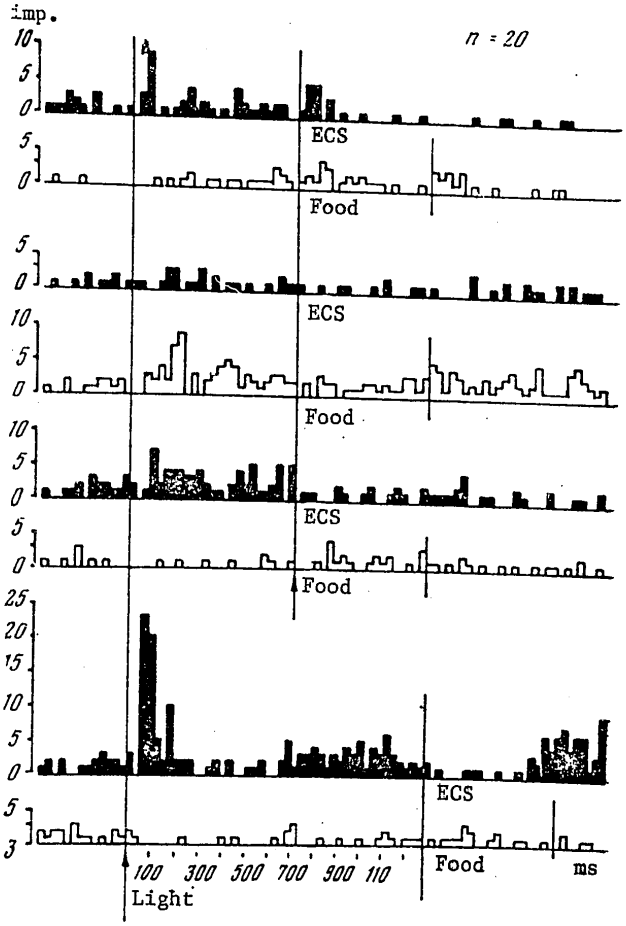


Figure 48. Reactions of four visual cortex neurons to conditioned flash with the same physical parameters and to ECS or delivery of juice in different behavioral acts. Black histograms refer to defense behavior and white to food. The first vertical line on the left is the flash mark and the second is the ECS (on black histograms) mark or moment that valve opens (white histograms). The third line marks the time of valve closing on the white histograms. Channel width 22 ms. Neuron indexes shown on the left

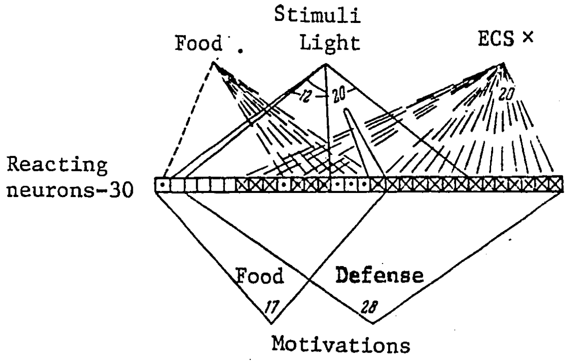


Figure 49. Diagram of inclusion of neurons of visual cortex in functional system of food-obtaining or defense behavior

Of the set of 30 reactive neurons (neurons represented by squares) motivation selects only those that led to achievement of a beneficial result in prior experience (food motivation 17 neurons, defense 28), thereby reducing superfluous degrees of freedom. Of all the neurons that were subject to some biologically specific motivational influences or other, only those that receive adequate visual afferentation (12 in food and 20 in defense behavior) react to a real visual stimulus, the flash of light. Motivation selects not only neurons that receive specific visual afferentation, and for this reason some of the visual neurons react to inadequate stimuli (9 to receiving food, marked by dots, and 20 to ECS, marked by "x")

On the other hand, by far not all neurons respond to light of those whose activity could be related to a specific motivation that determines the responses of visual neurons to "nonvisual stimuli" as well. Only the neurons whose activity corresponds to both motivation and the properties of real light are involved in the functional system of a specific behavioral act.

Motivation can cause activity of all neurons whose function had led at some time to achievement of one of the adaptive results, rather than those whose activity is related to the existing parameters of the light. In concrete behavior, of all the neurons purposefully selected by motivation, only those whose reactivity is specifically related to the parameters of the given photic stimulus are involved. Thus, both the time pattern of activity and composition of reacting visual neurons in the behavioral act are both goal-directed and reflect the properties of the photic stimulus.

There is an important consequence from this conclusion: since the same stimulus induces the activity of different sets of neurons in two different behavioral acts, we can refer only to an "information" model of the stimulus, and it is impossible to demonstrate activity that always corresponds unequivocally to the same stimulus. Thus, our data serve as proof of the thesis expounded already by K. Lashley, "that it is not excitation of the structure of specific sensory terminal organs that is an important element of a stimulus, but excitation of any terminal organs in a specific spatial or time structure" (1933, p 184).

It appears to us that these data warrant the assumption that, in a behavioral act, determination of activity of the organism by the goal is made by means of purposeful change in neuronal reactivity, i.e., by means of selective sensitivity to exogenous influences of only the set of neurons whose coordinated activity ever led to a result.

If we were to simplify the situation considerably, we could state that motivation as an hierarchy of goals is represented in pretriggering integration in the form of subliminal activation of the elements whose activity had ever led to satisfaction of this motivation in any situation. The situation is also represented as subliminal activation of those elements whose activity had ever led to any (even unnecessary at this time) results in the presence of environmental factors that were the same before as at the given time). Elements present in both sets concurrently have the highest probability of being involved in the functional system of the behavioral act upon appearance of the trigger stimulus, when there is implementation of one of the organizations contained in preliminary integration.

Neuronal discharges corresponding to different EP components play different roles in systemic processes of formation and performance of the behavioral act, but they are always part of the organized activity of the entire system of elements. On the one hand, this organized activity represents organization of endogenous physiological processes; on the other hand, it is determined by motivation and situation, i.e., information about the environment retrieved from memory.

Thus, the question of translation of exogenous information into organization of physiological processes can be generally answered with the hypothesis that the combination of specific informational elements of memory represented on individual neurons is also the organization of elementary physiological functions of these neurons.

In order to determine the concrete mechanisms of recombination of elements of memory and physiological functions in systemic processes of the behavioral act, we must first examine the problem of organization of memory.

Organization of Memory

The question of organization of memory is closely linked with the question of representation of information about the object-related environment in nervous activity.

At the present time, the anatomical pathways of passage of different afferentations to the brain are very well known. The problem of synthesis of different factors was first solved by means of conceptions of "point-by-point" transmission of information about the state of receptors to cortical representation of the corresponding analyzers and subsequent synthesis of different factors in "associative" regions. These conceptions were then replaced by the conception of "receptive fields," which is based on experimental data concerning the link between reactions of single neurons and stimulation of a specific, organized set of receptors or, more precisely, specific parameters of stimulation.

At first, a link between neuronal responses and specific localization of stimuli was demonstrated in the visual (Hubel, Wiesel, 1959, 1962) and somatic (Mountcastle, 1964) analyzers. Segments of the body surface or retina, stimulation of which elicited a response by the neuron under study, were referred to as the "receptive field" of the neuron.

In analytical experiments on anesthetized preparations, the receptive field appeared to be a constant property of some neuron or other, which characterized the aggregate of synapses stimulated by afferentation passing over anatomically fixed pathways. The receptive field of a neuron was viewed as a "group of elements of the underlying (or receptor) level of the system, which send signals to it" (Shevelev, 1971).

This thesis appeared to be so well-substantiated that the "link with parameters of stimulation" and "receptive field" for neurons on any level were used as synonyms. Since the link with parameters of stimuli was explained by the access of afferentation over projection pathways, it warranted references to "thalamic" or "cortical" receptive fields and studies of their relationship to stimulus properties as an attribute of fixed morphological connections with the periphery (Michael, 1969). "Simple," "complex" and "ultracomplex" receptive fields were distinguished in the visual analyzer (Hubel, Wiesel, 1962), and neurons were found that were specifically related to the most diverse parameters of a stimulus: direction, orientation, rate of movement of a point, line, slit, angle, etc. (see the surveys of the following authors: Creutzfeldt, Sakman, 1969; Chow et al., 1971; Tayal, 1971; Hamasaki, Winters, 1974); for the somatic analyzer this applied to the direction of movement of a stimulus over the skin (Whitsel et al., 1972; Werner, Whitsel, 1970) and angular rate of bending a joint (Mountcastle et al., 1963), etc. (see the survey of Darian-Smith, 1969); for the auditory analyzer this referred to detectors of vowels and consonants (Keidel, 1974), detectors of direction of sound (Sovijarvi, Hyvarinen, 1974), etc.

Subsequent studies revealed that the receptive fields of different neurons are not constant, and that they change with the most varied changes in experimental conditions. For example, retinal neurons respond to point illumination of their receptive field and do not respond upon stimulation of other points of the retina; if, however, the change in projection of stimulated retinal spot is induced by changing the position of the head, the neuron may response to illumination of the "new" receptive field and not to illumination of the "old" one (Horn et al., 1972; Denny, C. Adorjani, 1972; Schwartzkroin, 1972).

Changes in receptive fields were demonstrated with changes in background illumination (Nunokawa, 1973; Shevelev et al., 1974), in the presence of other exogenous stimuli (Weingarten, Spinelli, 1966; Slobodchikova, 1975), etc. From time to time, receptive fields change, even without any special factors (Donaldson, Nash, 1975).

It became apparent that a receptive field is a functional structure, an aggregate of synapses, the joint stimulation of which elicits a neuronal response under specific conditions. This receptive field was named the "physiological" field, unlike the "anatomical" receptive field, which is the aggregate of all anatomical synapses through which the neuron could potentially receive influences.

At first, the changes in receptive fields were related only to "modulation" of transient ["fugal"?] effects of throughput of special "communication channels," over which information about the physical parameters of a stimulus is transmitted. P. Wall (1967) and P. Wall et al. (1967) demonstrated that the receptive fields of spinal neurons could, under the effect of supraspinal influences, change not only in localization, but modality, for example, from tactile to thermal. Within a given modality, there is very fine adjustment of receptive fields (Kasprzak et al., 1970). Transient ["fugal"] influences were demonstrated, which also altered receptive fields in the visual analyzer (Meulders, Goldfraind, 1969), etc.

However, it was soon demonstrated that there was a dependence on specific parameters of stimuli of neurons that were not projectionally related to the stimulated periphery. Visual receptive fields were demonstrated, which were even specifically sensitive to the direction of movement of an object in the field of vision, in neurons of the motor cortex (Teyler et al., 1972; Garcia-Rill, Dubrovsky, 1971, 1974), as well as auditory receptive fields specifically sensitive to the properties of sound in neurons of the superior colliculi (Gordon, 1973) and visual cortex (Morrell, 1972; Fishman, Michael, 1973), etc. Evidently, these correlations with parameters of stimuli could not be related to arrival of afferentation over "specific pathways," and the concept of "receptive field" loses its original meaning in this case.

Indeed, on the one hand, it is known that divergence and convergence within a single analyzer already occur on the level of the "first relay." The history of this question was discussed numerous times in recently published monographs (Vasilevskiy, 1966; Yesakov, Dmitriyeva, 1971; Keydel', 1975; Som'yen, 1975). It was then learned that interanalyzer interactions are also possible on all morphological levels of the nervous system (Liege, Galand, 1972; Stein, Arigbede, 1972; Pityk, 1973; Farber and Volkova, 1970), including the level of the first "commutative relays" (Naumova, 1968). Moreover, there are centrifugal influences of diverse origin not only on all central levels (Livingston, 1959; Livingston, 1962; Amato et al., 1969; Durinyan, 1968; Adrianov and Mering, 1968; Gelarducci et al., 1970; Silakov, 1973; Daniel et al., 1973), but on primary neurons (Limanskiy, 1969; Dominik, 1970; Ignatov, 1973; Brown, Short, 1974) and receptors (Dodt, 1956; Spinelli, Weingarten, 1966; Yerchenkov et al., 1973; Klinke, Galley, 1974). Perhaps "interreceptor" interactions (Yesakov, Dmitriyeva, 1971) are also of substantial significance for integration of different factors into a single whole.

The numerous relations and efferent influences, even on receptors, do not enable us to relate first order neuronal discharges always to a change in peripheral afferentation. Any neuronal activity is generated by the convergence of many synaptic influences from different sources, and "where there are hundreds and even thousands of synaptic endings converging on one postsynaptic cell, none of them will have a decisive effect on its activity" (Som'yen, 1975, p 248).

Thus, the activity of a single neuron after a single peripheral stimulus is formed in accordance with the activity of the entire brain.

On the other hand, a unimodal stimulus that triggers a behavioral act elicits the activity of many neurons in virtually all parts of the brain. In the analytical sense, it would hardly be constructive to believe that all of them have, for example, "visual receptive fields." Extending this formal principle, one could think that all muscular elements involved in behavior also have "visual receptive fields."

These facts and considerations render the concept of "receptive field" inadequate to describe the relations between neuronal activity and parameters of a stimulus. For this reason, we consider it purposeful to suggest the term "functional synaptic field" to describe the functional relations of a single neuron expressly in behavior, and apply it to all neuronal associations, rather than only "underlying" or "projection" ones. The functional synaptic field is part of the "anatomical synaptic field," it consists of an aggregate of synaptic influences to which a neuron is selectively sensitive at a given time, regardless of the sources of these influences.

The appearance of reactions by a single neuron to stimuli that only have specific parameters and the fact that neuronal discharges arise in behavior with convergence to one neuron of influences from many different sources lead us to assume that a specific organization of reciprocal influences of neurons of the most diverse localization is related to the parameters of the stimulus, rather than peripheral afferentation, the correlation of which with stimulus parameters changes constantly during behavior due to transient [fugal] influences (Collet, 1974).

Thus, the link between the activity of a single neuron and stimulus parameters is not attributable to specific pathways to this neuron from the periphery or "receptive field," to organization of all interneuronal relations and the functional synaptic field (FSF) of a given neuron at a given time.

A neuronal discharge probably appears when some part of the synaptic influx coincides with the functional synaptic field. The selective sensitivity of a neuron to some part of the synaptic influx, i.e., its functional synaptic field, is mediated by neurochemical and metabolic intraneuronal processes (Sillito, 1974a, b; 1975), which in turn change under the influence of synaptic activations.

From the point of view we are presenting, information about the parameters of any individual stimulus, on the one hand, exists only as a specific organization of interneuronal interactions; on the other hand, organization of interneuronal interactions serves as the carrier of all information, rather than information about the stimulus alone. The link between "output" activity of a neuron and specific stimulus parameters probably means that the FSF "selects" only a specific organization of influences, which corresponds to information about these parameters, out of the entire synaptic influx to the neuron.

Thus, on the level of a single neuron that performs an elementary physiological function, its functional synaptic field is probably the "element of contact" with the environment.

Since specific physical characteristics of stimuli are usually changed in experiments, and the activity of different neurons changes only with change in specific physical parameters, the conception was formed that there are special "communication channels" for transmission of information expressly about the different physical properties of a stimulus.

For some time, the work of J. Lettvin et al. (1963), which demonstrated a link between the receptive fields of the forg's retinal neurons and specific forms of inborn behavior, stood alone, and comments such as "frogs are interested in beetles and flies, whereas only scientists are interested in boundaries and angles" did not influence the thesis that receptive fields are called upon to reflect the "physical properties of the stimulus." At the present time, however, more and more data are being accumulated indicating a link between receptive fields of neurons and specific behavior, not only in amphibians (Pigarev, Zenkin, 1973), but in mammals (see the survey by Collet, 1974).

In the frog, behavioral acts are largely fixed genetically, and there is a rather limited number of releasers that trigger specific behavior. For this reason, it was possible to disclose that the frog "breaks down" the outside world in accordance with the behavioral acts in its genetic memory. However, in mammals, whose behavioral capabilities are quite diverse, the link between neuronal activity and "physical parameters" of stimuli moved to the fore, whereas no link was demonstrated between this activity and a given form of behavior.

More and more data are presently being accumulated, which indicate that the "breakdown" [splitting] of the outside world by different neurons in mammals occurs in accordance with integral behavioral acts stored in memory, rather than "physical parameters," which is manifested, for example, by "adjustment" of auditory neurons to species-specific sonic signals that trigger specific behavior (Frishkopf et al., 1968; Wollberg, Neumann, 1972), by the relation of "receptive fields" of cortical neurons with "extrapersonal" space (Mountcastle et al., 1975) and by change in "receptive fields" with change in behavior (Wall, 1967; Bridgeman, 1973; Smith, Marg, 1975).

All this warrants the assumption that the link between neuronal activity and stimulus parameters is indeed a link with specific behavior, in which the neuron under study is involved and information is used about these parameters.

Ontogenetic studies revealed that the relations with environmental properties are determined by genetic mechanisms in only part of the neurons. Many "receptive fields" are created in the course of ontogenesis and learning (Pettigrew et al., 1973; Barlow, 1975), depending on the environment in which the animal is reared (Pettigrew, 1974; Blakemore, Mitchell, 1973; Cynader et al., 1973) and on "visual-motor interactions" (Imbert, Buser, 1975).

This circumstance enabled all of these authors to expound the hypothesis that life experience of the organism is fixed in the distinctions of the "receptive fields." The fact that many "receptive fields" are genetically determined is indicative of their link with integral behavioral acts present in the organism's genetic memory.

It should be mentioned that the idea of element of memory in the neuron as "an aggregate of potentiated synapses" had been voiced by Ye. N. Sokolov (1967, 1969) on the basis of other data, even before the conclusions that apparently became indisputable after the ontogenetic studies.

Since the link between neuronal activity and stimulus parameters is determined by its entire functional synaptic field, rather than only the "receptive field," it is expressly the FSF, which determines the capacity of a given neuron to respond to some parameters of exogenous stimuli that are familiar and make up the life experience of the organism in question (rather than respond to other factors that are "unfamiliar" to the neuron), that represents on the level of the single neuron both the "element of contact" of the integral organism with the organized exogenous environment and "element of memory about the exogenous environment." The parameters of FSF reflect organization of prior stimuli, and the entire aggregate of these fields in a single neuron represents all of the "life experience" of this neuron.

At the same time, the presence of a specific FSF in a neuron means that, in the past, a discharge of this neuron under the influence of specific environmental factors was useful for the organism in reaching some adaptive result. The "breakdown" of the environment in accordance with FSF of individual neurons is also the breakdown of this field, in accordance with the results of the organism's prior behavioral acts.

Thus, exogenous stimuli merely reproduce elements of stimuli in a definitive organism, information about which is stored in this organism's memory in the form of functional synaptic fields of different cells that were coordinated during prior, integral behavioral acts. Prior influences could render a neuron selectively sensitive to some factors or other and alter its FSF. At the present time, such changes have been demonstrated not only in mammals, but in frogs (Branston and Fleming, 1968), fish (Sandeman, Rosenthal, 1974) and crayfish (Wiersma, Yamagushi, 1967). However, these changes are possible only within the framework of the neuron's prior experience, i.e., they can "choose" one FSF of the ones that had ever been formed in this neuron in the course of ontogenesis and learning (Creutzfeld, Heggelund, 1975).

If we agree that the "life experience" of an organism on the level of single neurons is fixed in the organization of FSF, then both motivation and situation, which represent parts of prior experience, exist on the level of individual neurons as aggregates of FSF corresponding to behavioral acts leading to satisfaction of some need (motivation) and possible in a given, concrete environment (situation).

Thus, interaction of memory, motivation and situation in processes of afferent synthesis and decision making on a single neuron probably amounts to enhancement of expressly the FSF (if they exist in the memory of this neuron) that correspond both to the real environment and motivation.

Since the FSF of a specific neuron correspond expressly to those exogenous factors, in the presence of which constant physiological function of the neuron was used to reach some result (and survival), enhancement of specific FSF signifies concurrent retrieval from memory of certain organizations of physiological functions.

According to the conceptions we are developing here, the entire pattern of neuronal activity in the behavioral act is "endogenous," i.e., retrieved from memory, the early phases being caused by one goal and the late ones more definitely determined by it.

Since FSF serve as the memory substrate on the level of central neurons, it may be assumed that pretriggering integration is the selective organization of neurons whose FSF correspond to all possible future environmental factors and, consequently, all possible behavioral acts, while the acceptor of action results corresponds to selective organization of neurons whose FSF correspond to one future result-event and, consequently, one behavioral act.

The result and means of reaching it are chosen in accordance with the real environment. The real environment and future events, which are objectively related in the environment and, consequently, in the organism's memory, must be represented by interrelated FSF on the level of single elements. The activity of the organism in this environment will lead to the required result only if elements are selected for the functional system of the behavioral act that are activated through FSF, which correspond both to real and future (goal) information. In this case, organization of activity of the selected elements will be a means of "translating" one specific organization of the environment into another specific one.

In order to create such a set of elements, the FSF of the "required" neurons must be altered in accordance with current and future information. This change must occur in the course of systemic processes of afferent synthesis and decision making, i.e., during the first phases of EP. Consequently, the question of using current information and goal information to organize physiological processes could be put as a question of altering neuronal FSF in accordance with these types of information.

This is why we undertook the task of determining the correlation between FSF of individual neurons and parameters of current information and goal, during the different phases of EP in defensive behavior.

Use of Exogenous Information to Organize Purposeful Neuronal Activity in the Behavioral Act

The objective of our first series of experiments was to determine which parameters of information about the real environment correspond to neuronal FSF in different systemic processes. We used the behavioral act triggered by electrocutaneous stimulation as an experimental model. In this model, the variable ECS always triggered standard systemic processes of the defense act; on the other hand, it is an environmental factor, information about which is used to form purposeful defensive behavior. Since the behavioral act is the implementation of pretrigger integration, which is formed under the influence of motivation and situation even before the stimulus, of course the use of information about a single stimulus can be studied only with standardization of pretrigger integration.

Experiments were conducted on waking rabbits under stereotactic immobilization with the use of only novocain. Glass microelectrodes filled with 3 M KCl solution, with a tip about 1 micron in diameter, were used to record impulsation of somatosensory cortical neurons on a multichannel magnettor, together with EP derived from agar, which filled a trephination opening. ECS in the form of square-wave pulses from a Physiovar stimulator was delivered by means of needle electrodes. In order to maintain constant pretrigger integration throughout the series of stimulations, stimuli with the same parameters were delivered 25 times in a row at intervals of 5 or 10 s. The intensity of stimulation varied in different series in the range of 1 to 10 thresholds, which were determined by demonstration of EP. We tested the correlation between activation and duration of stimulation (1, 10, 100 and 500 ms) at two-threshold intensity. Threshold intensity usually constituted 5-10 V. We also changed the localization of stimulation.

Magnetic tapes were made with reduction of feed rate to one-eighth on the paper of an automatic ink recorder. AI-26 and AI-4096 analyzers were used to summate EP, and we plotted poststimulus histograms of neurons for every 25 deliveries of stimuli with the same parameters.

In this series, we analyzed the activity of 99 cells. Of this number, 59 neurons responded with some pattern or other to ECS of different parameters.

These patterns changed with change in ECS parameters, and this corresponded to a change in the entire pretriggering integration. The pattern changes often consisted of disappearance of one of the response phases. For example, Figure 50 illustrates a neuron which showed a primary response and late activation after stimulation of the front contralateral leg at an intensity of 50 V; upon stimulation of the contralateral hind leg, the primary response disappeared, whereas late activation persisted. With some of the changes in stimulus parameters, we observed disappearance of some phases and appearance of others that were previously absent. For example, Figure 51 illustrates a neuron that showed a primary response and late activation to 45-V stimulation of the contralateral front leg and a discharge in EP negativity in response to stimulation of the same intensity delivered to the contralateral hind leg.

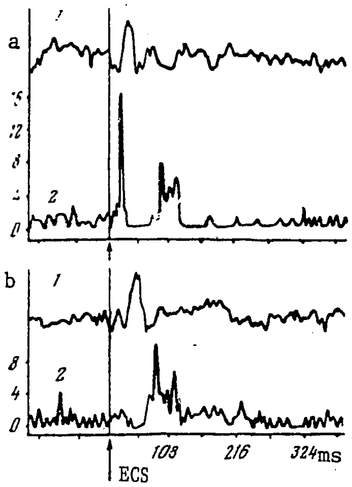


Figure 50.
Disappearance of primary response of somatosensory neuron and retention of late activation with change in localization of active electrodes
1) averaged EP
2) peristimulus histogram
Channel width 4 ms, n = 25
a) ECS of contralateral front foot, 50 V
b) ECS of contralateral hind foot, 80 V

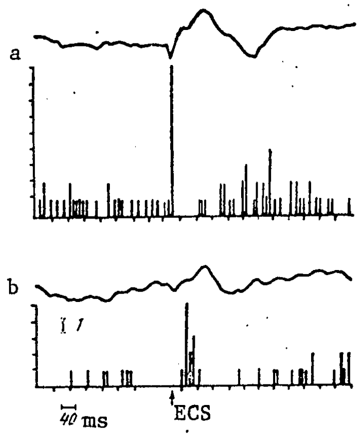


Figure 51.
Change in reaction pattern of somatosensory neuron with change in localization of electrocutaneous stimulation
a) stimulation of contralateral front foot, 45 V, primary response with late activation
b) stimulation of contralateral hind foot, 45 V, activation during negativity
Channel width 8 ms, n = 10

There were different correlations between different phases of the pattern and ECS parameters, even in the same neuron. For example, Figure 52 illustrates a neuron that showed a primary response and discharges in negativity of EP. The primary response did not change with change in intensity or duration, but disappeared with change in localization, whereas the discharges in negativity depended on both intensity and duration of ECS, and they appeared even with stimulation of the ipsilateral hind foot.

A difference in relation of different phases of the response to stimulus parameters was observed in spinal neurons (Brown, 1969), cortical neurons and primary afferent fibers (Handwerker, Sassen, 1972). A. Towe, R. Morse (1962) and H. Handwerker and M. Sassen (1972) also observed a similarity of response patterns of peripheral and central neurons in anesthetized preparations.

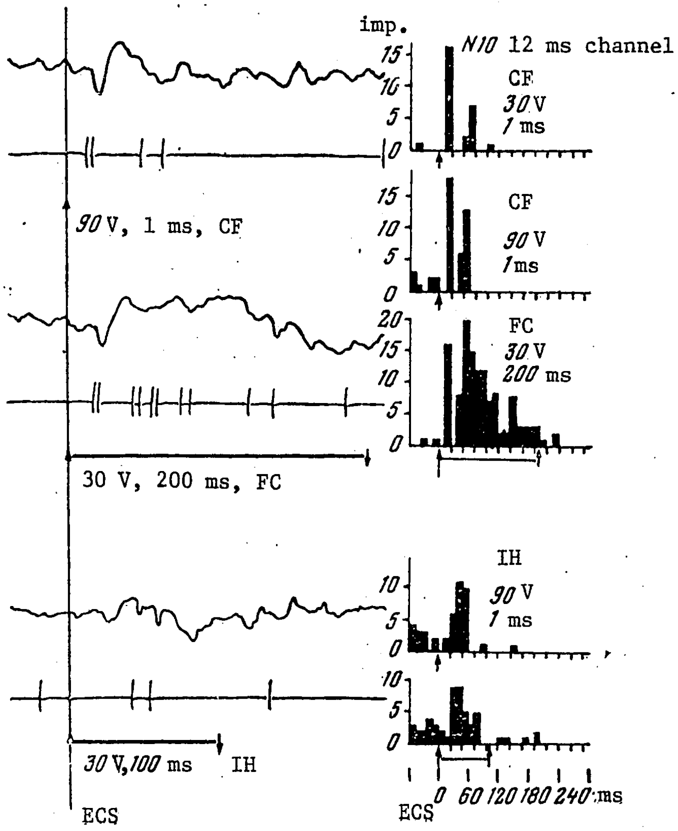


Figure 52. Properties of different phases of somatosensory neuron reactions
Left: examples of EP and single neuronal reactions; right: poststimulus histograms of neuronal reaction to ECS of different parameters. Stimuli are shown by arrows. Channel width 12 ms. Parameters of stimulation are shown on histograms; CF--ECS delivered to contralateral front leg; IH--to ipsilateral hind leg. Relation of discharges during EP negativity to intensity, duration and localization of ECS, and disappearance of primary response with change in localization are shown.

In order to determine the correlations between ECS parameters and functional synaptic fields of somatic neurons during different systemic processes, let us consider the dependence of different activation phases of these neurons on ECS parameters.

In our experiments, we were able to demonstrate primary responses of 19 neurons with different ECS parameters. All of these responses appeared only upon stimulation of local regions of the skin on the contralateral half of the body surface. With delivery of stimuli outside these regions, whatever the intensity (up to 10 thresholds), these responses did not appear or were even replaced by inhibition (Figure 53). Their dependence on ECS intensity with stimulation of a region varied for different neurons, but as a rule a maximum response appeared at a certain optimum intensity, a change in which in the direction of increase or decrease led to reduction or even inhibition of the response. But in some cases, a primary response that appeared with threshold intensity of ECS persisted throughout the tested range of intensities (Figure 52). Figure 55 illustrates primary responses of nine cortical neurons as a function of intensity of stimulation of their "receptive fields" in thresholds.

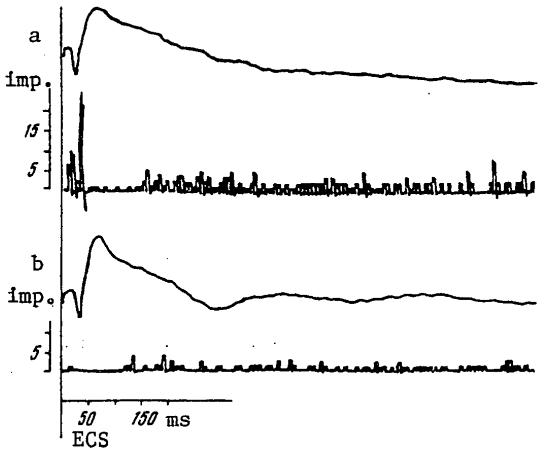


Figure 53. Change of primary activation to inhibition with change in localization of active electrodes

a, b) top: averaged EP; bottom, poststimulus histogram of neuronal activity, n = 25, channel width 5 ms.
ECS of 2 thresholds delivered to contralateral front (a) and ipsilateral hind (b) leg. Threshold = 10 V

As a rule, the primary response did not change with change in duration of ECS, but in 2 cases an increase to 500 ms led to alteration of the pattern and disappearance of primary responses (Figure 54).

The primary response contained only 1-2 spikes, which appeared in the interval of 10 to 20 ms after the start of delivery of stimulation of any intensity and duration; the probability of appearance of spikes, rather than number of impulses per response, was related to the stimulus parameters. In some neurons, appearance of a response was related to a specific localization and often to a specific intensity of ECS.

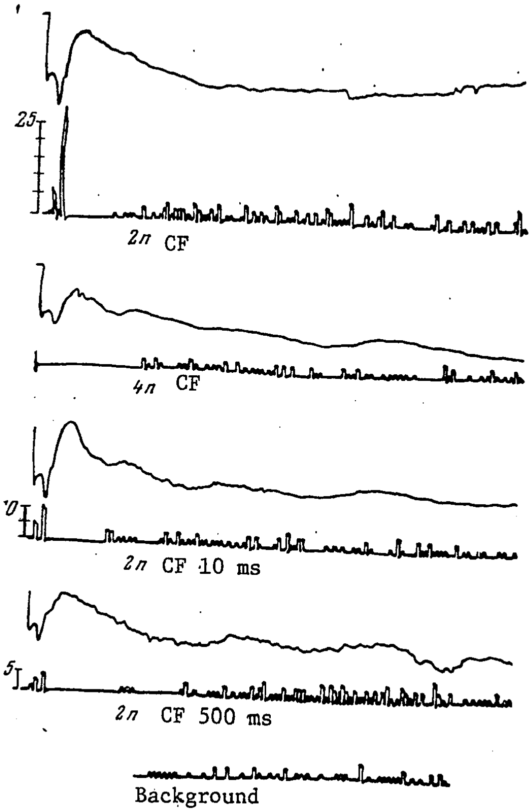


Figure 54. Primary response of somatosensory neuron as a function of intensity and duration of ECS
Top: averaged EP; bottom: poststimulus histograms, n = 25; channel width 5 ms. Marked primary response with 2-threshold intensity of stimulation of CF [contralateral front leg]. Increasing intensity to 4 thresholds leads to disappearance of primary response. Increasing duration of ECS has the same effect

Consequently, separation of the entire ECS into "signs" occurs in accordance with organization of FSF of different neurons, rather than the properties that the experimenter attributes to the ECS. These FSF during the primary response correspond to a specific localization, intensity and, probably, modality of the stimulus at the same time, as has been demonstrated for spinal neurons (Brown, 1969). Consequently, already in the first phase of realization of the functional system of a behavioral act, there is reproduction of information expressed only in terms of properties of specific FSF fixed in phylogenesis or ontogenesis, formed to reach some adaptive result. In this sense, this information is already subjective, since it reflects "refraction" of ECS parameters through the "life experience" of this rabbit.

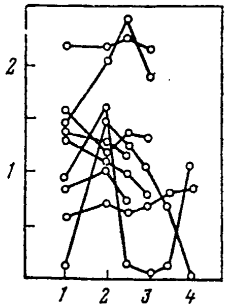


Figure 55.
Number of impulses in primary response of somatosensory cortical neuron as a function of intensity of ECS

X-axis, intensity of stimulus, in thresholds; y-axis, impulses per response, mean of 25 runs

In our experiments, ECS of the same parameters were delivered at equal intervals, which made it possible for the rabbit to "foresee" both the parameters and time of delivery of ECS. Consequently, a real ECS finds the FSF that were already potentiated in pretriggering integration. To check this hypothesis, we performed "reverse" averaging of summated activity and plotted "prestimulus" histograms (Figure 56).

This processing revealed that, in some neurons, an increase in frequency of "background" activity concurrently with increase in "anticipatory wave" on the EEG are inherent in the primary response, and the background reaches a maximum by the time ECS is delivered. We also found that the increase in background at the time of delivery of the stimulus could also be present in neurons without late activation in the "usual" place, i.e., those not used in actuating mechanisms of the preceding behavioral act. We have described comprehensively the phenomenon of change in background activity of neurons of the somatosensory cortex with delivery of ECS and development of a conditioned reflex in other works (Shvyrkov, 1968b, 1969), and here let us merely indicate that, at the time of the primary response, discharges are fired whose "pretrigger" FSF coincide with the parameters of real ECS; these FSF are enhanced in accordance with many possible variants of organization of elementary physiological functions into the actuating mechanisms of defensive behavior.

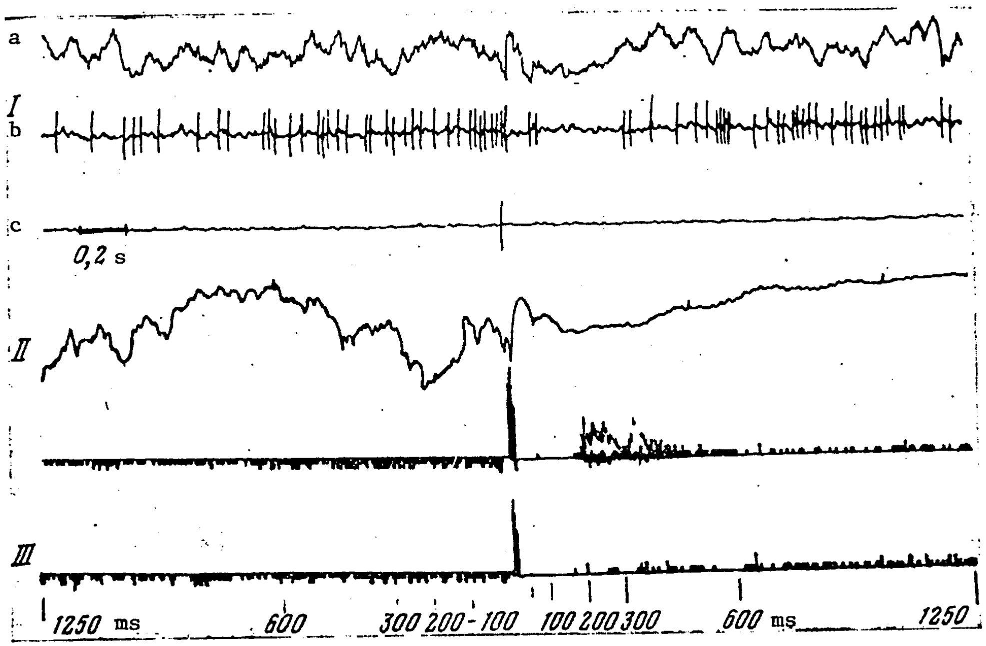


Figure 56. Increased background activity of three different neurons (I, II, III) by the time a stimulus is delivered, rhythmic stimulation

I) a--tracing of superficial EEG of somatosensory cortex; b--impulsation of first neuron; c--ECS mark

II) top--averaged superficial EEG; bottom--poststimulus histogram of second neuron; increased background impulsation and "anticipation wave" demonstrated by the method of reverse averaging

III) poststimulus histogram of third neuron. Arrow shows time of stimulation

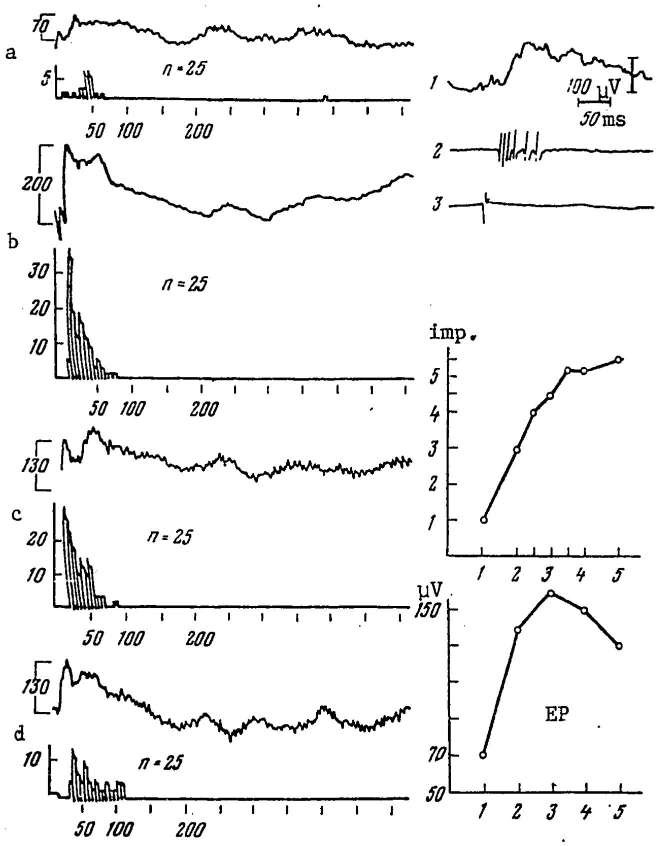


Figure 57. Negative phase of activation of somatosensory neuron as a function of intensity and duration of ECS

On the left, in a, b, c, d: top--averaged EP; bottom--poststimulus histogram of neuronal activity, channel width 5 ms. Stimulation of contralateral hind foot: a) 10 V, 1 ms; b) 50 V, 1 ms; c) 20 V, 500 ms; d) stimulation of ipsilateral hind food, 50 V, 1 ms

Amplitude of EP is shown in μV. On the right, single reactions to stimulation: 1) evoked potential; 2) neuronogram; 3) stimulus mark; on the graphs: number of impulses in neuronal response as a function of intensity of ECS, in thresholds

Thus, at the moment of the primary response, exogenous information activates an aggregate of elements that do not yet conform with organization of one specific act, which could also explain the absence of action at the time of the primary response.

Since the set of elements that show a primary response corresponds to many possible acts and not to any specific one, in other words, since this set is still scattered and is not an integral system of physiological functions, it may be assumed that information about the ECS as an integral environmental factor does not yet exist, and ECS is represented only by separate, uncoordinated FSF. Thus, the primary response can be viewed as a stage of analysis of exogenous factors in the interpretation of I. P. Pavlov.

We succeeded in demonstrating discharges in 20 neurons at the time of the negative EP component with different stimulus parameters. Discharges corresponding to EP negativity appeared with latency periods of 20 to 80 ms. These responses gradually depended on all tested parameters of ECS, but this dependence differed in nature in different neurons. In some neurons, the number of impulses during this phase and duration of the response were related in gradual stages to intensity and duration of ECS, and a response was also observed with ipsilateral stimulation (Figure 52). Other units did not show a change in duration of discharges, but presented a gradual relation of number of spikes to both intensity and duration of stimulus (Figure 57).

With a 1-ms stimulus, the correlation between number of impulses per discharge and stimulus intensity could be close to logarithmic or exponential. For example, Figure 57 illustrates a neuron, in which this relationship was described by the exponential function $N = (I - I_0)^k$ with $k = 0.5$. Figure 58 illustrates the number of impulses per response as different functions of intensity for 13 neurons.

In some units, a discharge in negativity appeared only with specific localization of electrodes (Figure 51), or else a reaction of different intensity was observed with different localization (Figure 57). A relationship to duration could also be observed for some points of the body and not for others.

Thus, both parameters of activation during negativity--number of impulses and duration--could be related to different combinations of stimulus parameters. As was the case for primary responses, for discharges in EP negativity there was an inherent link with several parameters of the stimulus, which the experimenter singled out as separate, but unlike the primary responses, discharges in negativity were related to a wider range of intensities and broader localization (often the entire skin surface).

The graduated dependence of discharges in negativity on intensity, like graduated dependence on amplitude of negative EP oscillations (Rosner, Goff, 1967; Beck, Rosner, 1968), cannot be explained as "conduction of stimuli" from the periphery, since the discharges in negativity were widely represented in different brain structures, while only two gradations of intensity were reflected in peripheral fibers in the interval of up to 100 ms after the start of stimulation (Verner, Mountcastle, 1965).

This gradual dependence and relation to duration and wide localization of stimulation can be attributed to the fact that, during EP negativity, the FSF of each cortical neuron "expands" significantly and corresponds to several "single" or "elementary" functional synaptic fields, and, consequently, to several behavioral acts. The "graduality" of dependence on intensity and duration could reflect the gradual increase in number of elementary FSF appearing in a neuron with increase in intensity or duration of nociceptive ECS.

The specificity of the link between discharges in negativity and a specific "set of signs" of ECS indicates that these responses, in spite of their obvious dependence on physical properties of a real stimulus, are also the result of comparison of ECS properties and specific FSF of a given neuron, in which is fixed prior experience of many goal-directed, defensive behavioral acts.

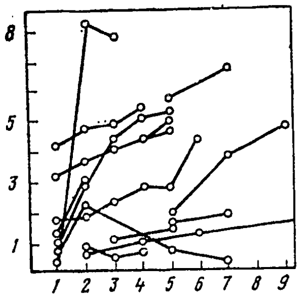


Figure 58.
Number of impulses of 13 somatosensory neurons in negative phase of EP as a function of intensity of electrocutaneous stimulation lasting 1 ms

X-axis, intensity of stimulus, in thresholds; y-axis, mean impulses per reaction, 25 runs

Since there is significant expansion of FSF of different neurons during EP negativity, exogenous information activates at this time the set of elements that correspond to all elements of memory represented in the "broad" FSF, rather than the real ECS alone. Evidently, the different elements of memory wihtin a single FSF of a single neuron are coordinated. "Expansion" of FSF may occur only as a potentiation of interrelated elements of neuronal memory (reflecting the link between specific elements of the real environment).

Inasmuch as different neurons have FSF during EP negativity that correspond to several behavioral acts, the discharges of the entire set of neurons at this time, like at the time of the primary response, cannot assure coordinated use of physiological functions to achieve the specific result of a defensive behavioral act. While it does not yet form an integral system, the set of elements that fire discharges in negativity cannot carry information about ECS as an integral environmental factor; however, expansion of FSF permits coordination, not only of different elements of memory on one neuron, but the FSF of different cells are also apparently more comparable. This is probably a transitional stage between analysis of information about exogenous factors and synthesis thereof.

We observed late activation in 20 neurons with different ECS parameters. Like separate activation, this phase could be demonstrated only when preceded by an inhibitory pause. The latency periods of such activations were quite variable, ranging from 50 to 500 ms. In other cases, late activations were actually the continuation of discharges that had begun in other phases, and their latency periods could not be determined (Figure 61). Some of the late activations depended on localization, like the primary responses. Other late activations appeared whatever the localization of electrodes. A dependence on intensity was demonstrable only when late activation was separated from prior and subsequent activities (Figure 59). This relation to intensity, with duration of 1 ms, was plotted for 10 such activations (Figure 60). As was the case for primary responses, late activations could have an optimum intensity, at which we observed the largest number of impulses per reaction, but in other cases there was virtually no relation to intensity.

There was literal reflection of duration of ECS in late activation of three neurons. One of these neurons is illustrated in Figure 61. With 1-ms ECS, this neuron showed a primary response and discharges in negativity, which were related in graduated stages to intensity of the stimulus. In this case, late activation appeared after an inhibitory pause with a latency period of about 200 ms and, like the primary response, it had an optimum at an intensity of 2 thresholds (not shown in Figure 61).

With significant increase in duration, the pattern changed and discharges continued throughout the period of stimulation, an "off effect" being demonstrated after stimulation. The bottom part of Figure 61 illustrates histograms of the responses of this neuron to stimulation lasting 500 ms of the ipsilateral hind foot. In this case, we observed only discharges in negativity. This indicates that, during negativity, this neuron had a broad functional synaptic field; during late activation this field "narrowed down" to one specific peripheral "receptive field."

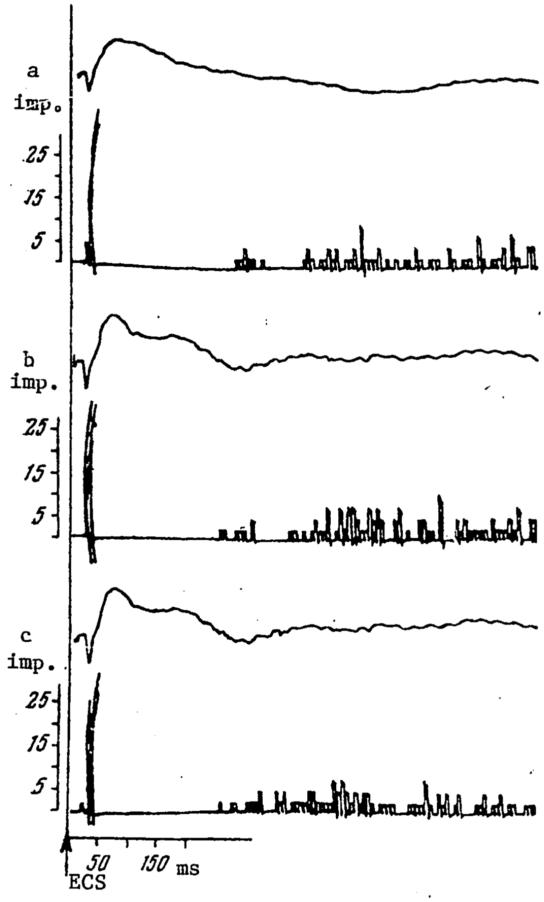


Figure 59. Primary and late activations of one neuron as a function of intensity of ECS
a, b, c) top--averaged EP; bottom--poststimulus histogram (n = 25, channel width 5 ms). In all cases ECS was delivered to contralateral front leg. Intensity: a--1 threshold; b--2 thresholds; c--3 thresholds, duration 1 ms

In other neurons, an increase in ECS duration could lead to a change in impulsation frequency or duration of late activation, or else did not change this activation at all. L. I. Peresleni (1974) also reported the dependence of late phases on duration of ECS.

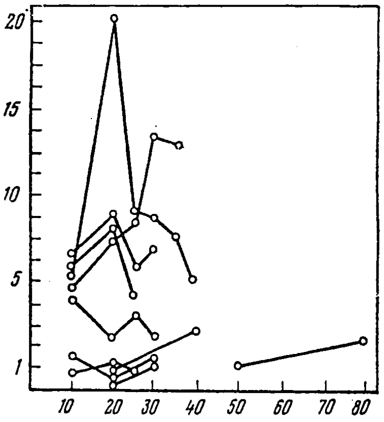


Figure 60.
Number of impulses in late activations of 10 somatosensory neurons as a function of intensity of ECS lasting 1 ms

X-axis, stimulus intensity, volts; y-axis, mean number of impulses per reaction (of 25 runs)

Thus, late activations have the widest diversity of forms of relationship to ECS parameters. In some neurons, late activation reflect, as do primary responses, correspondence of the stimulus with some single FSF throughout the period of stimulation and the entire behavioral act. The link between such late activations of single neurons and not only duration, but intensity and specific localization indicates (as in the case of other phases) that the effects on the organism are "broken down" during late activation, in accordance with FSF elements in memory, rather than special "channels" for coding the "intensity," "duration" and "localization" distinguished by the experimenter as separate entities.

Thus, the FSF of some neurons correspond during late activations only to one "set of properties" of real ECS and one "needed" behavioral act. In late activations of other neurons, the link with ECS is less selective, and during late activations such neurons have FSF that correspond to several different ECS. Finally, in some neurons, the link between late activations and stimulus parameters presents no pattern. With change in duration, localization or intensity of the stimulus, these activations do not remain constant, but we were unable to relate the observed changes to any quantitative changes in ECS parameters.

Late activations of such somatosensory neurons were found to be related to EMG activity (Figure 62), which could be indicative not only of involvement of late activations in the systemic process of implementation of the program of action, but that during late activation of such neurons their FSF were already organized in accordance with "feedback," i.e., information about the results achieved.

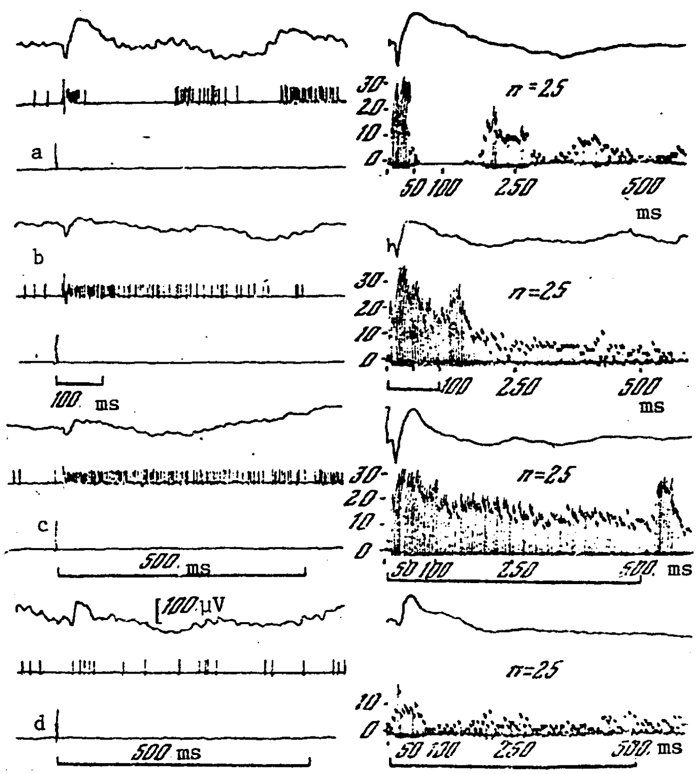


Figure 61. Late activation of somatosensory neuron as a function of duration of ECS

On the left: single EEG tracings, impulsation and stimulus mark; on the right: averaged EP and poststimulus histograms

a,b,c) stimulation of contralateral front foot, 20 V, 1, 100 and 500 ms, respectively

d) stimulation of ipsilateral hind foot, 20 V, 500 ms

Compare (c) and (d) (channel width 5 ms, n = 25)

During late activations, when neuronal activity is entirely coordinated to achieve one adaptive result, the FSF of different neurons should also apparently be coordinated and, consequently, conform on the whole with real ECS as an integral environmental factor. This stage probably represents synthesis of information about the exogenous factor (according to I. P. Pavlov). At the same time, it corresponds to synthesis of the integral functional system of the act from elementary physiological functions of different neurons.

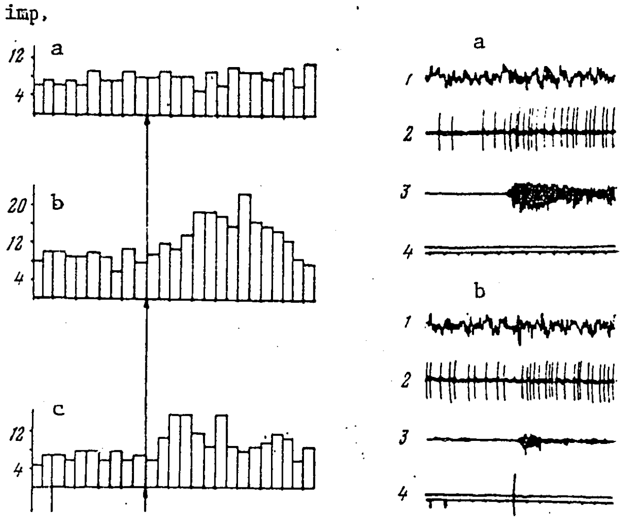


Figure 62. Inconsistent link between late activation of somatosensory neuron, intensity of ECS and EMG activity
Left: peristimulus histograms of neuronal activity with following intensities of ECS: a) 10 V; b) 20 V; c) 40 V. Channel width 70 cm, n = 10
Right: a) link between impulsation of given neuron and "intersignal" EMG activation; b) with EMG reaction to ECS
1) EEG 2) impulsation 3) EMG 4) stimulation mark

Our findings indicate that the FSF of many neurons correspond, during late activations, not only to real ECS, but some other elements of memory. It may be assumed that, at this stage, only neurons whose FSF correspond to both elements of real ECS and elements of the future result, i.e., elimination of ECS, are involved in the system. Then the coordination of neuronal activity at the stage of actuating mechanisms would be determined by both the real environment and model of the result, the objective link between which in the external environment is fixed in the memory of different elements in the form of coordinated FSF corresponding to these factors. We tested this hypothesis in the special experiments that we describe below.

As for the use of information about the real environment to organize the system of physiological processes, the submitted facts warrant, in our opinion, the assumption that it consists of the fact that, at all phases of development of the system of the behavioral act, discharges are fired by neurons with FSF that correspond to some elements of the exogenous object. At the stages of comparison and retrieval of information for input into afferent synthesis, FSF correspond to scattered elements of this object; at the stage of afferent synthesis and decision making, coordination of FSF, i.e., elements of memory, occurs at the level of individual neurons; finally, at the stage of actuating mechanisms, FSF of many different neurons are coordinated, reproducing a model or image of the entire object. The coordination of FSF of specific neurons in accordance with organization of the elements of a real external object leads to a specific organization and discharge activity, i.e., elementary physiological functions.

The hypothesis that there is use of information in stages, about the exogenous environment, is consistent with data obtained from studies of peripheral afferent structures. For example, analytical experiments revealed that the activity of primary somatic afferents begins to conform with the intensity of a stimulus 100 ms after it starts (Verner, Mountcastle, 1965). A similar pattern was observed for neurons of trigeminal nuclei (Darian-Smith et al., 1968) and retinal neurons (Wita, 1972). After 100 ms there was reflection of 7 gradations of stimulus intensity, or 2.4 bits of information about intenstiy; at the first moment there were only 2 gradations (Verner, Mountcastle, 1965).

In conclusion, we should like to note once more that, since one can observe neuronal discharges in virtually any brain structure in response to ECS, apparently information about ECS is used to organize the activity not only of somatic, but other neurons, i.e., the entire system of the behavioral act. At the same time, discharges of somatic neurons receiving influences from different neurons that are stimulated concurrently are formed under the influence of many types of information, rather than only information about effective ECS.

Information about a single factor exists only as part of the information about the entire environment, and it is reflected by enhancement of FSF that correspond not only to this factor, but the entire environment. For this reason, under different circumstances, the image of the same object can be represented by different sets of FSF and, consequently, by the activity of different sets of neurons.

Role of Goal in Organization Processes

In the aspect of information, the goal is a model of a prior event, i.e., one of the prior correlations between the object-related environment and organism as a whole. When this correlation was a reality it existed, on the one hand, as a specific organization of impulsation of many neurons, which led to achievement of a specific result and survival of the organism. On the other hand, this correlation with the environment existed as a specific organization of a set of stimulated functional synaptic fields of the neurons whose fields conformed in some way or other with the properties of the exogenous environment.

Thus, the goal is a model of a correlation between the organism and the environment, in which functional synaptic fields and, consequently, functional relations between elements provide for the generation of impulsation that is known to lead to the next result in the hierarchy of results leading to survival. Of course, goals do not exist in pretrigger integration as real correlations with the environment, but as those that are possible in a given environment and needed to satisfy the given motivation, i.e., in the form of potentiation of specific FSF corresponding to future events.

The object of our next series of experiments was to try to determine how information about future events is used in processes of organization of the functional system of a goal-directed behavioral act. This can be done by comparing the FSF of neurons during different phases of activation to the fields that would be actually activated in future events.

Since we have facts that enable us to assess the informational value of different phases of activations of somatosensory neurons in defensive behavior triggered by ECS, it was deemed expedient to consider the use in a defensive behavioral act of information about specific ECS properties, having made the ECS the future event. We did this by a procedure of developing a conditioned reflex, in which a flash of light was reinforced by ECS 600 ms later. The flash parameters were kept constant, while the ECS parameters were changed during the experiment, every 25-50 combinations, in order to track the correlation between parameters of future ECS and different systemic processes of the conditioned behavioral act triggered by the flash, by altering an event that is in the future, in relation to the flash.

As we have already mentioned, ECS cannot, of course, be considered a desired event on the way toward satisfying defense motivation. However, the behavioral act triggered by ECS must lead to some adaptive result, which we arbitrarily designated as "attenuation of deleterious effect." On the basis of general considerations, it must be assumed that the activity of elements that we recorded in the preceding series of experiments was directed expressly toward reaching this goal. The goal that is reached by the conditioned behavioral act triggered by the flash must also be hierarchically related to the former goal. For this reason, by changing ECS, which is a future event in relation to the flash, we also changed the goal of the conditioned behavioral act. Under such utterly artificial conditions, the ECS model could elicit a behavioral act analogous to the goals of natural behavior.

Experiments were conducted on 12 rabbits, using a method that was analogous to the preceding series in every respect, with the exception of the fact that a conditioned signal, a light flash synchronized with a click, was delivered 600 ms prior to ECS. The intervals between combinations constituted 20-120 s. After 20-30 combinations, the EP to a conditioned signal, like in response to ECS, usually consisted of a primary positive component, followed by negativity and a late positive component that changed into an "anticipatory wave" (Figure 63). The similarity of EP in conditioned and unconditioned behavioral acts was discussed in detail before. Conditioned EMG activation appeared with latency periods of 50-300 ms in different animals, and it coincided in time with the late positive component of EP (Figure 63).

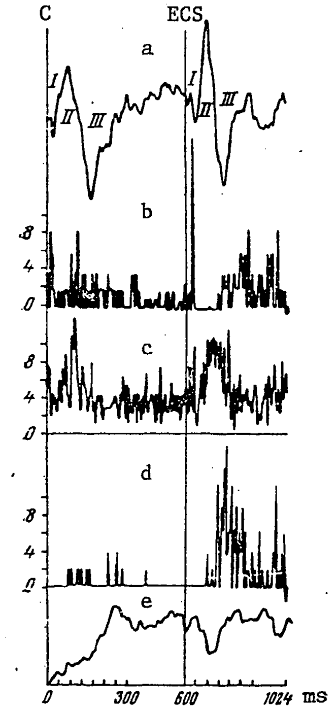


Figure 63.
Reproduction with conditioned signal (C) of types of responses of somatosensory neurons to ECS

- a) EP
  - I) primary component
  - II) negative
  - III) late positive component that changes into slow negative wave
- b) poststimulus histogram of neuron that presented a primary response with late activation to both stimuli
- c) histogram of neuron that fired discharges in negativity
- d) histogram of neuron with late activations
- e) envelope of EMG reactions

All of the curves are plotted from summation of 25 runs. Channel width 4 ms

This description was necessary to demonstrate that a rabbit, who is stereotactically immobilized and given only novocain, presents the usual adaptive behavior, characterized by the same parameters that were observed in free behavior. We have described elsewhere (Shvyrkov, 1968a) some of the distinctions of defensive behavior in a rabbit immobilized stereotactically.

Of the 83 neurons recorded in this series, 48 responded in relation to EP phases to ECS with different parameters: 12 neurons presented discharges during the primary response, 29 during negativity of EP and 24 showed late activations. The responses of these neurons to the conditioned signal often either entirely repeated the pattern of response to ECS, or contained the same pattern components in responses to the two stimuli (Figure 63). There was also reproduction of inhibitory responses. In those cases where we succeeded in "quasi-intracellular" demonstration of a neuron, the tracings also revealed segments with hyperpolarization (Figure 64).

The resemblance of patterns of reactions to conditioned and unconditioned stimuli in defensive behavior was reported repeatedly in the literature, and it was interpreted as a manifestation of "bridging" or "anticipatory excitation" (Vasilevskiy, 1968). We shared the latter opinion (Shvyrkov, 1968b, 1969).

However, since any spikes appear in order to reach the corresponding result, we must set aside the view, according to which any discharges may be the special correlate of the "afferent model of a future stimulus." The direct experiments of N. N. Vasilevskiy (1973, 1974) showed that a result, in the form of reinforcement of a specific discharge pattern, alters neuronal activity and organizes or disorganizes a specific configuration of impulses in accordance with the direction [sign] of reinforcement. We believe that our data are a convincing indication of the fact that the "afferent model of a future stimulus," i.e., goal, can be represented by functional synaptic fields organized in a specific way, whereas impulses always bear a performing [actuating] function, which is determined by information about the past, as well as the present and future.

The similarity of patterns of activity of many neurons of the somatosensory cortex in conditioned and unconditioned behavioral acts, like the similarity of EP configurations, is attributable, in our opinion, to the similarity of actions, results and all components of functional systems in the conditioned and unconditioned acts in the situation of "nonavoidance conditioned defense reflex." It reflects the similarity of processes of organization of elementary functions in two successive acts, in each of which only attenuation or only discontinuation of the nociceptive effect of ECS can be obtained.

As we have already mentioned, under relatively spontaneous conditions of behavior, when each act leads to achievement of its interim result, the similarity of discharge patterns of the same neuron in two successive acts is an extremely rare occurrence.

In spite of the fact that similarity of neuronal discharge patterns in conditioned and unconditioned behavioral acts is observed only in an unnatural situation, it shows that the time organization of processes in the somatosensory cortex under the effect of light and even ECS is not determined by the nature of the stimulus, but from the very first moment it is related to all systemic processes of a given behavioral act. Consequently, analysis of specific somatic information is made with development of systemic processes of the behavioral act, and it does not include any additional local or special processes occuring in a separate interval of time. Information processing is possible only as the use of information for organization in processes of organization of the functional system of the relevant behavioral act.

With change in ECS parameters and, accordingly, in pattern of the neuronal response to ECS, there is also a change in its response to the flash, which was not changed (Figure 65). This indicates that, on the whole, processes of organization in a conditioned behavioral act are determined not only by the trigger stimulus, but the model of a specific future ECS, represented in the form of preformed functional synaptic fields, already prior to the flash, i.e., in pretrigger integration.

Thus, we can assume that, by the time of exposure to the trigger stimulus, in pretrigger integration the FSF do not simply change in accordance with some motivation as a hierarchy of all goals leading to satisfaction of some need, but chiefly in accordance with the model of the next event, in our case, the model of a specific ECS.

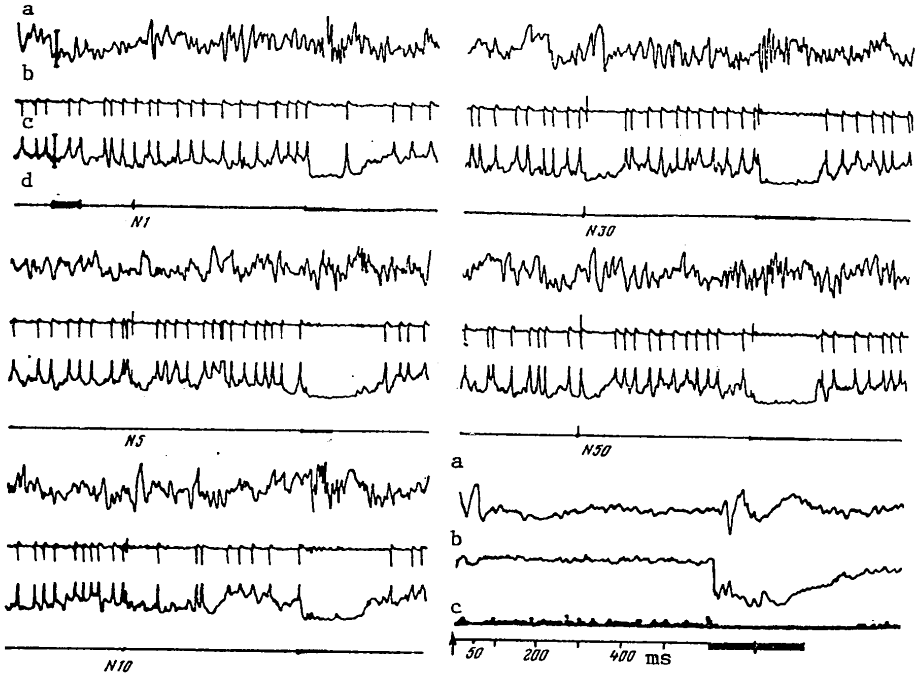
In order to determine the correlation between parameters of future ECS and FSF of somatic neurons in different systemic processes, let us consider the different phases of activation in a conditioned behavioral act triggered by the light as a function of parameters of future ECS.

The conditioned signal also induced a primary response in 10 out of 12 neurons, in which we demonstrated a primary response to ECS. On the histograms, these responses were often less marked in amplitude than the responses to ECS; their latency period ranged from 10 to 30 ms, and sometimes longer.

A change in parameters of reinforcement, which led to disappearance of the primary response to ECS, immediately also led to disappearance of the primary response to light, although the parameters of the latter remained unchanged. This was observed with change in both localization of electrodes (Figure 65) and intensity of ECS (Figure 66).

In two of the neurons that reacted to ECS we did not observe a primary response to light (Figure 67), whereas in three others primary responses appeared only to light and not to ECS (Figure 68). The responses to light disappeared with change in ECS parameters, even in neurons that did not respond to ECS.

These findings indicate that the sets of neurons showing primary responses to light and ECS are not entirely the same, but the entire set of responses to light is determined by the different properties of future ECS.



Calibration:
- a) 100 µV
- b) 1 mV
- d) 100 ms

Averaging is started at the time of the conditioned signal:
- a) averaged EEG activity
- b) averaged changes in membrane potential
- c) histogram of neuronal activity (n = 25, channel width 5 ms)

Figure 64. Neuron of somatosenory cortex with inhibitory reaction to conditioned signal

On the single tracings:
- a) EEG of somatosensory cortex
- b) neuronogram
- c) membrane potential
- d) marks; conditioned light flash and ECS.

Under each tracing is shown the sequential combination number from time of recording neuron and placing active electrodes in its inhibitory "receptive field"

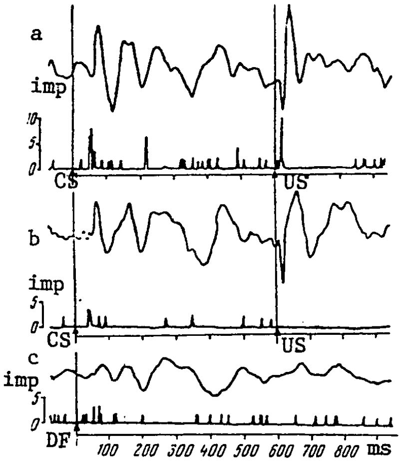


Figure 65.
Response of somatosensory neuron to conditioned flash as a function of localization of electrocutaneous reinforcement

a) primary responses to conditioned (CS) and unconditioned (US) stimuli during stimulation of contralateral front foot, 60 V
b) absence of primary responses when active electrodes are moved to contralateral hind foot, 60 V
c) no reaction to differentiation light flash (DF)

In a, b and c: top--averaged EP in somatosensory cortex; bottom--peristimulus histograms of neuronal activity (n = 25, channel width 3 ms)

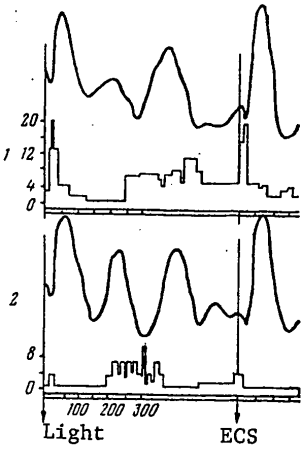


Figure 66.
Reactions of somatosensory neuron to conditioned light as a function of intensity of electrocutaneous reinforcement

1, 2) top--EP (stimuli shown by arrows); bottom--poststimulus histograms; channel width 4 ms, n = 25
1) reinforcing ECS delivered to receptive field of indicated neuron (contralateral hind foot), corresponds to parameters of receptive field in intensity (40 V) and elicits primary response; conditioned light also elicits a primary response; late activation of neuron after flash precedes delivery of ECS
2) an increase in intensity of ECS to 60 V leads to nonconformity between parameters of stimulus and receptive field, and to inhibition of neuron in response to ECS. Two phases of inhibition also appear in response to light: early and prior to delivery of ECS

Since responses to light of different neurons appear only with a specific future ECS, at the time when there is still no ECS in the real environment, it must be assumed that, during the primary response to light, the FSF of somatic neurons corresponding to elements of the future, specific ECS are already coordinated and, on the whole, conform with ECS as an integral factor.

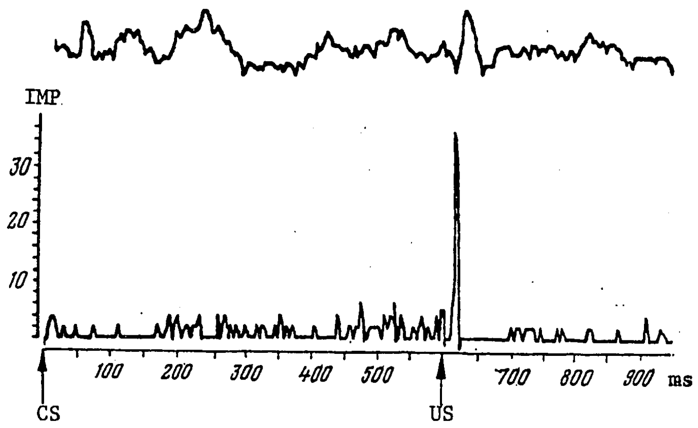


Figure 67. No reproduction of primary response to ECS with conditioned signal in somatosensory cortex
Top: averaged EEG activity; bottom: histogram of neuronal activity with n = 25, channel width 4 ms; CS--conditioned flash; US--ECS of contralateral front foot, 50 V, 1 ms

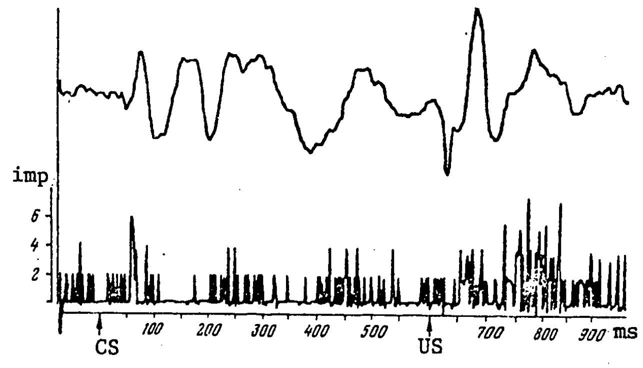


Figure 68. Primary reaction to conditioned flash by somatosensory neuron, which reacted to ECS with late activation
Top: averaged EEG activity; bottom: conditioned flash; CS--conditioned flash of light; US--ECS of contralateral hind foot, 60 V, 1 ms

Of course, the presence in a neuron of FSF corresponding to a future event does not rule out the presence of FSF corresponding to the real somatic environment "cut" by the flash. Our data probably indicate that, already at the time of the primary response, there is potentiation of only the FSF that correspond to the real environment, which are related to FSF corresponding to the goal. The link between these fields should reflect the link between different factors of the real environment and the future event.

Thus, both information about future ECS and information about the current status of the somatic environment is used in forming the aggregate of primary responses of somatic neurons. Discharges at the time of the primary response reflect the degree of conformity of the real properties of the environment not simply with prior experience, as we demonstrated in the preceding experiments, but with the part of prior experience that is prepared in advance to conform with the goal.

We succeeded in demonstrating discharges at the time of the negative component of EP in response to ECS in 29 neurons, only 17 of which showed responses to the conditioned signal (Figure 69). We were unable to demonstrate a response to the conditioned signal in 12 neurons, in spite of using the most diverse variations of ECS parameters and large numbers of combinations (Figure 70).

As a rule, reactions to the conditioned signal with different ECS parameters could be observed only in neurons whose responses in negativity to ECS appeared with different parameters of stimuli (Figure 71). Responses to light did not appear in neurons whose responses to ECS showed a marked dependence on ECS parameters (Figures 70 and 72). These two groups of neurons also differed in that a discharge usually appeared against the background of depolarization (Figure 73) in the "quasi-intracellular" tracings, in the first group, whereas in the second it usually appeared against the background of hyperpolarization (Figure 72).

We report the last finding only as an argument in favor of the conclusion that there is a difference between the two sets of neurons that fired discharges during negativity of EP; the origin and meaning of this phenomenon remain unclear to us.

The dependence on intensity and duration of ECS indicates that expansion of FSF of these neurons during EP negativity occurs in the direction of maximum conformity of integral characteristics expressly with ECS. Since discharges did not appear in such neurons after the conditioned flash, it can be assumed that, at the moment of negativity of EP in the conditioned act, the FSF of such neurons correspond only to the parameters of future (past) ECS and do not include FSF that correspond to the real somatic environment "cut" by the light. Because they do not receive a synaptic influx corresponding to their fields after the flash, these neurons do not fire discharges in the conditioned behavioral act.

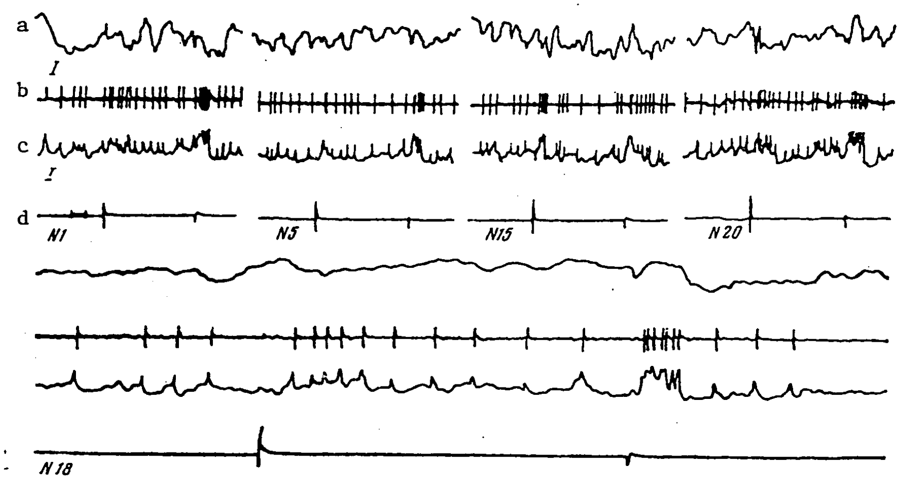


Figure 69. Appearance of discharges during negativity of EP in response to light flash in a somatosensory cortex that fired discharges in EP negativity in response to ECS

a) EEG of somatosensory cortex
b) neuronogram
c) membrane potential
d) marks of conditioned flash and ECS

Under each tracing the number of the combination from start of ECS with new parameters is indicated. Calibration: a) 100 µV; c) 1 mv; d) 100 ms Combination No 18 is illustrated with 4-fold increase in paper feeding rate

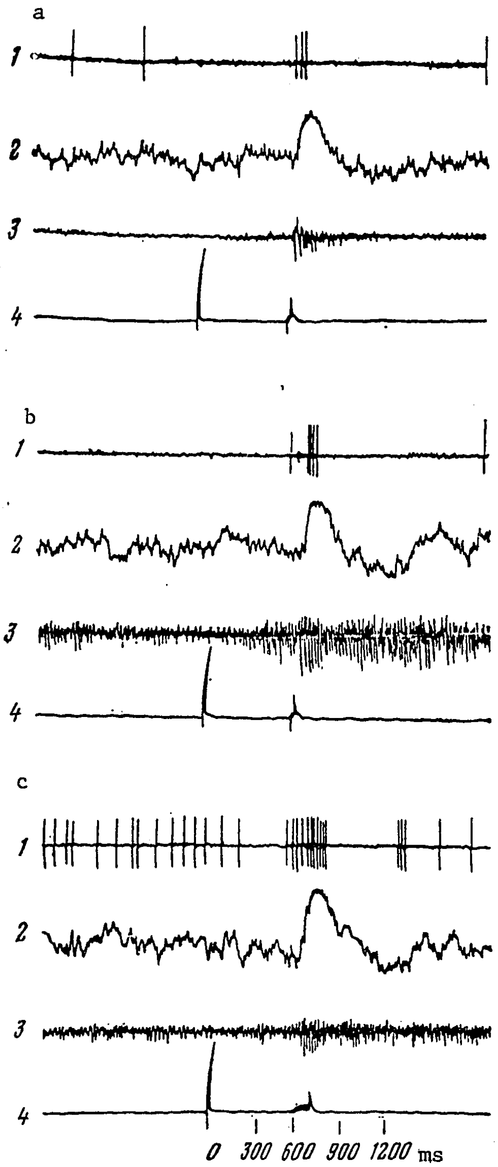


Figure 70. Absence of reaction to conditioned signal by neuron whose activation during negativity of EP in response to ECS depends on duration of ECS

a) first combination
b) 38th combination, duration of electrocutaneous reinforcement 50 ms
c) 80th combination, electrocutaneous reinforcement extended to 100 ms

1) neuronal impulsation
2) EEG of somatosensory cortex
3) EMG of cervical muscles
4) marks for flash and ECS

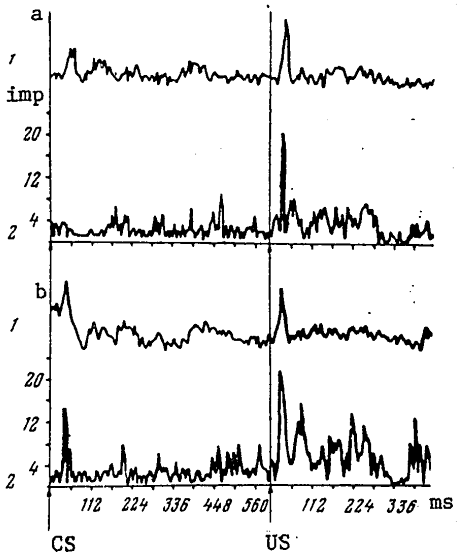


Figure 71.
Appearance of reaction in negativity of EP to conditioned flash in somatosensory neuron with change in ECS parameters

1) averaged EP
2) poststimulus histogram; channel width 4 ms, n = 25

ECS of contralateral front foot: a--40 V, 100 ms; b--70 V, 1 ms

Neurons, the discharges of which during negativity of EP in response to ECS appear with any intensity, duration and localization, apparently have very expanded FSF at this time. The presence in such neurons of discharges in EP negativity even after the flash indicates that, at this time, their fields could also correspond to the parameters of light in the somatic environment "cut" by the light.

In such neurons, responses to light appear only with specific ECS parameters (Figure 71), although after ECS they appear with all parameters. This indicates that the FSF of such cells at the moment of EP negativity to light are related to FSF corresponding to specific future ECS.

Thus, a change in ECS parameters only determines the presence or absence of discharges of somatic neurons during negativity of EP in response to light, but not the number of impulses or duration of activation. It can therefore be assumed that the FSF of somatic neurons correspond at this time only to one specific future ECS. In this case, fields corresponding to the "discrete" properties of future ECS on different neurons should also be coordinated, as is the case during the primary responses.

We were able to observe late activation in response to ECS in 24 neurons, and the flash induced activation in 20 of them (Figure 74). As was the case in the behavioral act triggered by ECS, late activation in response to light was referable to the most heterogeneous group. Some of these activations, especially of neurons that also presented primary responses, depended entirely on ECS. This is illustrated in Figure 74, and particularly Figure 66. In Figure 66, the primary response and late activation to light, which occur with ECS of 40 V, are illustrated. An increase to 60 V leads to disappearance of the primary response to ECS and development of marked inhibition during the primary response and at the site of late activation referable to unchanging light. In other words, like the primary response, late activation develops or does not develop, depending on the parameters of future ECS.

Another part of the late activations, as was the case in the responses to ECS, was related to EMG activation. This link was also present in the case of "intersignal" EMG activation (Figure 75).

Finally, other late activations, which corresponded to the most accurate use of information about the real environment during ECS, were probably not reproduced at all in response to the conditioned stimulus (Figure 76). This figure illustrates a neuron whose activity in response to ECS depended on localization, as well as intensity and duration of ECS. In response to the conditioned signal, it presented only a "hint" of a primary response. Probably, these neurons had FSF in the conditioned behavioral act that were entirely determined by the properties of future ECS, and they were unrelated to FSF of the real environment. Without receiving appropriate information from the exogenous environment, they did not discharge in the functional system of the conditioned behavioral act.

Interestingly enough, neurons that were activated after ECS probably reproduced this activation in response to the conditioned signal (2 cases), as demonstrable only when we analyzed individual tracings. In the case of summation, the neurons were areactive, due to variability of time parameters of conditioned activation (Figure 77). During such activations, the FSF of neurons could apparently correspond to the model of absence of ECS, rather than the model of ECS, i.e., the real goal of defensive behavior. Because of the small number of cases, this question remains open.

To sum up the results of these two series of experiments, on the whole it can be stated that goals in both pretrigger integration and in each systemic process are represented by the functional synaptic fields, activation of which would lead to a result. Information about the current state of the environment is represented by the real activation of the part of these functional synaptic fields that corresponds to the real environment. Unlike the information about the real environment that is submitted to analysis and synthesis in the course of the systemic processes of the behavioral act, from the very beginning and, probably, in pretrigger integration information about the goal is directly represented in "integral form."

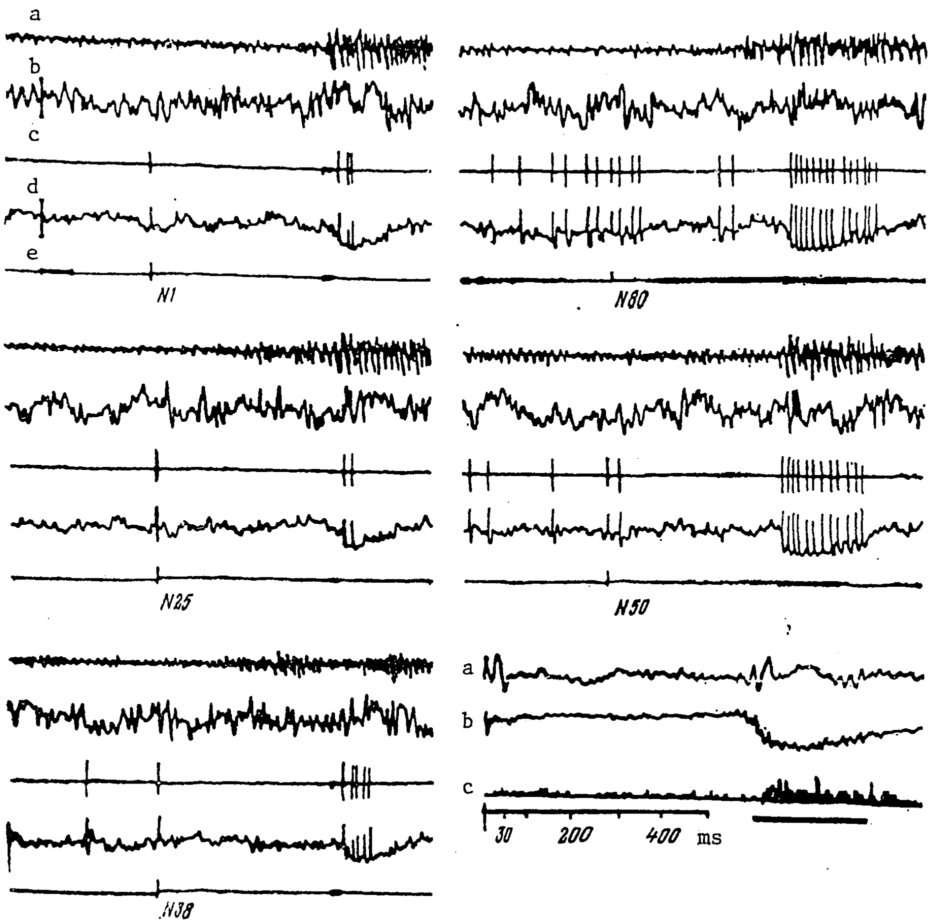


Figure 72. No activation in response to conditioned flash by somatosensory neuron whose response to ECS depends on duration of the latter and arises during hyperpolarization. Single tracings:

a) EMG of cervical muscles
b) EEG of somatosensory cortex
c) neuronogram
d) membrane potential
e) marks for conditioned flash and ECS. ECS increased from 20 to 50 V after 30 combinations, time increased from 20 to 200 s after 70 combinations

Calibration:
b) 10 μV
c) 1 mV
e) 100 ms

Averaging started at time of delivery of conditioned stimulus:
a) averaged EEG activity
b) averaged membrane potential
c) histogram of neuronal activity
Channel width 5 ms, n = 25

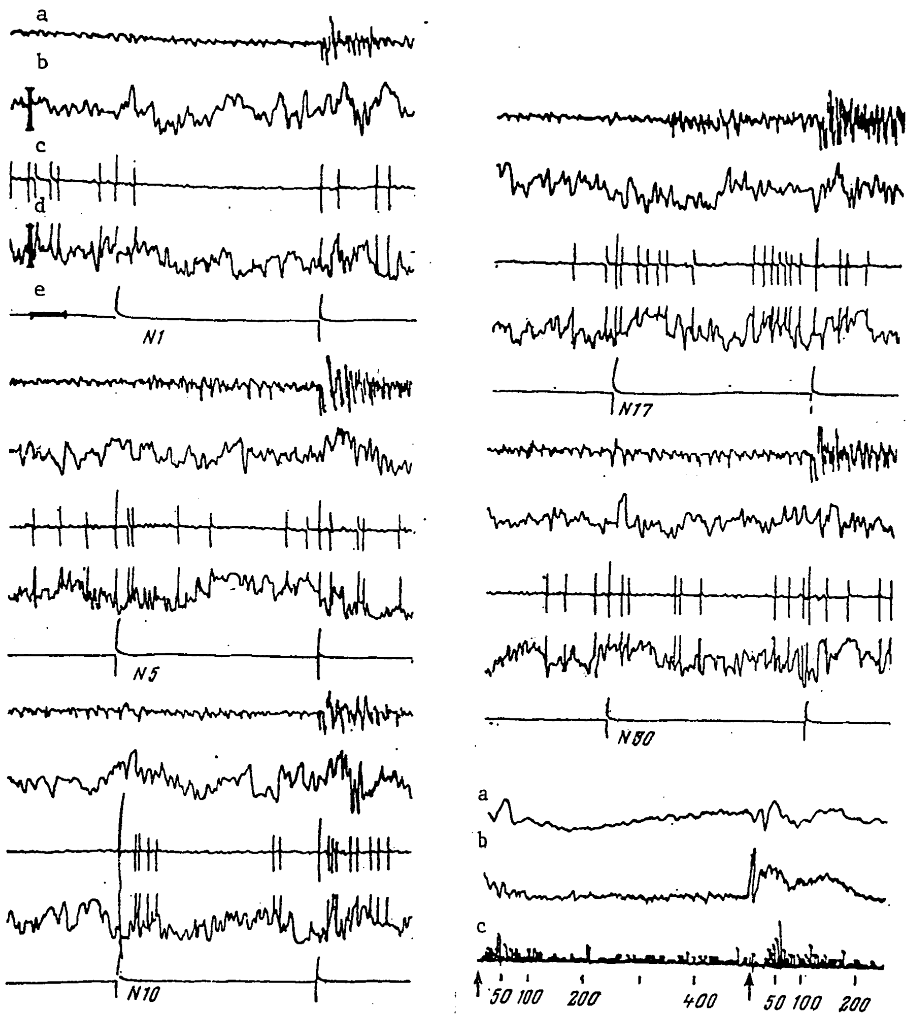


Figure 73. Reproduction of somatosensory neuron discharges in response to conditioned signal in negativity of EP appearing in depolarization. Single tracings:

a) EMG of cervical muscles
b) EEG of somatosensory cortex
c) neuronogram
d) membrane potential
e) marks for flash and ECS

Combination No shown under each tracing. Calibration: b--100 μV, d--1 mV, e--100 ms Averaging from delivery of conditioned flash: a--averaged EEG activity, b--averaged membrane potential; c--histogram of neuronal activity; n = 25, channel 5 ms

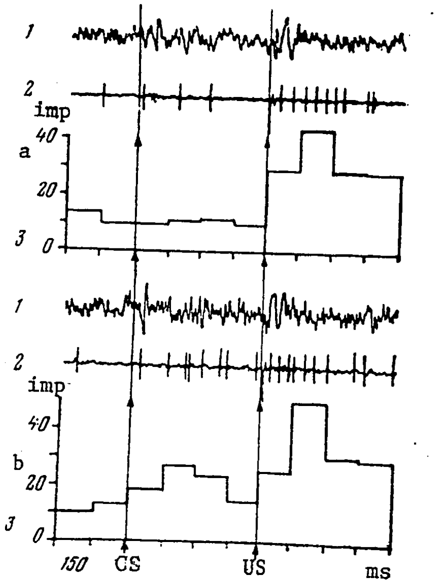


Figure 74.
Appearance of late activation of neuron of somatosensory cortex in response to conditioned light flash (CS) with change in parameters of electrocutaneous stimulation (US)
1) EEG
2) neuronogram
3) peristimulus histogram; n = 15, channel width 150 ms
a) electrocutaneous reinforcement delivered to contralateral hind foot, 80 V
b) discharging electrodes shifted distally by 5 cm

This warrants the assumption that the future event or goal is represented by potentiation of all FSF corresponding to a specific goal, whereas the exogenous environment only activates some of them. Since formation of an integral reflection of the object-related environment by means of coordination of FSF corresponding to different environmental elements probably occurs only on the set of neurons whose FSF are already coordinated in accordance with a concrete goal, this could lead to activation only of elements whose discharge activity and, consequently, elementary physiological functions are coordinated to achieve a specific result in a specific environment.

Involvement of Different Regions of the Brain in the Functional System of the Behavioral Act

Different forms of energy-related effects of integral objects on the organism are perceived by different specialized receptors having predominantly morphological links with specific brain structures. This circumstance, as well as numerous clinical observations, determined the trend to relate functions of processing of specific forms of information to specific regions of the brain. According to these conceptions, vision for example is implemented by the visual analyzer, hearing by the auditory analyzer, etc. It appears to us that there was a confusion here of different aspects of analysis of activity of the nervous system.

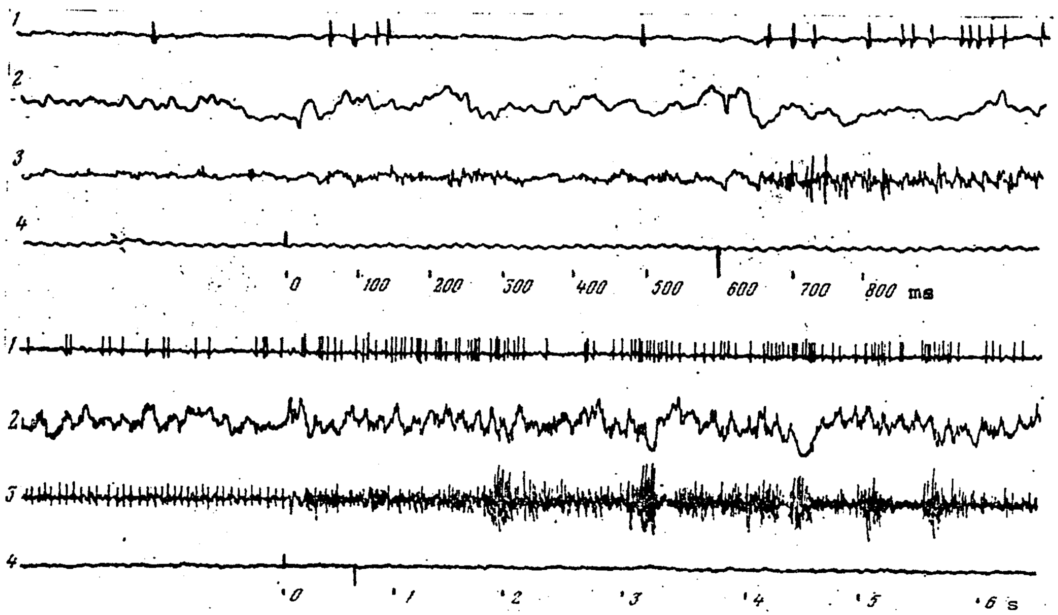


Figure 75. Reproduction with conditioned signal of activation of a neuron, which begins at the time of late positivity of EP and is related to the EMG reaction

a) 35th combination [a and b not shown in figure]
b) same neuron at slow paper feed rate (link is shown, not only with conditioned and unconditioned, but "spontaneous° EMG activation)

1) neuronal activity
2) EEG of somatosensory cortex
3) EMG of front foot
4) marks for light (top) and ECS (bottom)

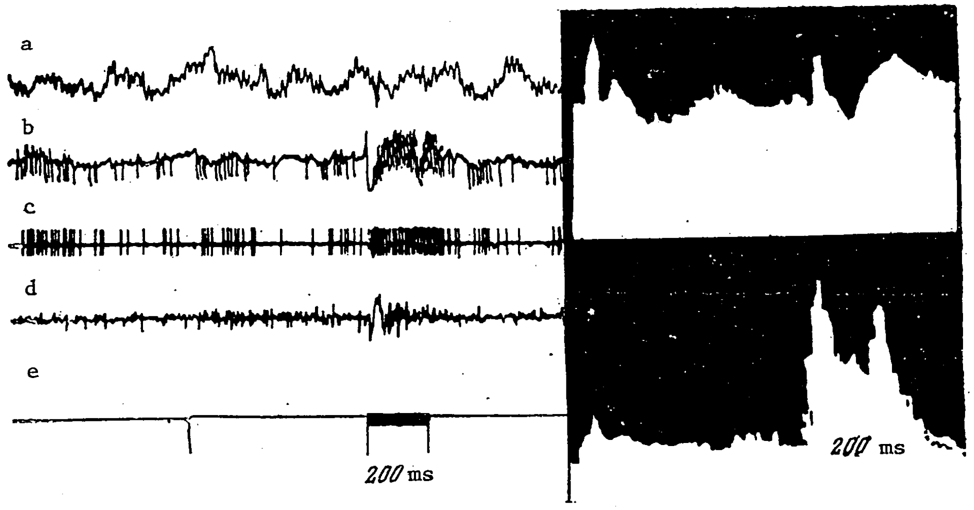


Figure 76. Absence of conditioned activation of somatosensory neuron, late activation of which reflects duration of electrocutaneous stimulation

a) EEG of somatosensory cortex
b) local potential recorded with microelectrode
c) neuronogram
d) EMG of muscles of ipsilateral front foot
e) marks of conditioned flash and ECS lasting 200 ms

Right, top: averaged EEG activity
Bottom: histogram of neuronal activity, n = 25, channel width 4 ms
Photograph taken from screen of AI-256

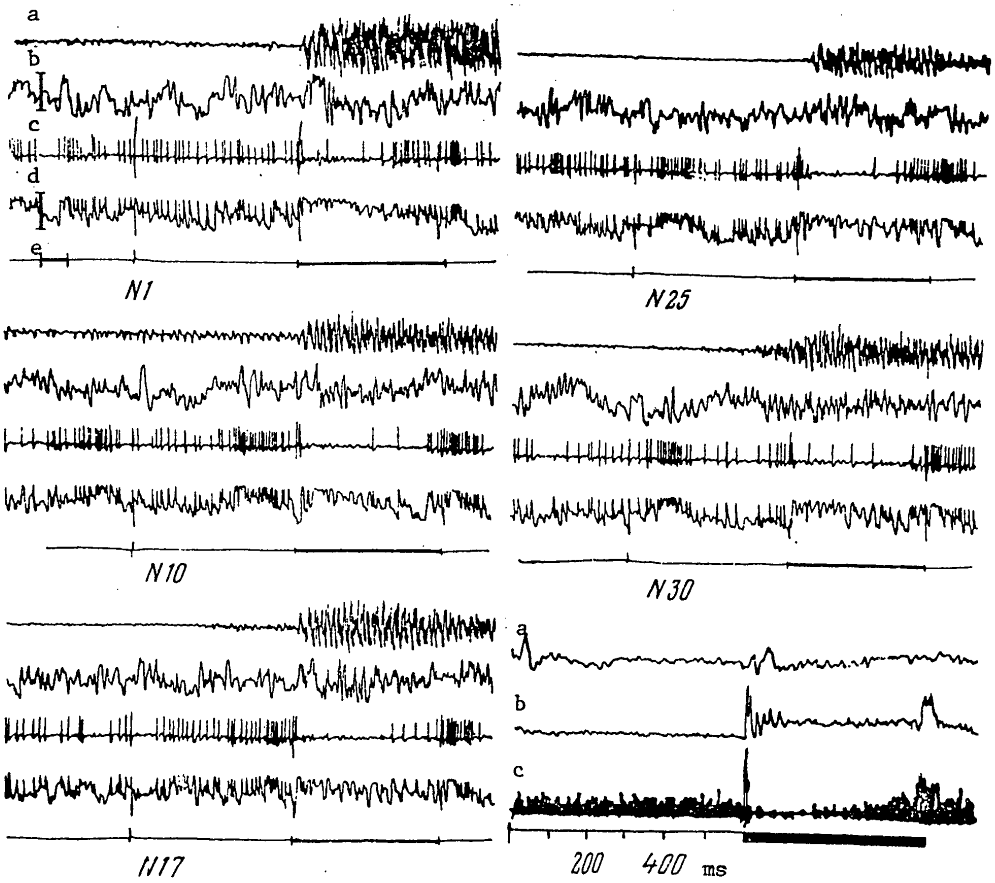


Figure 77. Appearance of late activation in response to light flash in somatosensory neuron that presented the "off reaction" to ECS. On the single tracings:

a) EMG of cervical muscles
b) EEG of somatosensory cortex
c) neuronogram
d) membrane potential
e) marks of conditioned flash and ECS lasting 500 ms

Combination No shown under each tracing

Calibration: b--100 mV, d--1 mV, e--100 ms

Averaging starts at time of conditioned stimulus:

a) averaged EEG activity
b) averaged membrane potential
c) histogram of neuronal activity; n = 25, channel width 5 ms

The instability of the latency period levels out the conditioned reaction in averaging.

As noted by P. K. Anokhin, "in the aspect of the problem of localization, one should make a distinction between function of substrate, tissue and function of the organism, which always has its own architectonics, its own complex integration" (1940, p 33). From this point of view, for example, vision, i.e., use of visual information to organize behavior, is unquestionably a function of only the entire organism, i.e., a systemic function. At the same time, each structure performs specific physiological functions in the system, which are determined by the specifics of its associations. These physiological functions should apparently be described in terms of "influences" on other structures.

Without going into the problem of localization of functions, let us only mention that the physiological specifics of some structure or other are apparently determined by the constancy of "outputs," rather than constancy of "inputs" that are used differently in different behavior. Discharges of the same element of a specific structure always have a constant physiological meaning, by virtue of its efferent associations, and this is true regardless of the cause of their appearance.

The question of using or not using the constant physiological function of a concrete neuron in a given form of behavior is answered through systemic processes of the behavioral act. Adaptation of organisms expressly to the objective environment requires organization of physiological functions in accordance with information expressly about objects, which is always multimodal.

Each neuron "breaks down" [separates] all factors of the exogenous environment in a behavioral act in accordance with the experience of using its own physiological function in behavior, rather than in accordance with the energy of these factors, since it has only FSF with activation of which its activity had been useful at some time for survival. These FSF may correspond (in the general case) to any modalities of exogenous factors, since they determine neuronal activation upon receipt of synaptic influx via many "intercentral" pathways. Of course, this does not rule out the possibility of different meanings or "weights" of different inputs to a single unit; however, purposeful use of neuronal physiological function in behavior is possible only with consideration of all influences that are organized in accordance with the objective external environment.

A given modality of environmental factors may be represented by part of the entire FSF of a neuron and, consequently, may emerge as part of the information about an integral object.

As shown by experimental data, the elements forming the functional system of the behavioral act are situated in virtually all regions of the brain with specific morphological structure and associations. The activity not only of neurons of the somatosensory cortex, but those of the visual cortex, as well as reticular formation and other structures, in the conditioned

[redacted]

behavioral act depends on the parameters of the future ECS. This is not in contradiction with conceptions of specific physiological function of each reason, but it shows that functional synaptic fields of specific "visual" or reticular neurons are formed with involvement of information about a future event, which is probably not limited to the parameters of ECS, but includes all factors of the exogenous environment that have an effect during delivery of ECS.

Thus, already during pretriggering integration the functional synaptic fields of different neurons are organized in relation to future events in all "modalities."

During pretrigger integration, FSF correspond to all means of reaching a goal. Let us try to imagine how reduction of these fields, or "degrees of freedom," occurs in systemic processes of the behavioral act triggered by conditioned light.

At the moment of the primary response, i.e., 10-20 ms after the trigger stimulus, discharges are fired simultaneously by neurons of the most diverse regions of the brain. As shown by the studies of K. Toyama et al. (1973), primary responses appear in neurons of the visual cortex that have both simple and complex visual receptive fields, according to the analytical nomenclature.

These fields probably correspond to only parts of all FSF of neurons of the visual cortex; other parts of these FSF may correspond to other modalities of the environment "cut" by the light flash, since we have seen that the primary response of a visual neuron depends on many factors.

In the somatosensory cortex, during the primary response the neuronal FSF probably contain parts that correspond to the real somatic situation during the light flash. In the reticular formation, the primary response is specifically related to biological sign of activation (Shevchenko, 1976a).

In addition to dependence of primary responses of reticular neurons on defense or food motivation, the following observation also leads to this hypothesis. In some neurons of the reticular formation, a primary response appears to both conditioned light and ECS (Figure 78); in others it is observed only to differentiation light (attenuated to one-quarter) and ECS, whereas non is observed in response to conditioned light (Figure 79). Evidently, differentiation light and ECS have only one property that distinguishes them from a conditioned stimulus: they temporarily eliminate anticipation of the next ECS, whereas the conditioned stimulus intensifies this expectation and, consequently, intensifies fear.

Thus, the primary respones of one part of the neurons of the reticular formation are related to attenuation of fear or "defensive" activation, and the responses of the other part are related to intensification thereof.

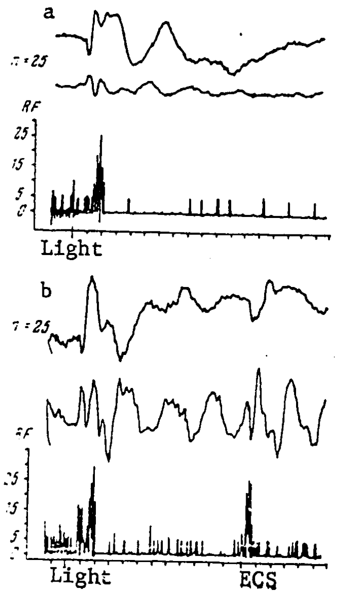


Figure 78.
Reproduction of primary response to ECS with conditioned signal in neuron of reticular formation, which reacted to light before conditioning by firing discharges in negativity of EP
a) before combinations
b) in 1st to 25th combinations
Top: averaged EP in visual cortex and RF [reticular formation]; bottom: poststimulus histogram; n = 25, channel width 4 ms; 600 ms between flash and ECS

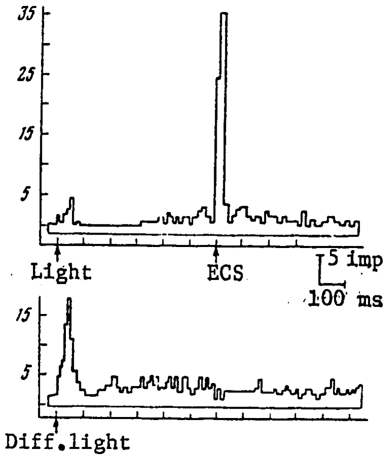


Figure 79.
Primary responses of reticular neuron to ECS and differentiation light
Top: poststimulus histogram for 25 combinations of flash and ECS (hind foot, 90 V, 1 ms); bottom: with 25 presentations of differentiation light. Channel width 4 ms

The FSF of reticular neurons probably correspond to very complicated sets of environmental elements; nevertheless, in this structure also we observed selective activation of neurons with specific functions during the primary response, which "broke down" the environment in accordance with experience of using specific activating physiological function of the reticular formation in different forms of behavior.

On the one hand, the aggregate of primary responses contains "superfluous" elements, since there is representation of FSF corresponding to many means of reaching a goal in pretrigger integration. On the other hand, this aggregate is not sufficient to reach a single goal, since it does not contain all of the elements necessary to reach the goal, but only those whose FSF were comparable to elements in the environment at the time of the trigger stimulus. Thus, the aggregate of all primary responses in all brain structures reflects retrieval from memory of integration of physiological functions that is partially superfluous and partially inadequate for a single means of reaching the goal.

An afferent signal may induce and include in afferent synthesis responses with short latency periods (15-30 ms) by neurons of the motor cortex (Voronin, Ezrokhi, 1971; Buser, Imbert, 1964), as well as the cerebellum (Fanardzhan, 1972) and spinal cord (Buchwald et al., 1961); however, this does not result in coordinated movement, since at this time the necessary level of coordination of physiological functions of elements has not yet been reached, and the general systemic mechanism of "program of action," within the framework of which only physiological motor mechanisms can be used in the behavioral act, is not yet functional.

There is constant change in neuronal FSF under the influence of changing motivation and situation; for this reason, any factor of the exogenous environment induces different [single] impulses which constitute constant "background" impulsation of both afferent fibers (Iggo, 1963) and many neurons that does not differ in any way from the "primary" discharges. The trigger stimulus differs from all other factors probably in that the FSF corresponding to it are present in the set of neurons coordinated with the goal by other parts of their FSF. For this reason, in real behavior, appearance thereof signifies the moment when specific environmental elements in many modalities coincide simultaneously with the properties of FSF prepared in advance and coordinated.

Under artificial conditions of independent appearance of a trigger stimulus, in relation to the rest of the situation, demonstration of the primary response in different regions appears in the form of a "widely generalized" spike. Under such conditions, coordinating influences triggered expressly by the trigger stimulus play the main role in generating the primary response in different regions, but they travel to different neurons via different "intercentral" pathways, rather than from the periphery. Since functional synaptic fields of a specific set of neurons are coordinated in pretriggering integration, "transient" [fugal] and "associative" influences reach only a specific set of neurons, in which spikes appear as the result of relatively chance coincidence of FSF generated by these influences with properties of the situation "caught unawares" by the trigger stimulus.

Indifferent signals, which activate FSF of a small number of cells that correspond to these signals, induce relatively local processes (Olds et al., 1972), since the FSF of most neurons are not coordinated in relation to the goal. If, however, the functional synaptic fields are quite broad in pretrigger integration and correspond to a large number of events, as is observed, for example, in the presence of high motivation or, on the contrary, if FSF are narrowed down and very accurately adjusted to one another, as is the case in "prestart" states, it is sufficient to have only partial coincidence between environmental properties and FSF to trigger the entire system. This mechanism is probably the basis of "incorrect" behavior with both heightened motivation and the dynamic stereotype.

The possibility of generalization of primary spikes is well demonstrable with the use of chloralose anesthesia, when the FSF of many neurons are found to be coordinated, apparently simply because of their expansion to the dimensions of anatomical synaptic fields. As we know, under chloralose anesthesia, an afferent stimulus induces responses with short latency periods, which are virtually synchronous, in many structures of the brain.

Obviously, the spikes that appear in the primary discharge extend over different areas in accordance with the morphology of links between discharging neurons. These influences converge on neurons of the next "time" order, which fire discharges during negativity of EP, regardless of whether or not these neurons reacted during the primary response. As we have seen, in this phase, the neuronal FSF differ significantly from FSF during the primary response. We must relate these changes to delivery to a neuron of a specific combination of primary discharges.

Since, according to the morphology of afferent associations of each neuron, these combinations include influences from the most diverse brain regions, neuronal FSF during negativity are formed with consideration of the most diverse information retrieved during the primary response. For this reason, neuronal FSF during negativity correspond, as shown by our experiments, to a specific set of environmental elements, and this already leads to partial translation of heteromodal exogenous information that continues to be received into organization of endogenous processes.

According to the hypotheses we are expounding here, reciprocal convergence of different influences on neurons during negativity represents afferent synthesis. Output spikes, which appear as a result of this convergence, correspond to decision making. Since different sets of influences converge on different cells situated in different regions of the brain during negativity, both afferent synthesis and decision making are specific in composition of different regions and even neurons. The decision becomes common and coordinated in subsequent convergence of all these impulses on the same and other neurons during the next phase, implementation of the program and acceptor of results of action, when integration reaches the stage of execution.

Convergence of discharges, which appeared during negativity, on neurons referable to the next "time" order alters the functional synaptic fields of these neurons in different directions, as shown by the above-described experiments, but on the whole it is in the direction of a more divided relationship to environmental elements, which is probably related to the start of function of already coordinated subsystems on the physiological level. The aggregate of discharging elements during late activations is already necessary and sufficient to achieve a specific result in a specific environment.

Late activation is observed in both the visual and somatosensory cortex, as well as the reticular formation (Shevchenko, 1976b)and, of course, the motor cortex (Evarts, 1966, 1972). These activations are already related to translation of organization of processes in the organism into new organization of environmental elements, i.e., achievement of a real result. This is achieved by the function of different physiological subsystems with their own systemic mechanisms, which were coordinated at the preceding "general cerebral" stages. Analysis of the hierarchic organization of subsystems on the physiological level is not included among our tasks here.

The above hypothetical scheme of neuronal mechanisms of systemic processes in an elementary behavioral act is illustrated in Figure 80. We had to depict the successive stages of development of the system in the form of discharges of different neurons; in the bottom part of the diagram, divergence and convergence at different stages of organizations can be perceived as a progressive process in the neuronal network.

In actuality, this scheme is called upon to demonstrate that different sets of neurons are involved in the system at different stages of organization, but there cannot be any question of any "progressive [forward-going] movement of stimulation."

In a behavioral act, successively occurring processes in any structure are local manifestations of successively developing general cerebral systemic processes, each of which involves different structures and neurons at the same time. Local and special processes included in the system of the behavioral act occur only within the framework of systemic processes, and it is only within the framework of systemic processes that different neurons perform their special functions in the system, in accordance with their afferent and efferent morphological associations.

The same time organization of processes in different brain structures by no means precludes the specificity of physiological functions of different structures of the brain and different neurons; in the course of general systemic processes, each structure and each neuron perform their own specific function, which is determined by the specifics of their properties and associations. The same time organization merely signifies that different structures and neurons do not function on their own, but are regulated by general systemic processes, as a result of which there is interaction of an enormous amount of elements, the highest form of coordination of their physiological functions or "degrees of freedom."

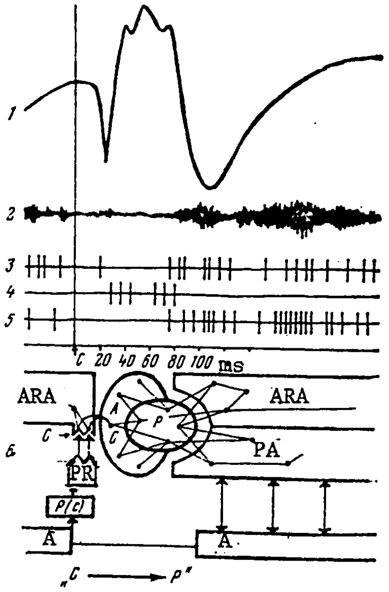


Figure 80. Hypothetical scheme of correlation of components of evoked potential and corresponding neuronal reactions with key mechanisms of the functional system of an elementary behavioral act. The dots connected by lines within the "blocks" reflect convergence and divergence of impulses appearing in different phases of formation of the functional system of a behavioral act

1) EP to trigger stimulus
2) EMG showing start of running program of action
3) neuron showing primary response and late activation
4) neuron responding in negativity of EP
5) neuron showing only late activation
6) diagram of key mechanisms of functional system of elementary behavioral act in continuum of behavior
"C-P") "stimulus-reaction" interval

ARA) acceptor of results of action
C) comparison of parameters of real stimulus (result) and "anticipatory reflection" thereof
PR) parameters of result
P(c) result of prior behavior (it is also the trigger stimulus)
A) action
AC) afferent synthesis
P) decision making
PA) program of action

The activity and special function of the same neuron can be used in different systemic processes, in both mechanisms of integration and of execution. Within the same systemic process, neurons with afferent and efferent special functions fire discharges simultaneously. Consequently, physiological mechanisms of analysis of the stimulus and mechanisms of formation of action are used simultaneously in the behavioral act, with development of systemic processes common to the entire organism. In the performance of behavior, only systemic processes are forward going [successive], but not "excitation" of afferent and efferent structures that are morphologically separated by only a few "synaptic stops [lags]," which could expalin only a few milliseconds of shift between the start of systemic processes in different regions.

CHAPTER 5. MECHANISMS OF INVOLVEMENT OF A SINGLE NEURON IN THE FUNCTIONAL SYSTEM OF THE BEHAVIORAL ACT

Mechanisms of Generation of a Goal-Directed Pattern

All of the foregoing appears to convincing, in our opinion, of the fact that processes on the neuronal level are a reflection of general systemic processes of the behavioral act in the integral organism. The problem of determination of activity of a single neuron is a problem of correlation between an element and the entire system. Heretofore, we have discussed these correlations from the systemic point of view; however, systemic processes themselves are formed by processes on an elementary level and, for this reason, the same correlations must also be examined from the "point of view" of the element.

Goal-directed activity of elements in the functional system of a behavioral act is determined by purposeful changes in their functional synaptic fields, and we had to assess this indirectly, according to their impulsation "output." It is difficult to assess changes in FSF, even in the case of intracellular registration, since activation via any synaptic inputs provides qualitatively the same EPSP.

At the present time, it is methodologically impossible to directly demonstrate on the neuronal membrane the "mosaicism" of synapses, to the activation of which a neuron is sensitive at a given time, just as it is impossible to directly determine the entire set of terminals carrying impulses to a neuron at a given time. However, some information can be obtained about organization of the functional synpatic field of a neuron by altering its state through microionophoretic delivery of biologically active substances. In analytical experiments, this method demonstrated, for example, that there are significant changes in receptive fields of peripheral and central neurons with ionophoretic application of some substances (Zieglgansberger, Herz, 1971; Zieglgansberger et al., 1971; Wallingford et al., 1973; Hess, Murata, 1974; Sillito, 1974, 1975).

The objective of our next series of experiments was to try to identify organization of processes on the level of a single neuron that determines its involvement in the functional system of a behavioral act. Since such involvement is referable to participation of neurons in some systemic processes, the problem was to determine the mechanisms of generation of a goal-directed pattern of neuronal discharges in the behavioral act.

We know from the analytical data that generation of neuronal spike activity is determined not only by current synaptic activation, but the state of the neuron, which usually refers to excitability, state of generator mechanisms, presence of pacemakers, etc. (Bullock, 1961; Sokolov, 1969, 1974, and others). It is also known that only some synaptic influences converging on a neuron are "detonators," i.e., induce generation of spikes, whereas others, i.e., "integrators," only modulate neuronal sensitivity to activation through specific detonator synapses (Andersen, Lomo, 1967). For example, the influences arising upon stimulation of the hypothalamus can modulate responses of neurons of the visual cortex to adequate stimulation (Khayutin, 1973).

Discharge activity of a neuron and its special functions are thus under the constant influence of integrator synaptic effects from other elements in the system. These integrator influences, which change constantly in behavior, create the variable "integrative state" (Anokhin, 1974a) of each neuron.

Like the entire behavioral act, the purposeful pattern of a single neuron must be the result of afferent synthesis. However, while there is interaction of "motivation," "memory," "situational afferentation" and "trigger stimulus" in afferent synthesis on the level of the integral organism, i.e., interaction of factors that characterize the behavioral act and organism as a whole, on the level of a single neuron afferent synthesis already emerges in the form of interaction of "molecular memory" and synaptic influences, the maximum composition of which is determined by the specific morphological connections of a neuron, converging on this neuron. While integrative brain activity consists of creating a goal-directed behavioral act from interaction of components of afferent synthesis, the integrative activity of a neuron consists of creating a "purposeful" pattern of activity that aids in reaching the goal of the entire behavioral act through interaction of heterogeneous synaptic influences and memory (Anokhin, 1974a).

On the level of the entire organism, motivation, memory and situational afferentation create pretriggering integration even before delivery of a stimulus. On the level of a single neuron, this pretriggering integration is reflected by a specific integrative state of the neuron, which is manifested by specific functional synaptic fields in relation to the system. While the goal-directed behavioral act is the result of interaction of triggering afferentation and pretriggering integration on the level of the entire organism, on the neuronal level the goal-directed pattern is the result of interaction of synaptic activation traveling to the neuron after the stimulus and the functional synaptic field that is prepared by integrative influences before the stimulus. The synaptic influences delivered to a single neuron immediately after the stimulus are already organized into a time and space pattern by the same pretriggering integration; for this reason, we used the direct change in state of only a single neuron with the use of ionophoretically administered substances to study interaction between synaptic influences and the integrative state of a neuron. By virtue of the local ionophoretic effect, it could not, of course, alter all of pretriggering integration and organization of synaptic influx to the neuron in question.

Experiments were conducted together with B. N. Bezdenezhnykh on 20 waking rabbits, using the same method as in the preceding series: a light flash was reinforced by electrocutaneous stimulation 600 ms later. We used four-channel glass microelectrodes constructed by the method of V. P. Belyy and V. V. Sherstnev (1973) to record impulsation. The recording channel was filled with 3 M KCl and the rest with 1-2-molar solutions of L-glutamate, GABA, atropine or acetylcholine. The substances were delivered to the neuron under study by 5-50 nA current throughout series of 20-25 combinations (15-20 min). A series of combinations without phoresis was conducted between series of combinations with phoresis as a control of the effect of each substance.

We shall describe below the results of analysis of activity of 70 neurons. First, we shall examine the changes in reactions of these neurons to ECS under the influence of phoresis; then we shall compare the changes in activity of these neurons in conditioned and unconditioned behavioral acts.

A response in some pattern or other to ECS was demonstrated in 29 neurons. Three of them presented a primary response, in five the phases of activity coincided only with the negative wave of the evoked potential, while six showed only late activation. In addition, 15 neurons presented multiphasic reactions: discharges were observed in 2 of them in all phases of the evoked potential, a primary response and discharge in the negative phase of EP were noted in 1, a primary response and late activation phase were observed in 3 neurons, while 9 had a response represented by a negative phase and a phase of late activation. The rest of the neurons (18) did not respond to ECS or presented an inhibitory reaction (23 neurons).

Of the 29 neurons that responded with some phasic reaction or other to ECS, 22 were tested for the effect of L-glutamate; GABA was tested on 13 neurons, atropine on 6 and acetylcholine on 3.

We could evaluate the change in state of a neuron under the influence of phoretically administered substances by the change in their background activity. As was the case in experiments of other authors (Salmoiraghi, Stefanis, 1967; Curtis, Crawford, 1969), glutamate always alleviated background activity, GABA always depressed it, to the extent of total elimination, atropine depressed it in 5 neurons and did not change it in 1; acetylcholine alleviated it in 1 neuron and depressed it in 2.

All of the agents we used were able to alter the pattern of evoked neuronal reaction. These changes consisted of both elimination of all reactions or different pattern phases, and appearance of new phases, the new ones also coinciding with some components of EP.

Glutamate altered the reaction of 19 neurons out of 22; in the case of monophasic reactions, it alleviated the response of 2 neurons, depressed or eliminated the response of 4 (Figure 81) and did not alter it in 1; in the case of multiphasic reactions, it enhanced all phases in 3 neurons, eliminated all phases in 1 and did not alter the response of 2. Glutamate had a different effect on different phases of the pattern of 5 neurons: it eliminated one phase while alleviating or failing to alter another. In four cases, glutamate "created" new pattern phases (Figure 82).

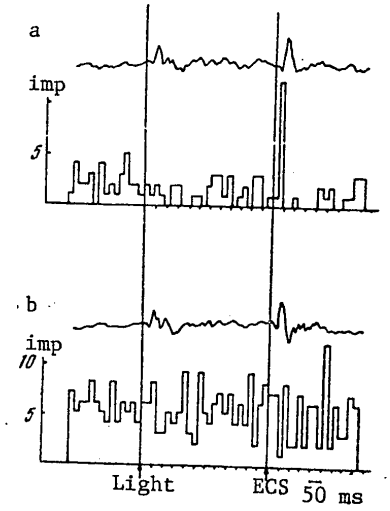


Figure 81.
Increased background and elimination of primary response to ECS under the influence of L-glutamate
a) before phoresis
b) during phoretic administration of L-glutamate (10 nA, 6 min).
Poststimulus histograms (channel width 24 ms); averaged EP shown above histograms, n = 15

In one neuron, acetylcholine did not alter background activity, but depressed the monophasic response; in another it depressed both background activity and the primary response, but created a new phase (Figure 85). We tested the effect of acetylcholine on only one neuron with a biphasic response: the negative phase of the response did not change under the influence of acetylcholine, while late activation disappeared (background activity was depressed).

Thus, the effect of the same phoretic administration of an agent on background activity and different phases of the response pattern of a single neuron could vary. In six cases, the changes in evoked neuronal reactions consisted of appearance of new pattern phases, which also corresponded to the components of the evoked potential.

In 7 out of 12 neurons with phasic reactions, on which we tested 2 or more agents, various substances had an utterly different effect with regard to changes in reaction pattern. For example, Figure 84 illustrates a neuron, in which the initial pattern of "primary response with late activation" changed into discharges in the negative phase under the influence of glutamate; there was an

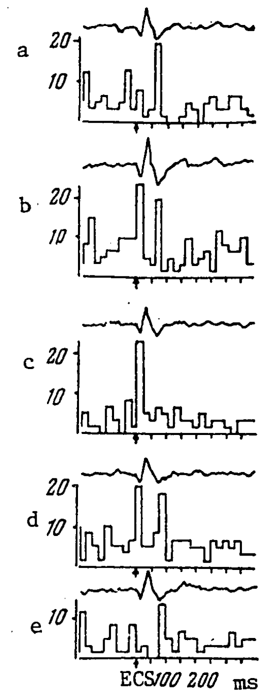


Figure 82.
Comparative effects of different agents on pattern of neuronal response elicited by ECS
a) initial neuronal response--late activation
b) L-glutamate (12 nA, 14 min) does not change late activation but "creates" primary response
c) GABA (+10 nA, 13 min) eliminates the first phase of late activation, but under its effect there is appearance of primary response
d) with atropine (+20 nA, 12 min) a primary response is "added" to the initial phase of late activation
e) control series after stopping atropine ionophoresis.
Same designations as in Figure 81, n = 25, channel width 24 ms

inhibitory reaction with administration of GABA, while the neuron became areactive under the influence of atropine.

Thus, the changes in state of a neuron and its functional synaptic fields induced by different biologically active agents are quite specific.

Analysis of the mechanisms of formation of the pattern of neuronal activity in an integral behavioral act must take into consideration that, by virtue of synchronism of processes in different brain structures and the same time organization of integrative processes in the functional system of the behavioral act, the synaptic influences going to a single neuron directly after the stimulus are already organized into a time and space pattern. However, the feasibility of altering the pattern of neuronal activity in such a manner that additional pattern phases appear by using phoretic delivery of agents to the neuron indicates that when a neuron is involved in a specific functional system it receives more synaptic influences than there are real phases in the response pattern.

Thus, we are convinced once more that the response pattern is not determined solely by organization of poststimulus synaptic influences, but also by the selective effectiveness of some of them, which make up the functional synaptic field of the neuron. This conclusion is also consistent with our previous conclusions, as well as the changes in receptive fields of neurons caused by phoretically applied biologically active agents.

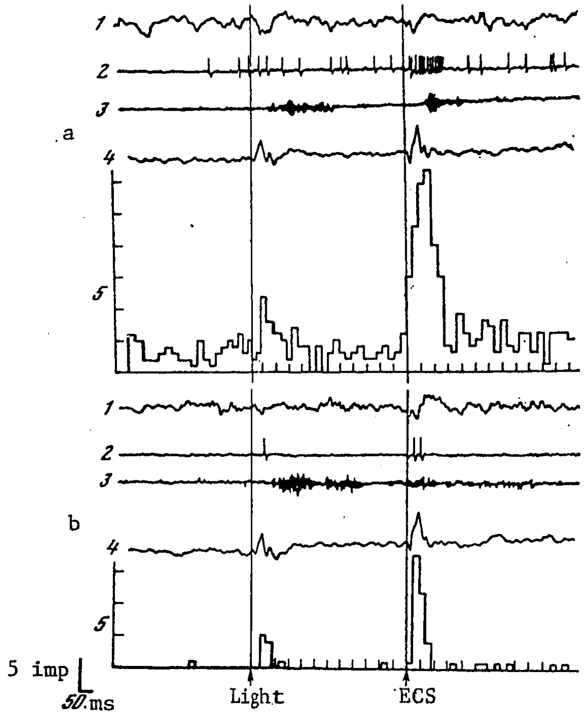


Figure 82. Depression of background activity and all phases of neuronal activation under the influence of GABA

1) EEG of somatosensory cortex
2) neuronogram
3) EMG
4) averaged EP (n = 25)
5) poststimulus histograms, channel width 24 ms, n = 25
a) before GABA
b) against the background of GABA

Analysis of sensitivity to the agents used of different elements of the pattern only enable us to state that in each phase the functional synaptic fields change under the influence of several agents. Thus, of the 9 neurons which demonstrated a primary response, 7 showed a change after phoresis of not only one, but two or even three agents which changed background activity differently (Figure 82). The primary response of different neurons was sensitive to different agents. Since synaptic influences are mediated by different mediators and changes in FSF are specific for different agents administered phoretically, the change in the primary response under the influence of different agents is indicative of the multimediator nature of synaptic activity at the time of the primary response.

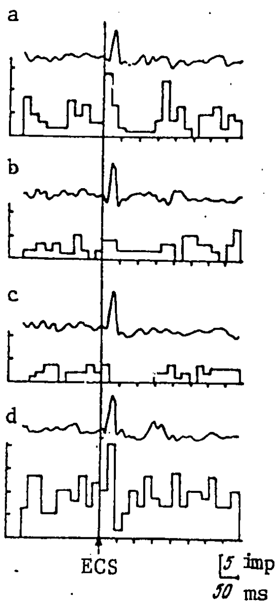


Figure 84.
Comparative effects of atropine, GABA and glutamate on ECS-evoked neuronal response; n = 15, on histograms the channel width is 24 ms

a) initial neuronal reaction (primary response and late activation)
b) elimination of response by atropine (+25 nA, 8 min)
c) inhibition of response by GABA (+10 nA, 7 min)
d) elimination of initial phases and appearance of new (negative) phase with L-glutamate (-15 nA, 8 min)

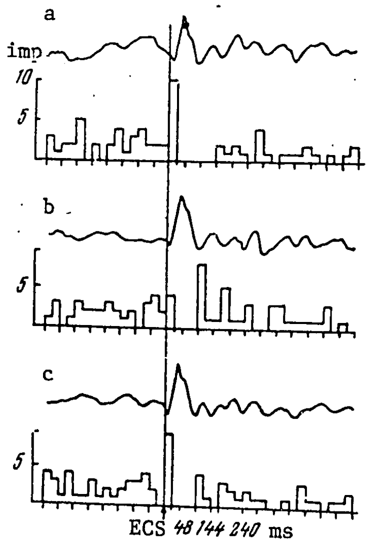


Figure 85.
Appearance of new phase in neuronal response with ionophoretic administration of acetylcholine

a) initial neuronal reaction--primary response
b) the primary response is eliminated by acetylcholine, but there is appearance of a phase of late activation
c) control series of combinations,

n = 10, channel width 24 ms

If we were to concur with the popular view (Orlov, 1974; Sherstnev, 1971; Marsden, 1973; Spehlman et al., 1974a, b) that neurons of different brain structures produce and use for synaptic transmission different mediators, it is logical to conlcude that not only the primary response of the entire set of neurons but, possibly, the primary response of a single unit is generated upon convergence on it of stimuli from many different sources. We had arrived at this conclusion earlier on the basis of other data. The same applies to the discharges in negativity, as well as the phase of late activation.

The fact that different phases of the pattern can differ in sensitivity to the same agent is indicative of differences in neuronal SFS in the course of various systemic processes according to the neurochemical criterion also.

Since a change in the state of a neuron under the influence of some agent does not lead to a chaotic reaction, but to elimination or appearance of additional phases, but always phases corresponding to some components of EP, it can be concluded that the state of the neuron per se does not lead to spike generation, but influences the output pattern merely by selectively altering the effectiveness of synapses making up the dynamic functional synaptic field, whereas initiation of phases is implemented by the phasic synaptic influx.

As we know, synaptic influences on a neuron induce two sorts of effects: "integrator," which are related to a change in state of the neuron, and "detonator," which induce spike generation. According to P. Andersen and T. Lomo (1967), integrating influences go to the distal parts of dendrites, while detonator ones come closer to the soma. This implies that there is morphological fixation of integrator and detonator links between neurons. P. G. Kostyuk (1974) believes that tonic and phasic influences are distinguished exclusively by their functional and dynamic features, and there can be both detonator and integrator influences from different sources on a given neuron.

Since influences that elicit a neuronal discharge also alter the state of the neuron, like the influences that do not elicit a discharge, we believe there is more justification for making a distinction between effects, rather than influences, on the assumption that any influence perceived by a neuron will have an integrative effect, while generation of spikes would depend on the entire set of influences and other conditions.

Under normal conditions, a given state of a neuron and selective effectiveness or "detonatory nature" of specific synpases are apparently related to corresponding integrator effects of all influences on a single neuron by other elements of the entire integration. In our experiments, the selective effectiveness as detonators of only some synaptic inputs and, consequently, the pattern of a neuronal response could be determined by constant integrator influences created by the motivation of fear and defense activation, which always appear in a situation of delivery of nociceptive stimuli. Since motivational influences are selective and elicit only neuronal states that led to acheivement of an adaptive result in the entire system in prior experience (Anokhin, 1968, 1974a; Sudakov, 1971), only the synapses whose activation would lead to purposeful activation of a neuron, aiding in achievement of this adaptive result, turn out to be effective. Although numerous exogenous influences converge on a neuron with electrocutaneous stimulation, a real pattern appears as the result of selective activation of the neuron only through specific effective synapes, which is what predetermines the appearance of a "purposeful" pattern in the reaction to current synaptic activation and involvement of the neuron in some systemic processes of the behavioral act. Thus, the neuron does not emerge as a summator, but as an "organizer" of influences coming to it: from the organization of incoming influences, which does not conform well with the goal, it creates an organization of discharges in time that conforms more fully with the goal.

There are two points of view that can be discussed to explain the interaction of different synaptic influences on a single neuron. According to one of them, the only form of interaction of synaptic influences is their summation on the neuronal membrane. According to the other view, integrative neuronal activity is not limited to summation of membrane potentials: some synaptic processes induce specific chemical changes in subsynaptic regions that are integrated in a change in metabolism of the entire neuron, and through the metabolic change they have a specific influence on the effectiveness of other synaptic inputs using different mediators.

This intersynaptic integration, which is a reflection of all interneuronal integration on the level of a single neuron, leads in turn to intermolecular integration, which is the object of fixation in molecular mechanisms of memory (Anokhin, 1974; Matthies, 1973, 1974; Huttunen, 1973).

Phoretic administration of agents, which blocks or alleviates neuronal activation with regard to some inputs, of course elicits a very complex change in the synaptic input, which could also be related to different presynaptic effects and some of its influences on adjacent elements. Nevertheless, phoretically administered agents, such as glutamate and GABA, always alter background activity unequivocally, which can be interpreted as an indicator of change in neuronal excitability, regardless of which specific mechanism is involved in obtaining this change. If we accept the summation hypothesis, we must conclude that changes in the background and reaction must proceed in the same direction, and this is what is usually observed when the neuronal membrane potential is changed by means of polarization (Kaburneyeva, 1971). However, as noted by many authors, when biologically active substances are delivered to a neuron the change in background activity often fails to be correlated with the change in reaction (Kozhechkin, Zhadina, 1973; Schmidt et al., 1974; Hess, Murata, 1974). In our experiments, glutamate, which depolarized the membrane (Krnjevic, 1970; Bernardi et al., 1972), increased background activity, but could eliminate the entire response or one of the phases of the response, while GABA, which hyperpolarized the membrane (Krnjevic, 1970; Altman et al., 1973) and blocked background activity almost entirely, could alleviate significantly the neuron's evoked reaction (Figure 86). At the same time, different agents, even those that changed background activity in the same way, could alter very differently the pattern of neuronal reaction. The difference in directions of changes in background activity and the evoked reaction, as well as different phases of neuronal reaction under the influence of the same agent cannot, in our opinion, be attributed to simple summation of membrane potentials evoked by phoretic and natural synaptic activation.

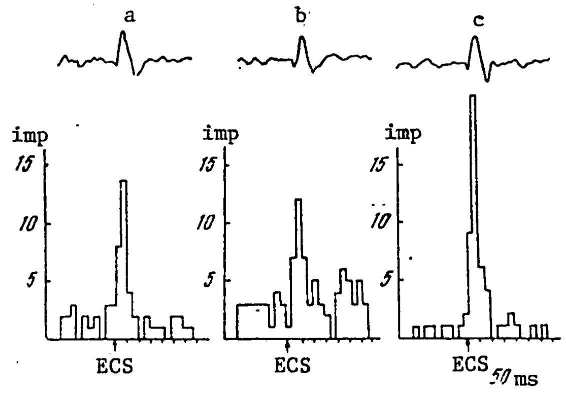


Figure 86. Comparative effects of L-glutamate and GABA on neuronal response evoked by ECS

a) initial neuronal response contains a negative phase
b) with L-glutamate an additional phase of late activation is added to the initial phase
c) with GABA, the initial reaction is alleviated, while background activity is depressed. On the histograms, channel width is 24 ms, n = 20

Within the framework of the summation hypothesis, this difference in directions could be explained by means of additional hypotheses to the effect that different components of the synaptic influx change differently under the influence of the same agent. However, these hypotheses appear contrived to us, since the absence of reaction change under the influence of glutamate, which depolarizes the membrane and increases background activity in all cases, would have to be attributed to the fact that the heightened excitability of the neuron is "compensated" proportionately to the decrease in synaptic influx, whereas blocking of the reaction (as, for example, in Figure 82) would have to be related to blocking of only one group of synapses, and one that is not isolated by the morphological criterion, but the functional time criterion. Analogously, under the influence of GABA, for example, in the case illustrated in Figures 86 and 87, we would have to assume that there is unexplainable intensification of synaptic influx under the influence of a universal inhibitory agent, and this intensification of synaptic influx is so great that it overcomes even a significant decrease in excitability of the neuron.

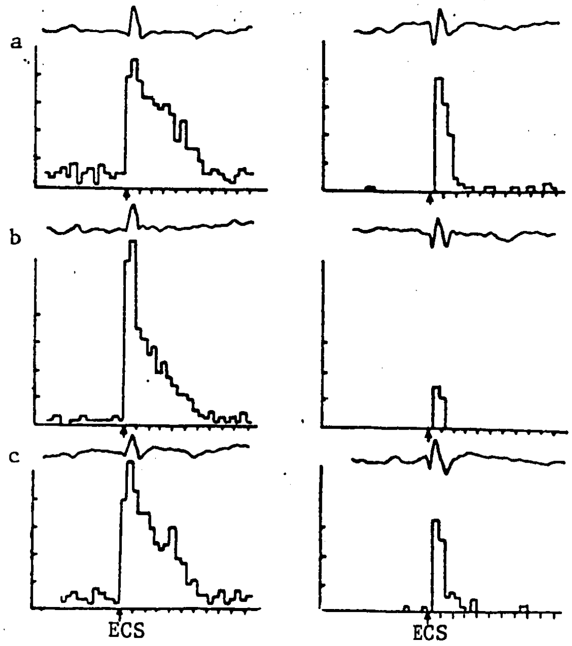


Figure 87. Effect of GABA on neuronal responses as a function of parameters of ECS.

Left--responses of neuron to ECS of contralateral front foot, 15 V, 1 ms:
- a) initial neuronal response consists of negative phase and phase of late activation
- b) GABA (+6 nA, 14 min, which depresses background activity, alleviates negative phase and depresses phase of late activation
- c) control series

Right--responses of neuron to ECS of contralateral hind foot, 30 V, 1 ms
- a) initial neuronal response consists of negative phase
- b) GABA (+6 nA, 14 min), which depresses background activity, also depresses negative phase of response
- c) control series of combinations

Channel width 24 ms, n = 20

These hypotheses turn out to be unnecessary, if we assume that constant phoretic activation or blocking of some synaptic inputs leads, in addition to change in membrane potential, transsynaptically to an increase in effectiveness of some synapes and concurrent decrease in effectiveness of others, which are activated immediately after the stimulus.

Since different synaptic inputs can be implemented by various mediators (Orlov, 1974; Sakharov, 1974), the difference in direction of the effect of the same agent on effectiveness of these inputs could be attributed to a change in neuronal sensitivity to different mediators. According to the integrative hypothesis, this selective change in sensitivity must be related to a change in general intraneuronal metabolism induced by the influence of a phoretically delivered agent.

Since different agents can change the pattern of neuronal reaction in different ways, it can be concluded that the change in metabolism induced by phoretic application of an agent is rather specific, i.e., that there is a specific link between activation of a certain functional synaptic field, metabolic changes within a neuron and new functional synaptic field, i.e., new organization of effective synapses.

This specific conformity is apparently determined by molecular processes in neuronal protoplasm and constitutes the "substrate of neuronal memory."

Thus, the integrative state of a neuron is mediated by neurochemical mechanisms. The general hypothetical scheme of correlation of neurophysiological processes on the level of a single neuron and of neurochemical processes is conceived as follows: when a neuron is involved in pretriggering integration, different integrative synpatic influences induce specific chemical changes in subsynaptic regions, which are integrated into a change in metabolism of the entire neuron, and through the change in metabolism they have specific influences on the effectiveness of synapses that use different mediators. Probably, the neuron "recognizes" a specific integration of synaptic influx as organization of mediators.

At the present time, there are already several hypotheses concerning the link between synaptic activation, molecular processes in neuronal protoplasm and impulse output of the neuron (Anokhin, 1974; Matthies, 1973, 1975; Matthies, 1974). The concrete intermolecular mechanisms of integration are beyond the area of competence of the neurophysiologist. We only have to stress the fact that, on all levels of this hierarchy, selection of different mechanisms into the functional system of an integral behavioral act occurs in accordance with a single evolutionary principle, namely the criterion of their cooperation in achievement of a useful adaptive result and, ultimately, survival of the organism. This entire hierarchy of integrations, which could be continued in both directions (in the direction of "molecular memory" and in the direction of "memory of the organism"), is established during formation of the functional system of a behavioral act during trial behavioral acts, and it is fixed by the useful adaptive result.

In accordance with the general direction of integrative activity of the nervous system toward reduction of "degrees of freedom" and selection of one behavioral act out of the many possible ones, integrative activity of a neuron consists of reducing the "degrees of freedom" referable to time of appearance of discharges and choosing one pattern of responses out of the many possible ones (Anokhin, 1974). On the basis of the facts we have submitted and data in the literature, it can be assumed that reduction of "degrees of freedom" of neuronal discharges is achieved on the basis of a general "principle of conformity." This principle is already manifested on the periphery, and it consists of the fact that neuronal responses appear only when there is conformity of stimulus properties with the properties of the peripheral receptive field. In the experiments described above, this principle was manifested by the fact that, although many synaptic influences converge on the neuron after ECS, a real pattern appears as the result of conformity between "endogenously"(through metabolic mechanisms) effective synapses with those that are really activated. As a result of all this, neurons, whose set of elementary functions corresponds to the goal and real information, become involved in the functional system, and behavioral acts are retrieved from memory that correspond to motivation and situation.

Since motivational influences that determine pretriggering integration are selective and induce only neuronal states that led to achievement of a given adaptive result in prior experience, only the synapses and FSF whose activation would lead to purposeful neuronal activity corresponding to achievement of one of the adaptive results are endogenously effective. Additional reduction of degrees of freedom of the neuron is related to the influence of numerous situational afferentations through which the change in all of pretriggering integration narrows even more the area of neuronal FSF.

Thus, the role of pretriggering integration in generation of a purposeful neuronal pattern consists of reducing the degrees of freedom of the neuron by means of formation of functional synaptic fields out of selectively effective synapses, the use of which in prior experience had already led to a useful adaptive result in a given situation.

Correlation Between Functional Synaptic Fields in Pretriggering Integration

The final choice of one degree of freedom in the behavioral act, i.e., the final organization of one system of orderly and purposeful relations, among all neuronal interactions that are possible due to divergence and convergence of their axonal collaterals within FSF selected in pretriggering integration, is established only after making a decision, when the actuating mechanisms of the behavioral act begin to function.

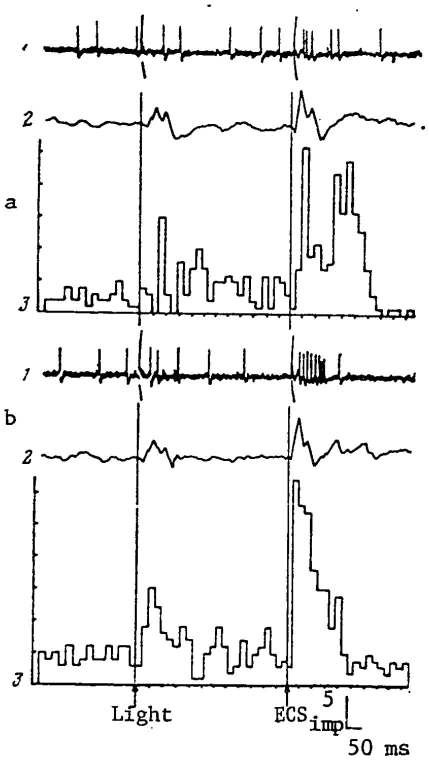


Figure 88.
Effect of glutamate on identical two-phase patterns of neuronal responses evoked by conditioned and unconditioned stimuli. Channel width 24 ms, n = 25

a) initial responses of neuron are represented by negative phase and phase of late activation
b) glutamate alleviates negative phases and depresses phases of late activation
1) neuronogram
2) averaged EP
3) poststimulus histogram

According to the conceptions we are developing, during pretriggering integration the FSF corresponding to future events related to the given motivation and situation should be effective.

We tested this hypothesis by comparing neuronal activity in conditioned and unconditioned behavioral acts with phoretic delivery of different agents. The logic of such comparison consists of the following: as we have established in the preceding experiments, neuronal activity in a conditioned behavioral act is determined by a model of a specific future event--electrocutaneous stimulation with specific parameters; the activity in an unconditioned behavioral act is determined by a model of some other future event, apparently, discontinuation of the nociceptive effect of ECS. These two goals are hierarchically related, the latter being "larger" in the entire hierarchy of goals constituting defense motivation.

By comparing the effects of the same agent delivered constantly on neuronal activity in the two behavioral acts, we hoped to separate FSF corresponding to different hierarchically organized goals.

Of the total of 70 neurons, 21 responded to conditioned light. Delivery of some agent to eight neurons that presented identical patterns in the two acts altered these patterns in six cases, in the same direction (Figure 88). In two cases, these patterns changed independently: with delivery of the same agent, neuronal activity was depressed in the first act and enriched by additional components in the second one (Figure 89). There was also independent change in reaction in the two behavioral acts in seven neurons that originally presented

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SYSTEMIC MECHANISMS OF BEHAVIOR

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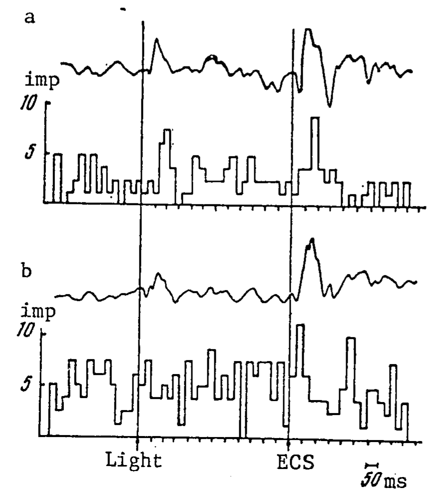

Figure 89.
Different changes in patterns of neuronal responses to light and ECS under the influence of glutamate. Channel width 24 ms, n = 15
a) initially, neuron responded with negative phases to light flash and ECS
b) L-glutamate eliminated negative phases in both responses and "created" a primary response and late activation in response to ECS

different patterns (Figure 90); the changes in reactions to light and ECS were induced by different agents. Conditioned responses appeared in 5 out of 14 neurons that had responded only in the second act after delivery of the agent (Figure 91). In six neurons that presented phasic responses only to the conditioned stimulus and did not react or were inhibited with ECS, no reaction to the unconditioned stimulus appeared under the influence of application of the agent, although responses to the conditioned stimulus could change (Figure 92). Delivery of agents to 35 neurons that were inhibited or did not react in both acts elicited a response to the conditioned stimulus by only one neuron and to an unconditioned stimulus by another one.

In 12 neurons, we succeeded in altering the parameters of ECS in at least one instance. In seven of them, this elicited a change in pattern of reaction, not only to ECS, as shown in Figure 87, but to the conditioned stimulus, and this was also associated with a change in effects of phoretically delivered agents (Figures 93 and 94). Interestingly enough, with change in ECS parameters, the patterns of conditioned reactions and sensitivity to different agents also changed in three neurons that did not react to ECS of any parameters before (Figure 94).

Let us discuss these findings from the vantage point of the questions we have posed. As it appears to us, the independence of changes in conditioned and unconditioned patterns with change in state of the neuron induced by ionophoretic application of agents, as well as the possiblity of appearance of conditioned activation with retention of the pattern for ECS, indicate that the pattern of conditioned activity of many neurons cannot be determined by generator mechanisms or the synaptic inputs that really activate the neuron and induce the unconditioned pattern.

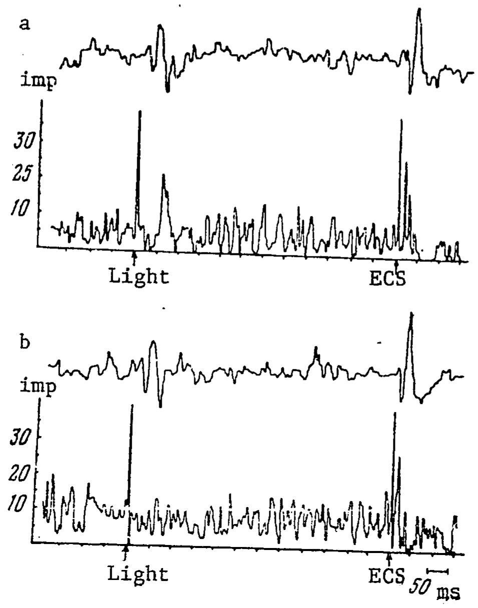

Figure 90.
Effect of L-glutamate on different patterns of neuronal responses in conditioned and unconditioned acts. Channel width 4 ms, n = 25
a) initial neuronal responses: late activation to light and primary response to ECS
b) with L-glutamate, late activation to light is eliminated, primary response to ECS does not change

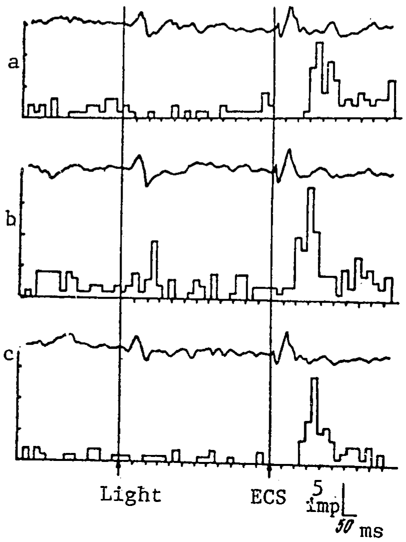

Figure 91.
Appearance of late activation in response to conditioned light under the influence of acetylcholine; on histograms: channel width 24 ms, n = 15
a) before acetylcholine
b) with acetylcholine
c) control series

Indeed, the independence of changes in pattern of activity in the first and second acts with delivery of some agent means that the neuron is activated in these two acts through different synaptic inputs. If we assume that the functional synpatic field of a neuron in the conditioned act is determined by "detonator" influences, which really activate the neuron after ECS, the changes in these influences, which were observed with ionophoresis, should have also altered the pattern of the response to the conditioned signal in the same direction. Appearance of spikes in some neurons in response to a previously ineffective conditioned signal, with unchanged pattern after ECS, also indicates that the functional synaptic fields determining the response to light could change, in the presence of the same pattern. The dependence of parameters of future ECS on "conditioned" activity of even neurons that do not generally respond to ECS, as we observed not only in neurons of the somatosensory cortex, but those of the visual cortex, speaks in favor of this conclusion.

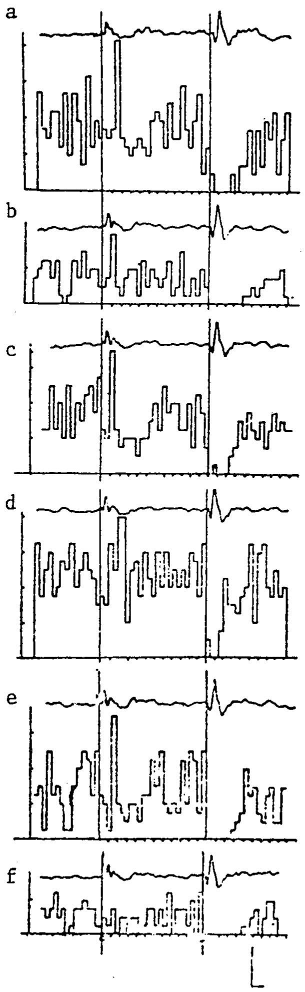

Figure 92.
Effects of different agents on a neuron that is inhibited in the unconditioned act.

a) initial activity
b) with atropine
c) control series
d) with L-glutamate
e) control series
f) with GABA

Poststimulus histograms, channel width 24 ms; above histograms are averaged evoked potentials, n = 25

First arrow--light, second--ECS.

Calibration: 5 impulses, 50 ms

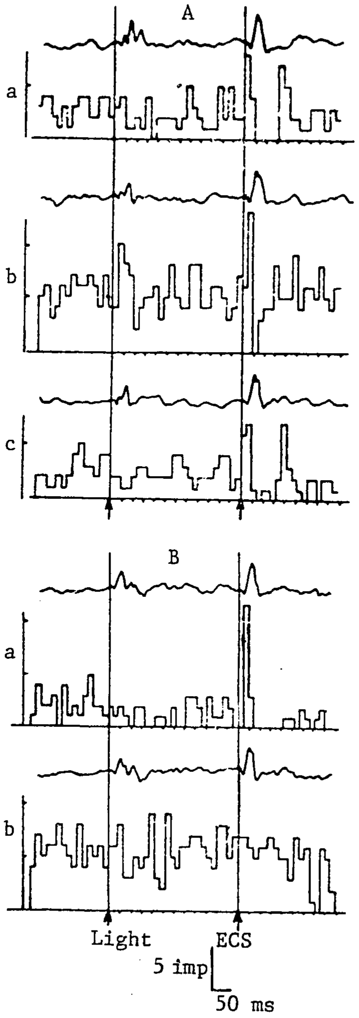

Figure 93.
Effect of L-glutamate on conditioned and unconditioned responses of the same neuron as a function of parameters of reinforcement

A) electrocutaneous stimulation of contralateral hind foot (30 V, 1 ms)
   a) initial activity
   b) with L-glutamate, a response appears to conditioned stimulus
   c) control series

B) ECS of contralateral hind foot (50 V, 1 ms)
   a) initial activity
   b) L-glutamate eliminates primary response to unconditioned stimulus

In both cases, the L-glutamate dosage was the same (-10 nA, 6 min).

Channel width 24 ms, n = 10

The state of the neuron very definitely determines the conditioned pattern, and it does so to such an extent that a change in state of the neuron by ionophoresis could even create a new response in neurons that did not react to light previously. A change in state of a neuron alters the response even of neurons that do not respond to ECS. Thus, we arrive at the conclusion that it is expressly a specific organization of internal metabolic processes that determines the functional synaptic field and, consequently, the pattern of the neuronal response in a conditioned behavioral act.

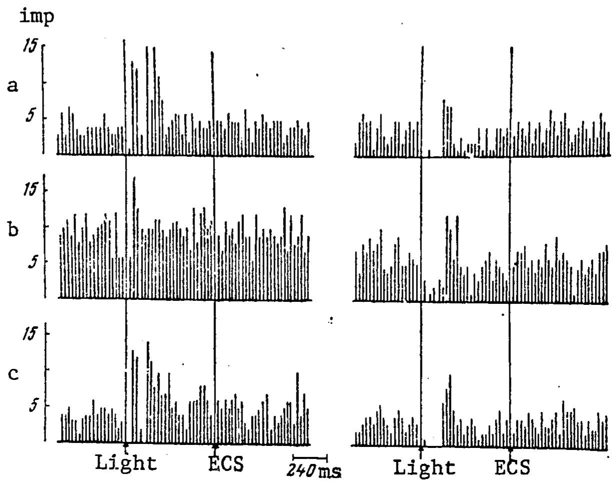

Figure 94. Effect of acetylcholine on conditioned response of the same neuron as a function of parameters of reinforcement.

a) initial activity with ECS of 40 V, 1 ms, contralateral hind foot (on the left) and 30 V, 1 ms, contralateral front foot (on the right)
b) against the background of acetylcholine
c) control series

Channel width 24 ms, n = 15. In both cases the acetylcholine dosage is the same (+50 nA, 8 min)

Normally, a given state of a neuron determining its FSF is probably produced by all influences going to this neuron from elements related to it, which have an integrative effect. Organization of these influences is determined by motivation and situation. As it changes constantly, this organization of interneuronal interactions leads to constant changes in endogenous metabolic processes which, as they determine neuronal FSF for each subsequent moment, in turn determine organization of interneuronal interactions.

In our experiments, it is logical to relate organization of integrator influences to defense motivation, which always appears in the situation of delivering electrocutaneous stimulation. The change in effects of phoretically delivered agents with change in parameters of ECS (Figures 93 and 94) and the fact that delivery of an agent to neurons showing different patterns in the two acts usually also elicits different changes in these patterns and, in general, could influence only one of the patterns, indicate that organization of integrator influences of defense motivation creates different FSF in many neurons, to be used in the system of the conditioned and unconditioned act. It may be assumed that, in such neurons, the FSF in the conditioned act are created by the "metabolic model of electrocutaneous stimulation," whereas in the unconditioned act they are created by the model of "discontinuation of electrocutaneous stimulation." This is also indicated by the fact that, with change in parameters of ECS, there is also a change in effects of the agents we used.

In those neurons that present similar patters in the two successive acts, the functional synaptic fields in the two systems are probably created by motivation as the hierarchy of all goals and future events, which is what determines the similar sensitivity of similar patterns to ionophoresis of the agents.

Neurons whose activity does not generally change (i.e., "areactive" ones) and, perhaps, inhibitory neurons probably simply do not have "metabolic models" and, consequently, no synaptic fields referable to the given motivation. For this reason, any change in the state of such neurons by means of electrophoresis cannot create metabolic changes that would be specific in relation to organization of synaptic influx.

Thus, determination of FSF by motivation emerges as an overall change in metabolism, which ultimately leads to satisfaction of this motivation. Determination of FSF by the model of a concrete event, which is possible in a given situation, emerges as definition [specification] of metabolic changes by integrator influences from the situation. On the level of metabolic mechanisms of memory, the same "law of conformity" probably applies: metabolic processes that would implement synthesis of specific biochemical receptors for specific mediators that could be received at a future time are probably initiated only when there is a conformity between the receptors present at this time and real mediators.

Of course, all these hypotheses, which have been expounded on the basis of studies of only "output" impulse activity of neurons, require verification in special experiments that would enable us to monitor [control] metabolic processes in a neuron during a behavioral act.

The operational architectonics of systemic processes must be invariant on all levels of the hierarchy of systems (Anokhin, 1973). In order to form an hierarchy, the operational architectonics of the functional system of a behavioral act and functional system of a neuronal discharge must be functionally identical. To continue the analogy to organization of systemic processes of a behavioral act, it can be assumed that a spike (or discharge within a single phase of EP) is the realization of an elementary program of action of the corresponding functional system. According to functional system theory, generation of spikes is the product of integrative activity of the neuron, in which convergence of different synaptic influences can be interpreted as elementary afferent synthesis, while establishment of "metabolic conformity" between the integrative state and detonator activation, i.e., functional synaptic field, as elementary decision making. Since the neuron is under the constant influence of other elements of the system and through its discharges influences the state of the entire system, appearance of a spike in the collaterals of its axon should alter the state of the entire system. This change can be interpreted as a result elicited by the spike; the reverse influence of the system on the neuron emerges as "feedback."

Any "anticipatory reflection" is based on anticipatory change in metabolism (Anokhin, 1962a); this anticipatory change in metabolism and preparation of subsynaptic membranes for feedback that it elicits can be interpreted as an elementary "acceptor of results of action." Thus, organization of intraneuronal intersynaptic integration allows for analysis of its functional architectonics from the standpoint of functional system theory.

The "principle of conformity" also applies in the performance of a single behavioral act; although pretriggering integration allows for achievement of the same result by different means, which corresponds on the level of a single neuron to potentiation of several FSF, real afferentation after a stimulus activates only one functional synaptic field in each neuron and determines implementation of a single [only] means of reaching the goal. In the course of different systemic processes, the integrator influences organized by each systemic process successively "narrow down" functional synaptic fields, rendering them more adequate to the goal and situation.

Complete exclusion of "superfluous degrees of freedom" and determination of the pattern of neuronal activity of the neuron in actuating mechanisms of the behavioral act by the only goal of this act and specific environment are achieved by the set of integrator influences created at the stage of afferent synthesis and decision making of expressly this elementary behavioral act. Evidently, these integrator influences, created by neuronal discharges during negativity of EP, determine the purposeful and selective sensitivity of neurons to synaptic influxes, which appear during performance of action until the result of a given behavioral act is achieved.

CHAPTER 6. FUNCTIONAL SYSTEM THEORY, AND THE PSYCHOPHYSIOLOGICAL PROBLEM

Impossibility of Direct Correlation of Mental and Neurophysiological Processes

The nature of mental processes and their material substrate have always been the subject of enormous interest to mankind. And the present time, "the study of psychosomatic correlations continues to be a most pressing problem, proper work on which would be inconceivable without the first and foremost involvement of neurophysiology"(Dubrovskiy, 1971, p 271).

As he began to study the brain by objective methods, I. P. Pavlov observed: "In essence, there is only one thing in life that interests us, our mental content" (Pavlov, 1949, p 351).

Associationism in psychology and reflex physiological conceptions led to interpretation of neurophysiological mechanisms of the psyche in the teaching on higher nervous activity on the basis of the idea of sameness of "an elementary mental phenomenon"--association and "the purely physiological phenomenon"--the conditioned reflex. I. P. Pavlov believed that "here there is total fusion, total absorption of one by the other, identification" (1949, p 521). For a long time this was the idea that guided the research of both physiologists and psychologists.

The neurophysiological mechanisms of the behavioral act, interpreted as a reflex, were limited in essence to conduction of excitation over a specific route, and they could be described as a succession of physiological processes occurring in different parts of the brain. In the very same way, mental processes were directly compared to physiological ones, which were studied (as we mentioned in the first chapter) in the absence of behavior and mental activity.

It turned out that these processes could not be compared, by virtue of absolutely objective properties of physiological processes that are always very definite in time and space, as well as mental processes localized only within the entire brain and organism, and within the time of the entire behavioral act. This circumstance led I. P. Pavlov to the need to exclude psychological concepts from analysis of mechanisms of behavior: "As shown by all of the experiments, the entire substance of studying the reflex mechanism, which is the foundation of central nervous activity, amounts to spatial relations, determination of the pathways over which stimulation spreads and collects. Then it is absolutely clear that the probability of learning everything on this subject only exists for the concepts in this field that are characterized as spatial concepts. This is why it must be clear that one cannot use psychological concepts, which are essentially nonspatial, to delve into the mechanisms of these relations. It is necessary to point with a finger to the site of stimulation and where it traveled. If you can conceive of this vividly, you will comprehend the entire force and truth of the teaching that we uphold and are developing, i.e., the teaching on conditioned reflexes, which has excluded entirely from its realm any psychological concepts, and which always deals only with objective facts, i.e., facts that exist in time and space" (1949, p 385).

Another solution to the problem of impossibility of comparing mental and reflex processes was offered by psychologists, and it refers to the fact that since "direct reconstruction ... of perception, feeling or a thought ... from the material of standard nervous impulses or graduated bioelectric potentials ... cannot be done, this impossibility of formulating the characteristics of mental processes in the language of physiology of endogenous changes in their substrate is the opposite side of the possibility of formulating them only on the language of properties and relations of their object" (Vekker, 1974, pp 14-15). This conclusion was very logically made by L. M. Vekker on the basis of an analytical reflex premis: "... any mental process, like any other act of human vital functions, originates from some human organ" (p 11).

Thus, mental and reflex mechanisms cannot be compared, both from the physiological and psychological points of view.

The organism always emerges as a whole in a behavioral act, and such psychological concepts as motivation, perception, memory or goal reflect conceptions about processes that are referable not only to the entire behavioral act, but to the entire organism that performs behavior, and they characterize it expressly as a whole. I. P. Pavlov observed that "mental processes are very closely linked with physiological phenomena, determining integral function of an organ" (1949, p 348). However, with the analytical approach, integral mental processes could only be compared to local and special physiological processes, since systemic processes uniting elements into a single whole had not yet been discovered.

We believe that it is expressly at this point that the "possibility" appeared of ruling out the mental factor from analysis of behavior, since the mental factor is something over and above the sum of purely nervous functions and, consequently, it also appeared to be over and above behavior. Efforts to compare integral mental and special neurophysiological processes also led to psychophysiological parallelism, or even directly equating mental processes with physiological ones, and the intensity of a subjective mental experience was compared to the force of excitation of the corresponding structure, while the content of this experience was compared to localization of excitation. For example, visual sensations and perceptions were viewed as excitation of the visual analyzer or as a process accompanying such excitation; motivation was interpreted as excitation or the "subjective aspect" of excitation of some hypothalamic center, etc. The concept of threshold made only a quantitative separation of purely physiological excitatory processes from the same excitation accompanied by an experience, and it did not permit posing the question of quantitative specifics of the nervous processes at the basis of psychological phenomena. At the same time, it is obvious that by no means any nervous activity is associated with mental experiences. This circumstance led to a search for the "center of consciousness," which was subsequently called "anatomization of abstraction" (Burns, 1969).

We believe that, by excluding the psychological element from mechanisms of behavior, reflex theory only created the illusion of the possibility of a purely physiological explanation of behavior. It appears to us that it appeared because the reflex was the basis of all conceptions of reflex theory, i.e., the phenomenon that occurs in spinal and anesthetized preparations, in which, of course, there is no integral adaptive behavior and, consequently, there is indeed no mind. Physiological reflex theory provided a "purely" physiological interpretation of the causes and mechanisms of behavior, in which reflection of objective reality by the brain was limited to physiological processes. In the reflex scheme of the behavioral act, which was an arc linking different effects to different reactions of different organs, there was simply no need for informational relations between the environment and the organism as a whole nor, consequently, for the mind. Since, however, there were few who were willing to negate the mind in general, the latter always emerged as an "epiphenomenon," which was not mandatory for performance of behavior.

For this reason, efforts to reconcile physiological and psychological descriptions of an elementary behavioral act were always within the framework of psychophysiological parallelism.

The Problem of Correlation of Systemic and Mental Processes

Analysis of the development of psychology and physiology from the systemic point of view led P. K. Anokhin to the conclusion that, in order to paint a complete natural scientific picture of brain function, it was not necessary to blend or equate physiological and psychological elements, but that a "conceptual bridge" was needed that would permit comparison of the concepts of these two disciplines and see physiological mechanisms behind psychological phenomena.

Since there are specific systemic processes of organization, qualitatively different from elementary ones, and integral behavioral acts are linked expressly with systemic processes, mental processes are based on systemic processes of organization of different processes into a single whole, rather than elementary physiological processes of excitation or inhibition. A comparison of neurophysiological and mental processes is possible only through processes on the systemic level.

A comparison of the concepts of systemic and psychological processes no longer involves the difficulties that arise if one directly compares mental and physiological processes. Indeed, in addition to time and space characteristics in common in physiological and systemic processes, the latter are also characterized by the parameters of integrity [wholeness] and organization. Like any processes of organization, systemic processes of the behavioral act are distinctive information processes, for which the "physiological level" emerges as the "material carrier." A comparison of these informational parameters of systemic processes to mental ones is then made using the same gage with regard to meaning, since both information and psychological processes are systemic properties of the organism as a whole.

The systemic nature of organization of processes is comparable to psychological processes in the sense of the latter's reflective function. Psychologists have provided convincing proof of the active role of perceptive actions in apprehension (Zinchenko, Lomov, 1960; Zaporozhets et al., 1967), and this compels us to question any physiological conceptions concerning purely sensory organization of information processing in analyzers, from "receptor to cortex." Some correlation or other can be demonstrated between reactions and a stimulus in any part of the brain and, consequently, this phenomenon cannot be interpreted as an indication of expressly mental reflection of the properties of a stimulus in the activity of some analyzer. Such properties of apprehension as activity, integrity and objectivity [in the nature of an object] cannot be compared to processes within a single analyzer, and they require a systemic foundation. At the same time, as we have tried to demonstrate, analyzers are also involved in such systemic processes as the program of action. Experiments with reverse masking (Donchin, Lindsley, 1964; Kostandov, Shostakovich, 1970; Massaro, Kahn, 1973) and direct comparison of evoked potentials to the reports of subjects (Rosner, Goff, 1969; Libet et al., 1967; Fox et al., 1973), revealed that about 100 ms are required, with presence of both early and late components of EP, for the appearance of subjective sensations.

At the same time, physiological experiments did not confirm the conceptions that are popular in psychology and based on the reflex principle to the effect that expressly the motor elements of perceptive actions, likened to the properties of an object, implement the creation of an adequate image of this object. Indeed, in afferent synthesis of the perceptual act, material in memory about movements can only be one of the components, along with information about the entire sensory situation (past, present and future).

Since information about any event is used, as we tried to show, during all systemic processes and for organization of activity of elements of the entire system, perception as a reflection of the properties of an exogenous object is linked with many central and peripheral structures, and with all the key mechanisms of the functional system of the perceptual behavioral act. Thus, the reflective role of the mind is thus comparable to the process of the organism's use of exogenous information (organization of environment) to build its own organization (organization of physiological processes).

As for the regulatory role of the mind, it could be compared to the systemic process of action: the higher the degree of organization of processes within the system, but more perfect the behavioral acts and the better the result is attained. Here, the process of afferent synthesis and decision making translates information (order [organization]) about the environment into an order of physiological elementary processes in the system, while reverse translation of organization of the system into orderliness of the environment occurs with the function of systemic mechanisms of the acceptor of results and program of action, when the action is performed, i.e., organized function of physiological actuating mechanisms, and real results of behavior are attained, i.e., new organization of the environment. Thus, the function of determination of behavior by the mind can be compared to the organizational parameters of systemic processes.

Insofar as systemic processes consist exclusively of physiological processes and organization of these processes creates a new quality--informational parameter of the system, comparable to the conception of the mind, physiological and mental determination of behavior are inseparable, and they do not exist without one another or without informational or systemic determination.

Although the "mental" factor is an attribute only of integration as a whole, this does not preclude the existence of a specific structure in mental processes. Since mental processes are based on integral behavioral acts, functional system theory, which describes the structure of behavioral acts, is also applicable for description of the structure of mental processes, and each of the key mechanisms of the functional system has, as can be seen from the submitted experimental results, very concrete neuronal implementation.

The properties of mental processes (for example, perception), demonstrated in psychological experiments, are found to be comparable to systemic mechanisms and, conseuqently, a very definite form of activity of concrete neurons. The activity of perception and apperception can be the consequence of presence in the functional system of the perceptual act of the system of the acceptor of action results, which actively requests the required information from the exogneous environment. Perception is objective [object-related] and integral [whole], because information retrieved simultaneously from the most varied regions of the brain and combined in pretriggering integration is involved in afferent synthesis; it is constant when the sensory situation changes, because material from memory is inputted in afferent synthesis, rather than the recoded state of receptors. Of course, this is only an example of possible comparison of properties of mental and systemic processes.

Functional system theory provides the same "operational architectonics" for any behavioral act; at the same time, psychology makes a distinction between several mental processes, such as perception, thinking, remembering, etc. In view of the fact that there is objective manifestation of the mind only through behavior and that the concept of activity (behavior for animals) is included in current conceptions of any mental processes, it may be assumed that the specific mental processes singled out by psychology can be compared to the specific characteristics of the same systemic processes corresponding to behavior, which is consistent with the thesis of integrity [wholeness] of the mind. The structure of systemic processes is, apparently, referable to the common features of "any mental process which constitute the basis for distinguishing between the mental and nonmental" (Vekker, 1974, p 10).

Functional system theory enables us to refer to the concept of quantity of information in the system and raise the question of dependence of properties of integration on informational and energy characteristics of the stimulus, as well as the problem of quantitative correlations between the properties of integration and sensation, to provide objective quantitative characteristics of sensation. Perhaps, the solution to these problems will relate the stimulus and sensation in a formula free of the objections that the psychophysiological law is presently encountering (Luce, Galanter, 1967; Pieron, 1966; Lomov, 1974). The approaches to the psychological solution of the problem of signal detection (Zabrodin, 1973) and the problem of reaction time (Stepanskiy, 1972; Oshanin, Konopkin, 1973) presently requrie analysis of the entire behavioral act and the entire experimental situation.

At the present time, we do not know at all which systemic characteristics will be comparable to some mental characteristics or other; however, the possibilities that are presently emerging of calculating such systemic characteristics as complexity, orderliness, wholeness, volume, composition, organization of a system, etc. (Ferster, 1964; Gorskiy, 1974) gives us hope that there will be a quantitative verification of this hypothesis.

The idea of expressly integrative activity of the nervous system has a long history (see, for example: Anokhin, 1968, pp 194-202). The conception of systemic organization of physiological mechanisms in behavior has been widely accepted in modern physiology, and it is winning increasing recognition by psychologists and philosophers.

Having proved the existence of specifically systemic processes of integration, qualitatively different from elementary physiological processes, functional system theory removed the main obstacle to synthesis of psychology and physiology, which consisted of the fact that, in analytical neurophysiological experiments, the researcher always deals only with local and special processes, whereas behavior and mental processes are related to function of the brain and the organism as a whole. Thereby, functional system theory made it possible to synthesize physiology and psychology while confirming the qualitative specifics of their objects of investigation. The solution to the psychophysiological problem apparently consists of the fact that organization of physiological processes into a single system occurs by means of qualitatively unique systemic processes; their substrate is physiology, while their informational content refers to the properties and relations of exogenous objects. Interpenetration and mutual enrichment of physiology and psychology are possible expressly on the level of consideration of systemic processes.

Functional system theory, first formulated in general terms in physiology as far back as 1935 (Anokhin, 1935), is becoming the logical basis of systemic conceptions that are presently also being developed in psychology (Lomov, 1975). The use of the same methodological approach to problems of consciousness and the mind in these disciplines opens up new opportunities for synthesis of a single natural scientific idea about the world.

At the same time, the systemic approach also imposes certain requirements not only of physiological, but psychological research.

At the present time, we can still encounter quite often interpretation of different mental processes as independent realities, which merely interact with one another. For example, it is assumed that processes of perception and memory, attention and thinking are independent, and determination is made of their influence on one another. This analytical, or "atomistic" approach, which was in its day a necessary stage of development of psychology, is now in contradiction with conceptions of integrity [wholeness] of the mind and unity of behavior and the mind. As noted by D. I. Dubrovskiy, this approach led to a situation where "the term 'mental,' which is one of the most widely used in modern scientific parlance, entails a variegated 'train' woven of different meanings and values. And in this form it appears as the cornerstone of psychology, reflecting its lack of theoretical organization" (1971, p 162).

At the same time, the integrity of mental phenomena, the impossibility of breaking them down into pieces, are usually mentioned as one of the fundamental features of the mind. It appears to us that the theses gained by psychology concerning the integrity of the mind and unity of behavior and mind constitute a good foundation for the systemic approach.

Correlation of Systemic and Neurophysiological Processes

This section is a summation of sorts of the conceptions that were discussed on the preceding pages.

We shall begin the comparison of systemic processes to processes on the neuronal level with consideration of memory ("life experience"). On the behavioral level, memory emerges as an hierarchy of goal-directed behavioral acts, which lead to survival of the organism under some conditions or other. On the neurophysiological level, different behavioral acts are the integration of a selective set of neurons with functions that are determined by organization of associations of each neuron.

On the level of a single neuron, its "life experience" consists of a set of functional synaptic fields that are used in any behavioral acts. These functional synaptic fields are hierarchically organized, and they are based on an hierarchy of metabolic processes within the neuron.

Thus, the behavioral act stored in memory is the possibility of coordination of activities, functions, functional synaptic fields and metabolism of many elements, which leads to survival under specific conditions.

Motivations are based on metabolic changes, which determine the appropriate organization of functional synaptic fields and, consequently, possible organizations of interneuronal relations.

The situation affects the hierarchy of life experience in the opposite direction: a certain organization of exogenous factors has a corresponding influence on coordination of neuronal metabolism through synaptic influences on specific functional synaptic fields.

All these correlations occur only through systemic processes: local changes in tissular metabolism, for example, in the hypothalamus, become motivation only through interneuronal and intertissular coordination of metabolism on the scale of the entire brain and organism; exogenous factors are considered as a situation only by comparing the effects to functional synaptic fields which, in turn, are determined by metabolism.

Since the situation and motivation change constantly, the interneuronal integrations, functional synaptic fields and metabolism of different neurons are in constant dynamic conformity with both motivation and situation. Goal-directed behavior develops when it is necessary and possible to alter this conformity in the direction of improvement.

In the continuum of behavior, pretriggering integration is formed while performing the preceding action and achieving interim results. At this time, impulsation is related to coordination of functions of the subsystems of the preceding action; at the same time, through integrator effects, it adjusts the functional synaptic fields to the properties of the future result of the entire behavioral act and thereby reduces the degrees of freedom of both individual neurons and the entire organism.

There is constant comparison of exogenous properties to the parameters of generated FSF; however, in the process of performing an action, the exogenous environment is compared to the parameters of FSF generated by subsystems on the physiological level. Performance of action leads to appearance in the environment of a result--event, which is then used to coordinate the functions in the entire brain and organism. For this reason, when a result appears in the environment, its parameters are compared to the prepared FSF in all analyzers, in accordance with the goal of a given behavioral act, which we considered to be the "preceding" one.

Comparison of the real multimodal parameters of the result to the parameters of the goal leads to appearance of a primary response that is synchronous in many structures of the brain. This response occurs only in the set of neurons whose FSF were prepared for the parameters of the result of action by the time it appeared. By virtue of hierarchic organization of FSF, only the fields included in the hierarchy of the entire motivated behavior can be prepared, and only in neurons whose function had ever been used to attain the future result.

Thus, at the moment of the primary response, pretriggering integration that contains the possibility of performing several acts becomes significantly reduced, and there is activation only of neurons whose FSF must meet one of two conditions: 1) ever been used to reach some goal under circumstances analogous to the state of the environment at the time of the primary response; 2) ever been used to attain the needed result under any circumstances.

The discharges of units with such properties through integrator effects lead to expansion of FSF in the direction of coordination with both the situation and the goal. This stage corresponds to afferent synthesis and decision making, and in the evoked potential it corresponds to negative oscillation.

At this time, discharges appear in the set of neurons whose FSF meet both conditions simultaneously, i.e., they had been used at some time to reach a given goal in expressly the given environment.

There can still be several integrations that could lead to a given goal in a given environment; of course, concurrent implementation thereof would disarrange the system and lead to diverse mistakes.

The final choice of one means of coordination of the activity of all elements on the scale of the entire brain and organism occurs next: when neuronal discharges corresponding to negative oscillation of evoked potentials alter FSF through integrator effects in such a way that discharges can appear only in neurons whose coordinated activity led in the past to the required result. This stage corresponds to complete reduction of degrees of freedom of both single neurons and the entire organism; this is the stage of the acceptor of results and program of action. From this time on, the different physiological subsystems that were coordinated in the preceding stages of formation of the functional system of the behavioral act begin to function in accordance with the hierarchy of results making up the acceptor of results of action in the behavioral act.

The real information about results in subsystems alters integration and prepares new pretriggering integration for appearance of the result of the entire behavioral act, etc.

CONCLUSION

All of the problems dealt with in our study of neurophysiological mechanisms of systemic processes require further development and definition. This applies to both the conceptual system and hypotheses, as well as conclusions.

Use of functional system theory in our approach to behavior opens up a wide range of problems that must be submitted to experimental and theoretical studies in both the physiological and psychological aspects.

We have barely touched upon the problem of hierarchy of behavioral acts in complex behavior and the problem of automation of the behavioral act, when it probably becomes a sybsystem on the physiological level. The very content of our discussion of systemic processes may change appreciably when adequate quantitative gages will be found to describe organization, integrity, composition, size and other systemic parameters.

The feasibility of comparing mental and physiological processes with the use of systemic ones raises the question of direct identification of neurophysiological bases of mental processes and states. For example, it may be that the "quantity of motivation" can be measured by the number of elements involved in integration and extent of expansion of their functional synaptic fields, and that the "quantity of perception" can be measured by the number of degrees of freedom removed by some perceived event from elements and the organism as a whole. These are all problems that can be solved directly through psychophysiological epxeriments from the positions of functional system theory.

The learning problem, i.e., formation of new functional systems under the system-forming influence of goals and results, requires systemic analysis, and it is becoming a part of general problems of systemogenesis.

Apparently, development of neurophysiology, psychology and other disciplines, the correlations between which are becoming possible by virtue of the sameness of the systemic approach in these fields, will very soon lead to significant clarification and even radical change in the initial theses of functional system theory, as is presently happening with Darwinism. However, the significance of functional system theory, which was expounded by P. K. Anokhin, is not that it is growing rigid, like a dogma, but that "a genuine idea is capable of attracting, like a magnet, only 'iron' facts from a pile of diverse facts."*

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*SOVETSKIY SOYUZ [Soviet Union], No 11, 1972, p 37.

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