The Neurophysiological Aspects of Human Mental Activity

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SECOND EDITION

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Preface to the First Edition

This book describes the fundamental stages in a study of the cerebral maintenance of mental processes and presents recent data, obtained from direct studies of human cerebral physiology, on the neurophysiological mechanisms of these processes.

Years of work on the diagnosis and treatment of patients by means of implanted electrodes are described. The approach has included observation of the dynamic pattern of cerebral physiological indices during the performance of mental activity and observation of the dynamics of spontaneous mental processes and of activity evoked by electrical stimulation of the brain.

These studies have made it possible to accumulate much new data on the physiological mechanisms of mental phenomena. An analysis of these data has led to the hypothesis that mental activity is maintained by a cortical-subcortical, structural-functional system with links of varying degrees of rigidity.

The book examines the theoretical prospects for an understanding of this problem and the possibility of expanding psychiatric and neurological treatment methods on the basis of new data on the human brain.

This monograph is intended for physiologists, neuropathologists, psychiatrists, and physicians in other specialties.

Preface to the Second Edition

The first steps in our study of the cerebral maintenance of mental activity were very difficult. Now, however, as the collection of data on the cerebral structural-functional organization of various types of activity by the implanted electrode method is becoming a normal diagnostic procedure, exceptional possibilities have opened up. Clinical physiological work has revealed the promise of therapeutic developments based on the hypothesis of a stable pathological state and the reactions that maintain it, the role of this general state in chronic diseases of the brain, and the therapeutic significance of overcoming it through a reorganization of the brain at a new level of functioning. The values of a complex surgical and drug treatment, multiple microlyses, therapeutic electrical stimulation of the brain, and the clinical application of an experimental biofeedback method have been demonstrated. A combination of biofeedback with therapeutic electrical stimulation, permitting the formation of new functional systems that facilitate an optimum use of the brain's reserves, is promising.

Our fundamental approach was to study the neurophysiological changes in the links of the brain system for maintaining mental processes, primarily those changes that underlie the "coding" and "decoding" of verbal stimuli in the brain. This study showed that changes in the impulse activity of neuronal aggregates occur in the brain depending on the acoustic characteristics of words, the frequency of their use, and the presence or absence of an appropriate basis for the engrams of long-term memory. These findings proved to have such significance that it seems appropriate to evaluate them at the start of a study of the neural code of mental processes—in the first place, in the study of the impulse code of words.

The significance of the new material and our need to trace the development of our work on the physiological mechanisms of mental activity led to this second edition.

N.P.B.

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Introduction 1

The assumption that there is a connection between the brain and the mind—between all that is now called mental activity and the central control of the functions of the organism—was made by thinkers who lived many hundreds of years before us (Hippocrates and others).

The impossibility of experimentally investigating the principles and concrete forms of the organization of cerebral activity in those far-off times sometimes gave rise to strange opinions. For about fifteen hundred years, the notion that the cerebrospinal fluid had a very important role in mental activity was supported by the authority of Galen. In the early stages of the natural sciences, a leading role in mental activity was assigned to various deep-seated formations (Descartes, Willis, Lancisi, and much later, Penfield) or conversely to the cortex. This latter point of view, for which there is practically no factual basis, appeared in a more or less schematic form in many early works and attained its apogee in the well-known, eighteenth-century phrenology of Gall.

These concepts were again advanced, but now on the basis of a large amount of clinical and anatomical data, toward the end of the first quarter of the nineteenth century. They were developed vigorously during the second half of the nineteenth century and gave rise to the theory of localization in the study of the structural-functional organization of the brain (Bouillaud, 1825; Broca, 1861; Wernicke, 1874; and many others).

The daily practice of neuropathology, psychiatry, and particularly neurosurgery continues to confirm the thesis that there is a connection between the brain and mental activity (Korsakov, 1890; Bechterew, 1900; Foerster and Gagel, 1933; Alpers, 1937; Grunthal, 1939; Buseh, 1940; Aleksandrovskaya et al., 1947; Gless and Griffith, 1952; Williams and Pennybacker, 1954; Orthner, 1957; Abramovich and Zakharova, 1961; Abashev-Konstantinovsky, 1961, 1964; Victor et al., 1961; Barbizet, 1963; Milner, 1962, 1967; Levita et al., 1967; and many others).

The tendency to connect the higher mental functions with specific regions of the cortex, which is so convenient in neurological and neurosurgical practice and which frequently enables one to determine so much about the patient's prognosis, survives in clinical practice in a more or less modified form even to the present day. However, the focal pathological processes—"natural models" simulating experiments involving partial ablation and stimulation of the brain—have contributed relatively little to our understanding of cerebral physiology or to an understanding of the organization of the brain systems responsible for the performance of complex mental tasks. And analysis of the neurophysiological mechanisms for the maintenance of mental functions in relation to clinical and anatomical observations has remained a purely verbal affair.

Nor has the massive nature of the changes in structure resulting from focal injuries to the brain provided a key to understanding how so many functions can be disrupted by an isolated pathological focus.

The most satisfactory approach to the evaluation of data generated by focal pathological processes has been and apparently to a considerable extent still is Hughlings Jackson's position that it is incorrect to make assumptions about the localization of functions on the basis of their disruption in injuries to any (one) region of the brain.

In clinical practice, without claiming to explain the general principles of the most complex cerebral activity, the localization model has been of great practical value. This has, as it were, compensated for its theoretical inadequacy.

As the trend toward using this model developed, however, it led to a logical absurdity when attempts were made to convert the brain and, above all, the cortex, into a patchwork state made up of diminutive sovereign principalities, each "solving" its own more or less complex problems, from the control of movement to religious feeling, from the control of speech to the social ego, and so on.

Although this sounds paradoxical, it was precisely the development of the localization theory which dealt it a serious blow.

Especially during the first half of the twentieth century, schematic charts of the localization of cerebral functions migrated from one textbook to another, although in neurological practice more and more evidence accumulated to contradict these concepts. The contradictions in clinical-anatomical and simple clinical data became so extensive that another extreme in the study of cerebral functions emerged: Lashley's unusual position on the equipotentiality of brain tissue (1958).

It may be noted that despite the well-known practical value of the localization theory (within certain limits) it is the equipotentiality theory that is coming to life in one form or another now. One of the most striking examples of this modernization of the equipotentiality theory is, perhaps, Pribram's view (1969) that complex mental activity is represented in the brain completely in each of its microvolumes, while its realization is connected with the involvement of the brain's macrovolume in the activity.

Counterbalancing the localization theory to a certain extent, statements appear frequently in the physiological and psychological literature in support of the theory, which seems so reasonable at first glance, that mental activity is carried out by the brain "as a whole." Actually, complex mental activity is a result of the activity, or potential for activity, of a very large number of brain areas. The view that the brain as a whole participates in mental activity is essentially a demobilizing scientific stance; at least it does not stimulate the search for the structural and functional organization of the maintenance of mental activity by the brain.

Penfield's extensive and valuable study (1958), though strictly focused, led to a revival of some of Meyer's concepts concerning the role of the cortex in more or less complex forms of memory and pointed toward the solution of the most complex problems of integration of the centrencephalic system.

Numerous papers have been devoted to the discussion and criticism of the localization and equipotentiality theories, holism, and the concept of the centrencephalic system. It can be stated with some justice that, particularly during the last few decades, almost as much effort has been expended on a critical analysis of completely or partially erroneous ideas about the physiology of the human brain as on the creation of working concepts, even if the latter may not always reflect the actual conditions in the brain with complete adequacy.

But to an equal and perhaps greater extent than in other areas of natural science, methods of studying the brain, facts about its function, and hypotheses constructed on these facts are also applicable to medical practice, physiological theory, and even philosophy. The cultivation of a "critical direction" led to the appearance in the biological and philosophical literature of statements in which, under a thin layer of verbal materialism, the outline of ideas about the isolation of mental functions from a material substrate were easily discernible. This is apparent in statements affirming the concrete presence of many mental processes and in the direct denial of the need to search for and the possibility of finding physiological correlates of mental phenomena. At bottom, these views are hardly very far removed from open dualism.

An objective analysis of many modern theoretical constructs again underscores the impossibility of true progress in this area without an adequate method for its study.

As is well known, the characteristics of higher nervous system activity in humans have been and are still being studied on an extraordinarily broad scale by psychological methods. It would seem that Sechenov's examination of mental mechanisms and Pavlov's analysis of the pathology of higher nervous activity in humans on the basis of data obtained in conditioned reflex experiments on animals must be regarded as the beginning of the physiological study of such activity in the strict sense of the term.

The genius of Pavlov's basic experiment cannot be denied. It firmly established the principle on which the exceptional potentials of the brain in humans and higher animals are based.

The great achievement of Pavlov and his school was to establish the probable pattern of structural-functional organization in the brain that is the basis of conditioned reflex activity and of the physiological mechanisms determining its various manifestations and to define the characteristics of these mechanisms as a function of the properties of the environment and the organism.

The experimental approach to the study of the physiology of the higher nervous system in human activity initially relied on the same methods that were used in animals (defense and salivation) and then was modified somewhat by means of a more "human" variant of the conditioned reflex method, i.e., a motor method with vocal reinforcement and later other "equivalents" of the conditioned reflex situation. By means of this variant, usually called the vocal-motor method or the motor method with vocal reinforcement (Ivanov-Smolensky, 1933), investigations were carried out in children and adults, patients and normal test subjects.

The universality assumed for the principles underlying higher nervous system activity was confirmed by a large number of observations, which served to define more accurately the typical variations in this activity produced by changes in the functional state of the human brain. Yet the application of conditioned reflex methods to humans has led to incomparably fewer scientific results than their application in animals. For the penetrating physiological study of healthy human beings, the methods proved too primitive, and when they were used in isolation the specific central mechanisms of the reaction could not be observed. In investigations of human mental activity, conditioned reflex and psychological methods had to be combined.

Recording the physiological indices of vital activity in the human brain became easier by the end of the 1920s when electroencephalography was introduced. The stages in the introduction of encephalography into clinical practice are well known. The EEG now occupies a secure place among diagnostic procedures and is widely used in neurosurgery, neurology, psychiatry, anesthesiology, and other clinical disciplines.

As long ago as the 1930s, attempts were made to observe the dynamics of the human EEG during conditioned reflex reactions (Durup and Fessard, 1935; Loomis, Harvey, and Hobart, 1935a,b; Knott, 1939). Investigations of this type in humans confirmed, deepened, and broadened many propositions of conditioned reflex theory. They made possible a very complete study of the relatively monotonous bioelectric pattern of the healthy human brain as well as the more varied pattern of the diseased brain.

It was shown that the bioelectric activity of the brain, as measured by the EEG, changes when conditioned reflexes are carried out. The changes may differ with positive and inhibiting reactions. The specific types of changes that develop depend primarily on the initial bioelectric background. Against the moderately synchronized background of the EEG of a healthy subject, positive conditioned reactions produce changes of the desynchronization type, whereas strengthened inhibiting reactions produce an increase in synchronization. Starting with a different background, although still under normal conditions, changes of every kind, even in the reverse direction, may be observed. In all cases the changes in the EEG initially develop very diffusely, which probably reflects both a "generalization of the stimulation" and the participation of many cerebral structures in the organization of the conditioned reflex reaction. The changes then become restricted, and this may be regarded as reflecting the concentration of nervous processes or the gradual development of the reaction on an optimal structural basis, or both.

With an initially stable desynchronization of the biopotentials, performance of the conditioned reactions caused practically no shifts in the EEG or at least no visible shifts. To a considerable degree, this may be related to the relative indirectness (via the meninges, cranial bone, aponeurosis, skin) of the recording method, which necessarily yields incomplete data. And when distinct changes in the EEG were observed, these same recording conditions would also limit the visualization of the components of the EEG and, hence, of their dynamics.

By comparison, observations made in experiments on animals by recording the electrocorticogram and subcorticogram with electrodes implanted directly in the brain provided considerably more information on cortical dynamics and made it possible to carry out an investigation not only of the EEG but also of the neuronal activity accompanying classical conditioned reflex activity.

The investigators were not satisfied, however, with the meager results obtained in humans; they proceeded to study the problem in three fundamental directions:

1. Patients with EEG changes caused by brain injury were studied. Here, the initial polymorphism of the EEG made it possible to observe "richer" dynamics for any activity, including conditioned reflex activity, than appeared in the normal brain.

2. Functional tests were diversified and made more complex. In place of the simple system of light, sound, proprioceptive, and other stimuli forming a "classical" conditioned reflex, various types of psychological tests were also used in the recording of the EEG.

3. With standardized "classical" conditioned reflex tests and with more complex psychological tests, the patient's EEG was specially processed to obtain the maximum amount of information. Analyzers, computer technology, and special methods of mathematical analysis of the EEG, including some developed for this purpose, were used.

By combining the conditioned reflex method and the EEG we obtained much interesting material. Of most interest were the findings on the role of various areas of the cerebral cortex in the performance of specific types of mental activity and on the interaction of large parts of the brain in mental activity in general.

A well-known advance in the neurophysiological study of mental activity was the discovery of the phenomenon of expectancy, represented by the E wave, a contingent negative variation (CNV) that occurs in the frontal regions of the human brain when the appearance of one stimulus determines or makes probable the appearance of a second stimulus (Walter, 1965; Walter et al., 1964). There were significant differences in the phenomenon, depending on the mental and emotional state of the subject and the degree of training of the test subject, reflecting, in the words of Gray Walter, "the subjective probability of an event." The reliability of E-wave appearance under specific conditions made it practically an ideal means of studying the development of readiness for action, the activity of a subject in a given situation, and the interaction between a human being and the environment. Clear evidence of subcortical involvement in this phenomenon, which was originally regarded as purely cortical, has now been obtained (Chernysheva, cited by Bechtereva and Chernysheva, 1969; Ilyukhina and Khon, 1973), and the cortical-subcortical mechanisms of its realization have been investigated.

Interesting as these observations proved to be, they have not made possible a broader and more profound study of the neurophysiological mechanisms of human mental activity. A study of the neurophysiological basis of human mental activity required the direct, multidisciplinary investigation of neurodynamics in different regions of the human brain.

Possibilities for a more profound study of the neurodynamics opened up with the development of surgery of the subcortical formations, particularly after the implanted electrode method was introduced into clinical practice (Fig. 1).

In the effort to obtain therapeutic results free of complications, one of the most important tasks was to avoid disconnection in the brain system maintaining mental functions.

Under conditions of direct electrode contact with the brain, the dynamics of the mental reactions produced by electrical effects were observed, and a detailed multidisciplinary investiga-

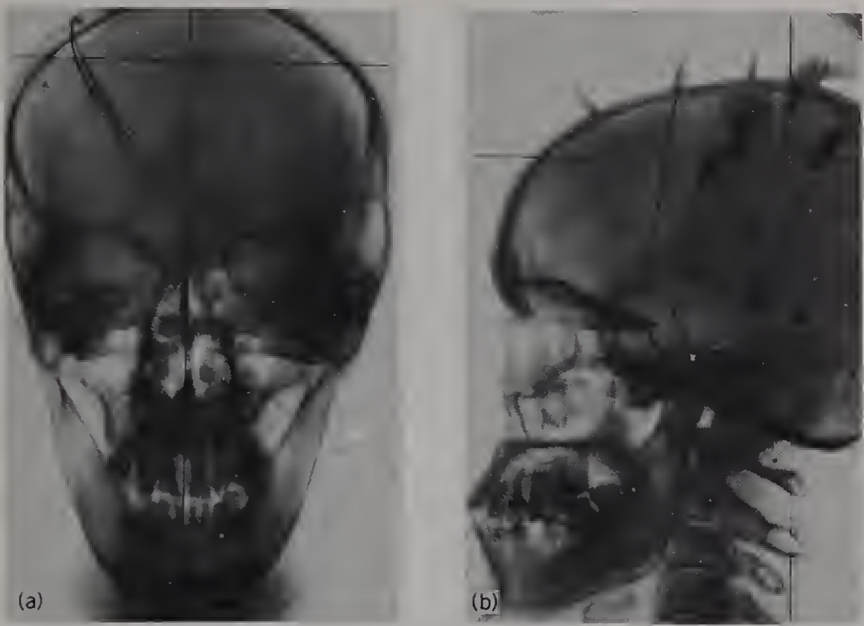


Figure 1. X-rays of the heads of patients with implanted electrodes. (a) Electrode clusters implanted through a single opening made by trephination; (b) electrode clusters introduced through separate openings.

tion was made of the activity of the brain during psychological tests (Bechtereva, 1965, 1971, 1974; Bechtereva, Bondarchuk, Smirnov, and Trokhachev, 1967) was carried out. This approach combined almost all of the advantages of animal experimentation with the unique possibilities of investigating mental activity in humans.

Many years of study involving the diagnosis and treatment of patients with implanted electrodes have established a complex approach to investigating the structural-functional organization and neurophysiological mechanisms of human mental activity. This approach includes, on the one hand, a study of the effects of local electrical influences on a given emotional-mental activity in progress and, on the other hand, an analysis of the local dynamics of many physiological indices of the brain state (electrosubcorticogram–slow electrical processes; available oxygen; impulse activity) in emotion-producing and psychological tests (Fig. 2). This approach has made it possi-

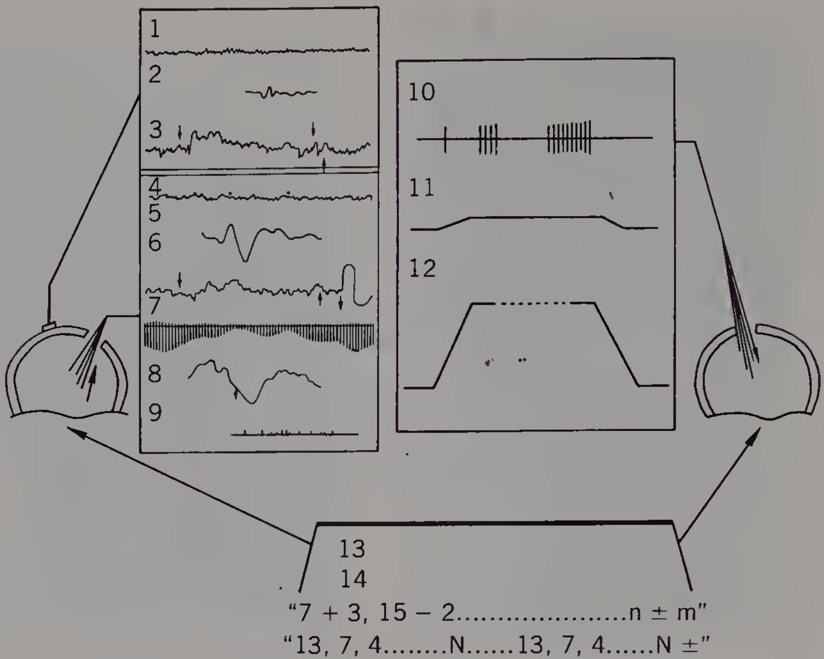


Figure 2. Diagram illustrating the complex method for the investigation of the structural-functional organization of the brain. 1, EEG; 2, elicited responses; 3, CNV; 4, subcorticograms; 5, elicited responses; 6, CNV; 7, slow electrical processes (SEP); 8, available oxygen; 9, cell activity; 10, electrostimulation; 11, electropolarization; 12, electrolysis; 13, functional tests; 13, psychological tests.

ble, by changing the conditions of observation and introducing and eliminating various factors in the external and internal environment, to study how, as a result of what shifts, and in which brain structures, any psychological problem that can be processed by the brain is solved. It might be mentioned in passing that the development of this complex method of studying the brain has proven extremely valuable in the study of the brain mechanisms of motor activity and in the solution of a number of practical diagnostic and therapeutic problems (Bechtereva, Bondarchuk, Smirnov, and Trokhachev, 1967; Bechtereva and Bondarchuk, 1968; Bechtereva, Bondarchuk, and Smirnov, 1969).

The information obtained up to the present time through examination of about 2000 zones of the brain, including deep structures within the different thalamic nuclei, the striopallidal system, the higher brain stem, and the mediobasal part of the temporal lobe made it possible to formulate and confirm a hypothesis concerning the principles of the maintenance of mental activity by the brain (Bechtereva, 1966).

General changes in the brain, in the background, that develop during the realization of mental activity and that possibly determine the optimum conditions for its performance have been investigated. The zones, the "points" in the brain that are most closely related to mental functions and that are apparently elements of the brain system maintaining the mental functions have been identified and are being studied. The relative importance and the role of these different elements—the neuronal (or, more accurately, the neuronal and the neuroglial) populations in the maintenance system are the subject of a continuing investigation.

It is a well-known fact that, in special investigations with psychological tests, subjects vary significantly in their performance. The nature of this variation is being analyzed. In the study of the neurophysiological aspects of mental activity, at this time, it remains expedient to select certain psychological tests from among the most standardized and best-studied tests and to analyze the dynamics of the physiological indices. The investigation of different physiological indices of the vital activity of the brain as psychological tests are performed has proven to be a significantly more subtle method than the observation of changes in mental activity with focal pathological processes, surgical local destruction, and electrical stimulation of the brain.

Specifically psychological tests, on the other hand, have proven to be more useful in the study of human mental activity, including its neurophysiological aspects, than classical conditioned reflex tests.

This complex approach has permitted a more thorough study of the structural-functional basis of mental activity than was previously possible and has demonstrated that those formations, which might as a result of specific disconnections and stimulations be incorrectly considered "silent" zones, also participate in mental activity.

Results obtained by stimulating the brain via implanted electrodes and by recording other parameters of the vital activity of the brain have often but not always been fully comparable. The data obtained by recording different parameters characterized different aspects of the phenomenon; they corresponded selectively or preferentially only to some of the problems formulated, and they might perhaps more adequately be regarded, although also within certain limits, as complementary characteristics (in the sense of complementarity as used in quantum mechanics). The limits in the use of this term are determined primarily by the fact that, in contrast to "truly" complementary phenomena, certain parameters of the vital activity of the brain can be recorded simultaneously, although it is naturally a very complicated matter to ascertain the level of "losses" in such recordings. The different physiological parameters have proven selectively useful with respect to different aspects of the phenomena investigated.

It is hardly justifiable to state at this time that the mental characteristics can be exactly superimposed upon the physiological. We still know relatively little about what takes place in the brain, particularly in the completely healthy human brain during mental activity, which is the most complex of all possible forms of activity in the living organism. Long and tedious work faces investigators in this area—which work, however, can be made a little easier by summing up the results obtained so far.

This book is organized to conform to the fundamental directions of our study. It describes changes in the EEG during conditioned reflex reactions, but presents practically no new observations concerning the mechanisms and levels of the closing of conditioned reflex reactions in humans. It is not the purpose of this book to analyze all factors in the electroencephalographic expression of conditioned reflex reactions—this has been the subject of reviews by Rusinov and Rabinovich (1958), by Mnukhina (1964), and by many others. A similar analysis was also undertaken by us in 1959. The work described in this book will help achieve a more precise definition of the general changes in brain state under the conditions studied, i.e., changes that reflect the process of optimization of the brain state for activity. It can be affirmed, however, that not one laboratory in the world possesses sufficient valid data for an assessment of the levels and mechanisms of closure of conditioned reflex reactions in humans. An analysis of these mechanisms was not one of the book's objectives, although they are being studied in an extremely fruitful manner (Anokhin, Livanov, Rusinov, Belenkov, Khananashvili, Vasilevsky, and many others in the Soviet Union and various countries around the world).

On the other hand, the available information on the structural-functional mechanisms of human mental phenomena is discussed in this book. For obvious reasons, no experimental laboratory studying animals has obtained data of this type.

It is not the purpose of this book to argue that there are significant differences between conditioned reflex and mental phenomena in humans. Without denying the importance of studying the mechanisms of classical conditioned reflexes in humans, however, we must recognize that the specifically mental element is the most important problem in the study of the human brain, and a problem that can be solved only by studying humans.

The technical revolution of this century, a product of human thought, in turn has made altogether special demands on the human brain, requiring the organism to maintain its activity within a very changed environment. The need for rapid adaptation of the brain systems of functional control to new time zones, to sharply different climatic conditions, to new linguistic and sometimes new social environments, have become a part of daily life for an ever-increasing number of people. The requirements for speed and accuracy of reaction have changed greatly in many areas of the national economy; modern, man-machine systems as a whole have also led, in many cases, to greater complexity in the necessary operations.

There have been many psychological and physiological studies of this problem of human reactions and their optimization in a world of increasingly more complex technology (Lomov, 1966; Zarakovsky, Medvedev, and Zinchenko, 1970). Not only the requirements of medical practice and the theoretical interest of the problem, but also the huge reserves of the brain revealed by this technological leap have prompted the study of the physiological principles and specific mechanisms that maintain these reserves.

Each stage in the study of the cerebral maintenance of mental activity is undoubtedly important in itself as a phase in the development of the natural sciences. Even a very small step forward in the science of the human brain can be extremely valuable in clinical practice when it concerns data that could improve treatment of nervous and mental diseases and broaden the spectrum of curable diseases.

Furthermore, progress in the investigation of brain physiology is important in the development of philosophy and sociology. Modern sociologists are anxious to know how the human brain will cope with the abundance of information and other demands made upon it in our time. The scientific-technical revolution, forged by the thought of geniuses and men of talent and secured by the work of millions, in its turn has made huge demands on the brain. Whether he wishes to or not, man receives a huge volume of information through his eyes and ears, and his brain—whether he wishes it to or not—reacts to this flow of information. Is there a real threat that the human brain may be unable to cope with such complexity?

Principles by which the brain has developed through interaction with the external environment and adaptation to it have been hypothesized. Physiologists studying the human brain must now attempt to answer the following questions: How is it possible to have not only a colossal improvement, the revelation of the brain's potentialities, but also an abrupt transition to new stages of interaction with the environment in a situation that is becoming ever more complex? And how has the human brain been able, in less than two generations, to adapt to what is in so many ways a new world? What will happen if the load on the human brain continues to increase at such a rapidly accelerating rate? Is there a mechanism of self-preservation and self-protection in the brain?

Many of these important questions must be answered by brain physiologists. Most of the questions require further investigation and reflection, but some of them can apparently be answered at the present time.

It is known that there is a brain mechanism which provides excess resources for dealing with each novelty. Those who have succeeded in "spying out" what takes place in the brain at the moment when a new situation is presented, when there is an unexpected transition to an earlier situation, or when there is at least some element of "surprise," can say that the brain in these cases does bring into play previously established states of readiness. A vast number of neural elements are activated, and many connections are "closed" between different areas and systems of the brain. It is not impossible that this same mechanism may, in part, maintain the resources of the brain, the resources of the species.

The mechanism for reacting is probably something like a natural conditioning of the brain which, by constantly providing excess readiness for novelty, has maintained the enormous potentialities of the brain over many centuries.

The greater the amount of novelty, the more times the brain will be "surprised" for short intervals of time, the more information will be received through the senses, the more rapid will be the development of a child's brain, the more fully the potential of the human brain will be manifested, and the greater will be the opportunities open to mankind. It is clear that the present-day scientific-technical revolution is the result of an interaction between the human brain and the external environment, which is being changed by this brain. Scientific-technical progress thus represents, on the one hand, the personal decisions taken by mankind and, on the other, a mass increase in mankind's potentials and a mass generation, clash, and mutual enrichment of ideas.

But the scientific-technical revolution also marks a great increase in the opportunities for studying the brain itself, for solving the problem of the nature of our brain. And here, again, we come across the social aspect of the problem.

Social needs arouse and activate interest in the brain. Progress in the study of the physiological basis of mental activity in turn acquires social significance because it provides clues to the control of the brain's potentialities. It is not within our power nor in our interest to slow down scientific-technical progress as a whole, and progress in the study of the human brain in particular, but it is within our power to give this progress the desired direction.

Current knowledge of the physiology of the human brain allows us to hope that, in the very near future, we shall acquire real power over the brain. This power must be used only in the interest of man!

Modern technical progress has made it possible to use the most subtle physiological methods in the diagnosis and treatment of brain diseases and has thereby provided unique possibilities for the investigation and modification of the mechanisms of the human brain. The use of mathematical methods to analyze the adaptive apparatus, and of analog and numerical computer technology to investigate physiological phenomena, together with solutions of a number of practical problems, has enabled us to design studies of the physiological code of human neural phenomena.

An early approach to a complete solution to this very complex problem is possible only if the many scientific groups studying the mechanisms of human mental activity pool their efforts. Thus, the object of this book is not only to summarize the results obtained so far, but to stimulate further investigations of the neurophysiological aspects of human mental activity.

2

The Functional State of the Human Brain during the Performance of Conditioned Reflex Reactions and Psychological Tests

The Electroencephalogram during Conditioned Reflex Reactions

The investigation of the physiological characteristics of the brain during conditioned reflex activity by means of electroencephalography has an almost thirty-year history of experiments on animals and, although this may seem paradoxical, a history of over thirty years of observations in humans.

The study of the EEG during conditioned reflex reactions in animals and in humans was carried on during these decades with a clearly defined purpose: it was assumed that it would be possible to find a reflection of the properties and dynamics of the basic neural processes in the EEG. Most reviews of this subject refer to one of the early papers by Livanov and Polyakov (1945), in which two rhythmic stimuli were used (light and electrical) and the phases of formation of a conditioned reflex in a rabbit were investigated. Analogous phase changes in the EEG were later observed in an experiment by Morrell and Jasper (1956) and co-workers. In the later work of Livanov and his co-workers, and also in a vast number of other investigations in Russia and elsewhere, the characteristics of the EEG changes in animals were shown to depend upon the nature of the stimuli and the type of conditioned reaction, the region of the biopotential leads, and the type of animal (Livanov and Ryabinovskaya, 1947; Kogan, 1949, 1967; Livanov and Korol'kova, 1949; Maikowski, 1955; Knipst, 1955; Angyan and Hosznos, 1951, Sakhiulina, 1955–57; Trofimov, Lur'e, Lyubimov, and Rabinovich, 1955; Roitbak, 1956; Jouvet and Hernandez-Peon, 1957; Rusinov, 1953, 1955, 1957; Anokhin, 1957, 1968; Yoshii, Pruvot, and Gastaut, 1957; Morrell and Jasper, 1956; Khananashvili, 1972).

In the investigations that were carried out it was possible to study many specific neurophysiological mechanisms of conditioned reflex activity, as well as a number of general biological characteristics of brain function (Anokhin, 1968). The data obtained from different animals on the bioelectric component of the reactions investigated were, however, difficult to compare with each other, not only in terms of the specific forms of the biopotentials but also with respect to the direction and degree of dissemination of changes in the observed patterns.

For this reason it was difficult to use the results of experiments of this type to interpret analogous mechanisms in the human brain. Additional difficulties in extrapolating from brain studies in experimental animals to those in humans arose from the conditioned reflex method itself. The mechanical transfer of methods used in animal experimentation to human investigation frequently did not produce the expected results in research on humans and, as a rule, led to findings of less general significance. A very important factor–the substantially greater complexity of brain mechanisms in humans–together with the non-comparability of some physiological indices of the animal and human brain made it necessary to conduct practically the whole range of investigations on human subjects.

In humans the study of EEG dynamics in conditioned reflex activity or in reactions similar to conditioned reflexes was begun as long ago as the 1930s (Durup and Fessard, 1935; Loomis, Harvey, and Hobart, 1935, 1936; Knott, 1939; and others). As in the animal experiments, the fundamental task in these and later investigations, which were sometimes almost primitive, was to study by means of electroencephalography the dynamics of the neural processes of the brain under model conditions of reproduction of the simplest mental scheme.

In the initial investigations, and in the overwhelming majority of the later studies, a light stimulus, proprioceptive stimulus, or both, was used as a reinforcement (when the light was turned on, the test subject was to carry out what was usually a simple motor reaction). The conditioned stimulus most frequently used as a sound, for which the orienting reaction had usually been extinguished beforehand (Loomis, Harvey, and Hobart, 1935; Knott, 1939; and others). The relative complexity of the problem varied according to the particular objectives of the study (which were as a rule very simple). Some experimental parameter was introduced or eliminated, and positive or inhibiting reactions were developed through coincidence or varying degrees of non-coincidence of the stimuli.

The results of even the initial investigations emphasized the importance of the given problem's complexity with respect to the nature and dynamics of the EEG patterns. This will be considered later in light of the effect of the exploratory components of the task on the stability of the conditioned reflex reaction itself and of the EEG changes related to it (Voronin and Sokolov, 1955; Anokhin, 1957; and others).

When special procedures were used, in which the approximate-exploratory component could not be extinguished, the alpha-rhythm depression in the EEG was very consistent. On the other hand, when the experimental conditions were simplified and standardized, it was possible to observe a gradual decrease in the intensity of the alpha-rhythm depression in response to repeated, coincidental stimuli.

When identical combinations of sound and light were repeated in the study by Knott and Henry (1941), the depression of the alpha-rhythm became increasingly less distinct with respect to both sound and light; this was attributed by the authors to central inhibition and adaptation. Later this finding was confirmed by many others and was also the subject of special study in individual investigations (Sokolov, 1956). The clearest explanation of this phenomenon was given by Anokhin (1962, etc.), who demonstrated the importance of what seemed to be biologically insignificant "reinforcement," i.e., the formation of a reflex reaction in these cases did not depend on a true unconditioned reflex. Jasper and Shagass (1941) studied the conditioned reflex reaction elicited by coincident and non-coincident presentations of the stimuli, using a combination of sound and light, to which the test subject was to respond by depressing a key. When the stimuli coincided, the conditioned reflex was easily elicited and was also easily extinguished after three to five non-reinforcements. Investigation of the dynamics of the EEG in the case of coincident, delayed, and trace-conditioned reflexes showed that alpha-rhythm depression precedes the reinforcement. In complete agreement with the results of the Pavlovian experiment, both of these experimental conditions—removal and delay—could produce a state of drowsiness in the subject. After the development of a differentiating reaction, the differentiating stimulus gradually ceased to affect the EEG.

A study of the dynamics of the bioelectric reaction over time in different regions of the cortex, in which the methods of Jasper and Shagass were used, was undertaken by a number of investigators, in particular, Mushkina (1956). Although the changes in the acoustic and visual regions of the brain were of the same nature when the conditioned reflexes were present, the changes observed when the light was removed were phasic in character. In the first stage of the development of the extinguished conditioned reflexes, the alpha-rhythm depression started simultaneously in the acoustic and visual regions; this was considered to be an EEG manifestation of the generalization phase of the neural processes. In the second stage, the depression of the alpha-rhythm in the acoustic region began while the sound continued, whereas in the visual region it began before the moment of visual reinforcement (the phase of gradual concentration). Finally, with the combined stimuli the alpha-rhythm depression in both cortical regions began to develop before the moment of light reinforcement.

The dynamics of the EEG during the development of differentiation was also explored in detail. The alpha-rhythm depression was first recorded in the visual and acoustic regions simultaneously. In a second phase of the reaction, the alpha-rhythm depression was extinguished in the visual region. A third phase of the reaction then ensued: complete extinction of the alpha-rhythm depression when any given combination of stimuli was applied in the regions where the "unconditioned" stimulus and the conditioned signal occurred. These dynamic changes were thought to reflect development of inhibition, initially in the region of the "unconditioned" stimulus, and its subsequent propagation to the region of the conditioned signal.

The reflection in the EEG of the delay process in a conditioned reflex motor action was studied by Maiorchik, Rusinov, and Kuznetsova (1954). In their study, when the extinction of the alpha-rhythm depression was changed, diffuse slow waves, which were gradually concentrated in the parietal region, appeared in the EEG. From an analysis of the data [EEG, electromyograms (EMG), etc.] and changes in the test conditions one could infer that the slow waves reflected an inhibition process. Similar EEG changes were observed by A. and K. Jus (1954) when the light "reinforcement" was removed. These investigators, like Jasper and Shagass, noted that during the development of such conditioned reactions, the test subjects became drowsy.

The absence of slow waves in the EEG in "inhibited" test situations in most investigations carried out on human subjects, was interpreted in the 1950s not as the absence of a relationship between a specific EEG pattern and a neural process, but as the reflection of a concentration of the inhibition process to a small area not shown in the EEG. This assumption seemed plausible in light of the history of clinical electroencephalography, and it was still tempting to assume that a relationship did in fact exist between the slow waves and inhibition, even if it were an indirect relationship.

When EEGs recorded during conditioned reflex reactions in humans are analyzed, it now seems probable that the appearance of slow activity in these conditions is primarily related to the development of a drowsy state. In healthy persons under reliable experimental conditions, slow waves in the "inhibited" test situation virtually do not appear unless the inhibition is of the type where the subject falls asleep.

The conditioned reflex change in the alpha-rhythm was followed in similar experiments (Shagass, 1952; Beritov and Vorob'ev, 1943; and many others).

There have been numerous other variations in the methods used to study the EEG changes during conditioned reflex activity (Gershuni and Korotkin, 1947; Gershuni, Kozhevnikov, Maruseva, and Cristovitch, 1948; Maiorchik and Spirin, 1951; Lur'e and Rusinov, 1955; Kratin, 1955; Makarov, 1956, 1957; Novikova and Sokolov, 1957; Lansing, 1957; and many others). A. G. Smolensky's method of recording EEGs during conditioned reflex activity was developed on the basis of the motor method with vocal reinforcement and has been widely used.

By the mid-1950s, a very large quantity of data on EEG dynamics during conditioned reflex activity had accumulated throughout the world. It was assumed that stimulation is reflected in the EEG by desynchronization—this seemed very probable. It was also assumed that inhibition might (or, more precisely, should) be reflected by slow waves or by synchronization. At the same time, the similar but not entirely equivalent experimental conditions of some of these studies made it difficult to compare the results. From this viewpoint and in keeping with the persistent belief of researchers in the possibility of detecting EEG correlates of neural processes, Gastaut, after making personal investigations in this area (1955–1956), organized a broad study of EEGs during conditioned reflex activity by a large group of investigators in a number of European countries (Gastaut, Jus, Morrell, Storm van Leeuwen, Bekkering, Kamp, and Werre, 1957; Gastaut et al., 1957).

From the very beginning of this study an element of selectivity was introduced in the choice of test subjects, so that the results cannot be universally applied. Rather than making a random selection of test subjects with different EEGs, subjects with well-developed alpha-rhythms and rolandic rhythms were chosen for study. On the other hand, only the most frequently repeated manifestations were isolated and described—anything that was not observed repeatedly was rejected as unessential.

The investigation was carried out as follows. The EEG, electromyogram (EMG), electrocardiogram (EKG), pneumogram, and "electrodermogram," were obtained. The EEG was evaluated visually and by means of a frequency amplitude analyzer. A sound stimulus was combined with a light stimulus (1) or with a passive (2) or an active movement of the hand. Depending on the experimental conditions, depression of the occipital or rolandic rhythms was evoked. And finally, (3) the sound stimulus was combined with a composite reinforcement–the sound was reinforced by light, in response to which an active or a passive movement of the hand took place. This variation of the experiment could lead to a depression, in response to the sound, of both the rolandic rhythms and alpha-rhythms (with the latter being depressed bilaterally) or of the rolandic rhythm only.

From their observations, Gastaut and his colleagues postulated that the region of primary suppression of the synchronized alpha-rhythm or the rolandic rhythm depends mainly on the nature of the reinforcement. With conditioned motor reflexes, they were able to observe a phase in which blocking of the rolandic rhythm appeared only in the motor region of the opposite hemisphere. Gastaut's findings, with respect to a correlation of the excitation and blocking of the alpha-rhythms and rolandic rhythms in the EEG, proved to be the same in principle as those of previous investigations.

When the test subjects were presented with a sound stimulus (inhibiting) with or without a light stimulus, for which they were instructed to make a fist, an initial reinforcement of the rolandic rhythm was noted, followed only later by its depression. The movement took place only against the background of the depression. The reinforcement of the rolandic rhythm was evaluated as a reflection of the inhibition as seen in the EEG. On the other hand, the spontaneous disappearance of the blocking during positive reactions was considered a manifestation of the development of above-threshold inhibition processes. When the combinations of stimuli were repeated, there was an increase in the amplitude and retardation of the cortical rhythms, up to the development of an EEG characteristic of light sleep (appearance of theta and delta rhythms). In this case also, a synchronization and retardation of the rhythms was observed under conditions in which inhibition might have been assumed to develop (see Table 1).

Table 1. Diagram of the fundamental spatial dynamics of synchronization and desynchronization phenomena during conditioned-reflex reactions in humans (according to Gastaut, et al.).

Reaction number	Stimuli		Nature of reaction	Region of manifestation of reaction
	Conditioned	Unconditioned		
1 2 3	Sound +	Light	Blocking of alpha-rhythm	Parietal-temporal-occipital regions of both hemispheres
1 2 3	Sound +	Hand movement	Blocking of rolandic rhythm	Central region of the hemisphere contralateral to the hand carrying out the movement
1 2 3 . . .	Sound +	Light, hand movement	Blocking of alpha-rhythm and rolandic rhythm	Parietal-temporal-occipital regions of both hemispheres and central region of the hemisphere contralateral to the hand carrying out the motor reaction
$N < M$*	Sound +	Light, hand movement	Blocking of rolandic rhythm	Central region of the hemisphere contralateral to the hand carrying out the motor reaction
$N < M + 1$ $N < M + K + 1$**	Sound +	Light, hand movement, and the word "good"	Blocking of rolandic rhythm	Central regions of both hemispheres
	Sound −	Light	Increased manifestation of [illegible]	Parietal-temporal-occipital regions of both hemispheres

		rolandic rhythm	contralateral to the hand carrying out the motor reaction
Sound —	Light, hand movement	Depending on the nature of the preceding positive reaction:	
		1. Increased manifestation of rolandic rhythm and increased manifestation of alpha-rhythm	Central region of the hemisphere contralateral to the hand carrying out the motor reaction
		or	
		2. Increased manifestation of rolandic rhythm	Parietal-temporal-occipital regions of both hemispheres, central region of the hemisphere contralateral to the hand carrying out the motor reaction

* *N*, any repeated combination of stimuli (generally less than 20, but with significant individual variations; *M*, combination of stimuli when the EEG expression of the positive conditioned reactions becomes indistinct.

** *K*, combination in which a "disinhibition" of the EEG reaction takes place in connection with some external or internal factor.

Gastaut and his colleagues assumed that they had confirmed the relationship in humans between inhibition in a conditioned reflex situation and synchronization and the development of slow waves in the EEG.

It should be noted that the interpretation of the EEG phenomena observed with the initial development of above-threshold inhibition followed by sleep has been influenced, in the studies of Gastaut and his co-workers and others, by a desire to perceive a similarity to Pavlovian data.

Gastaut and his co-workers, like the overwhelming majority of investigators before them, worked easily with known and unknown quantities: what developed in the EEG was considered a reflection of what should have developed according to the classical laws of Pavlovian physiology. On the basis of their own assumptions, they went on to assign to specific bioelectric phenomena a well-defined relationship with fundamental neural processes, and then the manifestation of any of these bioelectric characteristics was considered to be evidence of the development of the corresponding neural process.

Gastaut identified four fundamental types of phenomena: two related to stimulation—independent of and dependent on conditioned reflex activity—and two related to inhibition.

The development of widespread blocking of the alpha-rhythm during excitation was explained on the basis of an activation at the mesencephalic level of the reticular formation, and the development of local blocking (also related to excitation) was attributed to an activation of thalamic formations. Depression of the mesencephalic system when the stimuli were repeated was a distinctive part of the manifestation of this second EEG reaction. Gastaut, in this case, postulated an antagonism at these two levels of median structures that fitted his scheme, although it did not correspond very closely to reality (Bremer, 1962). Apparently, the lack at that time of sufficiently reliable data on synchronizing brain formations (Morruzzi, 1962) determined to a considerable extent Gastaut's view that inhibition in the mesencephalic and thalamocortical systems was the mechanism for the extinction of the alpha-rhythm blocking reaction and the increased synchronization in the EEG.

In reporting the results of his complex investigation, Gastaut also discussed the problem of identifying the brain levels when closing of the conditioned connection in humans occurs. He presented a number of schemes in which the center for both the bioelectric and the conditioned reflex events was confidently assigned to the thalamic level. Without essentially arguing against this assumption, it should nevertheless be pointed out that he incorrectly associated the nodal points, the "rhythm conductors," observed in the EEG with the regions of higher integration. And he did this at a time when the importance of the activating effects of the nonspecific mesencephalic system, subject to a very wide range of external influences, had already been studied sufficiently. Gastaut (1957, 1958) insisted that the role of the cerebral cortex in his interpretation of the physiological data was in no way "depreciated" since the thalamic closing of the reflex arc is always accompanied by activation of the corresponding thalamocortical link (Gastaut and Roger, 1962). It should be emphasized that these opinions of Gastaut are surprisingly similar in essence to Penfield's view of the centrencephalic system. The closing of the conditioned connection takes place in the median regions of the brain, and the cortex participates in the reaction–from this it would be plausible to assume that the cortex in this case fixes the experience of what is taking place or represents a past experience (memory) in the arrangement of the reaction being formed.

Returning to the evaluation of the neurophysiological aspects of the shifts studied in the brain, it is evident that Gastaut, without having added anything significantly new to what was known previously, defined more accurately and, by virtue of his detailed treatment of a large amount of comparable source material, verified that persons with an initially good alpha-rhythm show a widespread or somewhat more limited desynchronization or synchronization (which also included a retardation of the rhythm) under conditions in which, according to the classical laws of Pavlovian physiology, there are reasons to expect the emergence of widespread or limited excitation or inhibition.

In analyzing these studies, we must admit that if there were at least some evidence to correlate a state of excitement with desynchronization in the EEG, the situation is more complex in the case of inhibition. In the first place, it is complicated by its electroencephalographic expression: this had already been shown to be very "nonspecific." As mentioned, the first criterion for selecting the test subjects was a good alpha-rhythm at rest; this rhythm was identical or very similar to the EEG pattern during inhibition.

Second—and this is much more important—the relation between excitation and desynchronization and between inhibition and synchronization could be confirmed only for a particular group of persons with a resting alpha-rhythm. Under the same conditions, a large group of healthy persons without a distinct resting alpha-rhythm not only did not display any manifestations of excitation in the form of desynchronization in the EEG, but also failed to show any signs of inhibition in the form of synchronization. Thus, even if we accept the significance of the correlations detected between neural processes and EEG manifestations, the data at best only satisfy the principle of conditional probability (the operative conditions being an initially good alpha-rhythm and rolandic rhythm). The neurophysiological expression of fundamental neural processes and the precise neurophysiological mechanisms of human mental activity required further investigation, more data, and most importantly, new approaches.

The thoughts of these investigators were quite justifiably directed primarily along the lines of three basic approaches, which were often very closely interrelated. These approaches were determined by the hope of: (1) discovering more multifaceted, less monotonous EEG dynamics; (2) obtaining data about changes in the EEG under conditions of specifically human mental activity, and, finally (3) revealing in the EEG, by using mathematical techniques and sophisticated apparatus, dynamics that escape the investigator's naked eye.

Observation of the polymorphic dynamics of the EEG in humans was made possible by varying the physiological state of the test subjects and by studying patients. Additional information from the EEG was obtained by the application not only of standard instrumental methods, but also of certain special methods, including some developed for this purpose. The investigation of the EEG under conditions of specifically human mental activity suggested conducting the electroencephalographic measurement during the performance of different psychological tests (which naturally in no way excluded other ways of processing the data).

The dynamics of the polymorphic EEG during conditioned reflex activity were studied in healthy persons while they were falling asleep and in patients with brain injuries. The studies carried out during the period of falling asleep and development of sleep during the various phases of sleep showed, on the whole, spatial dynamics in the EEG similar to those observed in healthy persons in an awake state. The similarity increased when the test subjects were wakened by the first stimuli. But if the awakening were incomplete, the reaction might be the direct opposite of that noted in the awake state—a revival of the alpha-rhythm was observed in response to positive stimuli (Roger, Sokolov, and Voronin, 1957). The same studies showed the ease of extinguishing the reinforcing reaction and of intensifying the slow waves simultaneously with an increase in the depth of sleep. These and other studies involving EEG recordings in conditioned reflex activity, which can be combined with pharmacological tests (Livanov, Gavrilova, and Aslanov, 1966), provided convincing evidence of the importance of the initial EEG background in determining the specific form of the developing reaction and also demonstrated that the view that there is a well-defined relation between neural processes and specific electroencephalographic reactions is erroneous.

An investigation of the dynamics of the polymorphic EEG in patients with brain injuries during conditioned reflex activity revealed that the dynamics of the biopotentials, which are generally either widespread or limited according to the nature of the stimuli and the phase of development of the conditioned connection, may prove to be clearly "subordinate" to the cortical pathological focus.

These observations in humans not only confirmed once again the nonspecificity of the relationship between neural processes and the EEG, but also showed in a very graphic form the interaction of diffuse distant effects with the functional state of discrete cortical areas. In the EEGs of patients it was also possible to observe general rearrangements of the alpha-rhythm, if this rhythm was maintained. The dynamics of the slow waves in the region of the cortical focus were found to be much more distinct and did not depend directly on the site of the pathological focus in the brain or on the type of stimulus. Various other rearrangements of pathological forms of activity, which were related to the cortical focus, were also detected.

In addition, the increase or decrease in the intensity of the slow waves in the focal region could be seen immediately upon presentation of the reinforcing stimulus, etc., and might last only a short time or persist in the EEG even after the conditioned reaction was performed. These observations on the significance of the pathological focus in the dynamics of the bioelectric reaction could be explained by the theories of Ukhtomsky (1945) on dominance, which were elaborated by Rusinov (1953, 1955) and others. As far as the actual nature of the changes in the focal region is concerned, the development of slow waves at first seemed a convincing illustration of the Pavlovian concepts of above-threshold inhibition. Indeed, the changes could be explained in precisely this way, particularly if the appearance or spread of slow waves were regarded as evidence of the development of inhibition. Nevertheless, evidence to support such an explanation was not always present in manifestations of conditioned reflex activity. The slow waves in the focal region, including those located in the area where one or both types of the stimuli was presented, frequently developed most clearly during the first conditioned reflex reaction. This is not quite consistent with the theories mentioned above, although it could be assumed that the dynamics of the EEG were later "complicated" by increased excitability in the brain, particularly the cortex, relative to conditioned reflex activity. In the same patients, "extinction" of reinforcing reactions, which is presumably related to inhibition, was very indistinctly correlated with the development of slow waves. And finally, even with a focus of slow waves that was large and increasing in intensity and duration in the cortical zones of most importance for the reaction, the actual conditioned reaction was, as a rule, carried out.

There remained the assumption that:

(1) As a result of the development of a focal pathological process, new compensating patterns, "a redistribution of the control" of brain functions, had already emerged and that, precisely for this reason, even an increase in the focus of extinction (inhibition?) in the cortex did not cause a significant defect in the conditioned reflex activity elicited by the interaction of sound, light, and proprioceptive signals; or

(2) What had appeared in the form of slow waves did not indicate inhibition in the cortex, leading to its disconnection from activity, but rather was a reflection of the excitation developing at some other level of brain function initially.

The latter possibility (2) seemed probable from an unprejudiced analysis of the clinical data which showed that a sometimes quite broad circle of typically "cortical" activity in patients, with widespread as well as focal slow waves, remained. However, in EEG recordings from patients with an initially polymorphic EEG there was a real possibility of polymorphism in the electrographic expression of functional changes in the brain during conditioned reflex activity; also, these EEG phenomena could not be attributed solely to distant conditioning foci. The EEG changes that develop in the brain during conditioned reflex activity take place through the interaction of other brain areas with the cortex. The evidence for this, which is more convincing than a synchronization-desynchronization mechanism in the cortex, is the expression in the EEG of the interaction between an "induced situation" (a distantly conditioned EEG reaction) and an existing cortical pathological focus, in particular the EEG changes developing under these conditions in the region of the cortical pathological focus. This is an important principle in answering the question of whether it is possible to obtain from the EEG information on fractional, predominantly local cortical events, especially during inherently mental activity.

An investigation of the EEGs of patients with focal brain injuries, during inhibited conditioned reactions, showed that it was possible to observe different types of reactions, including increases and decreases in focal slow wave amplitude. Thus, even in response to inhibiting stimuli, the initially cortical slow waves followed a specific pattern which could be expressed by changes in the direction of these waves (Fig. 3).

Investigations carried out in these "model" situations, with an initial pathological focus in the cortex, emphasized both the complexity of the electrographic phenomena in conditioned reflex activity and the contradictory findings regarding the interaction of slow waves and inhibition. The fundamental importance of the thesis that slow wave activity and inhibition are not necessarily related, or that such a relationship would be unlikely, was also emphasized by Anokhin (1968). Nevertheless, clinical physiological investigations have shown that the focal slow waves, with movements in different directions, which were detected during the execution of both positive and inhibiting conditioned reactions, actually possess at least one of the functions of an inhibiting process—the preventive function [this property was proposed by Walter (1953), particularly with respect to slow waves].

In the course of joint investigations with neurosurgeons, we convincingly showed the relative safety of surgical manipulations in the focal zone of slow activity and the sharp increase in the frequency of pathological reactions in the case of a low intensity or virtual absence of slow activity in the region of the pathological focus as well (Bechtereva and Orlova, 1957).

An intensification of the slow waves was not the only form of interaction between the pathological focus and the input from the brain stem, and the thalamic, limbic, and other areas arriving in the cortex during conditioned reflex activity. The interaction between the focus and the input from these areas can occur in such a way that the bioelectric effect is a significant decrease in the intensity of the slow waves or an increase in the intensity of the fast waves, i.e., a type of spiked beta wave.

The assessment of these reactions proved to be valuable in the preoperative evaluation of patients. Whereas the presence and intensification of slow waves in the zone of pathological focus in response to stimuli was a prognostically favorable sign with respect to the patient's reaction to the operation, an increase in intensity of the frequent vibrations in the focal zone was an unfavorable sign. Unfavorable reactions during the operation were prevented by a special preoperative preparation of the patients (Bechtereva and Orlova, 1957); however, this is a special problem not connected with the subject of the present book.

A natural experiment–in brain disease–made it possible to investigate the same phenomena in cases of a primary injury to the brain stem.

One of the frequent manifestations of a pathological focus in the brain stem is the development of more or less pronounced paroxysmal activity, which is revealed in the form of bursts of beta- or alpha-like, theta and delta, or mixed rhythms. In patients studied with implanted electrodes these bursts are not only detected in the cerebral cortex, but may also, as it were, "permeate" the whole brain substance (this, of course, does not preclude the possibility that local bursts will appear as well).

The dynamics of the diffuse bursts that appear in the EEGs of such patients during conditioned reflex activity in many respects paralleled the alpha-rhythm dynamics observed in healthy persons. They were suppressed during the initial application of nonspecific stimuli and the repeated application of positive conditioned stimuli, and were maintained during repeated nonspecific stimuli; while in response to stable differentiated stimuli, the slow activity components of the bursts may not only be maintained but even increased according to the period (Fig. 4).

A desynchronization with a blocking of alpha-rhythm was observed under conditions in which development or intensification of the process of stimulation, relative to a conditioned reflex reaction, might be assumed to be the most frequent reaction in healthy stimulated subjects. A change in the physiological state of healthy persons–falling asleep–could, under the same conditions and with similar spatial characteristics, produce a synchronization reaction of the alpha-rhythm. Both of these electrographic reactions might clearly reflect distant shifts in the EEG. The "intervention" of a cortical pathological

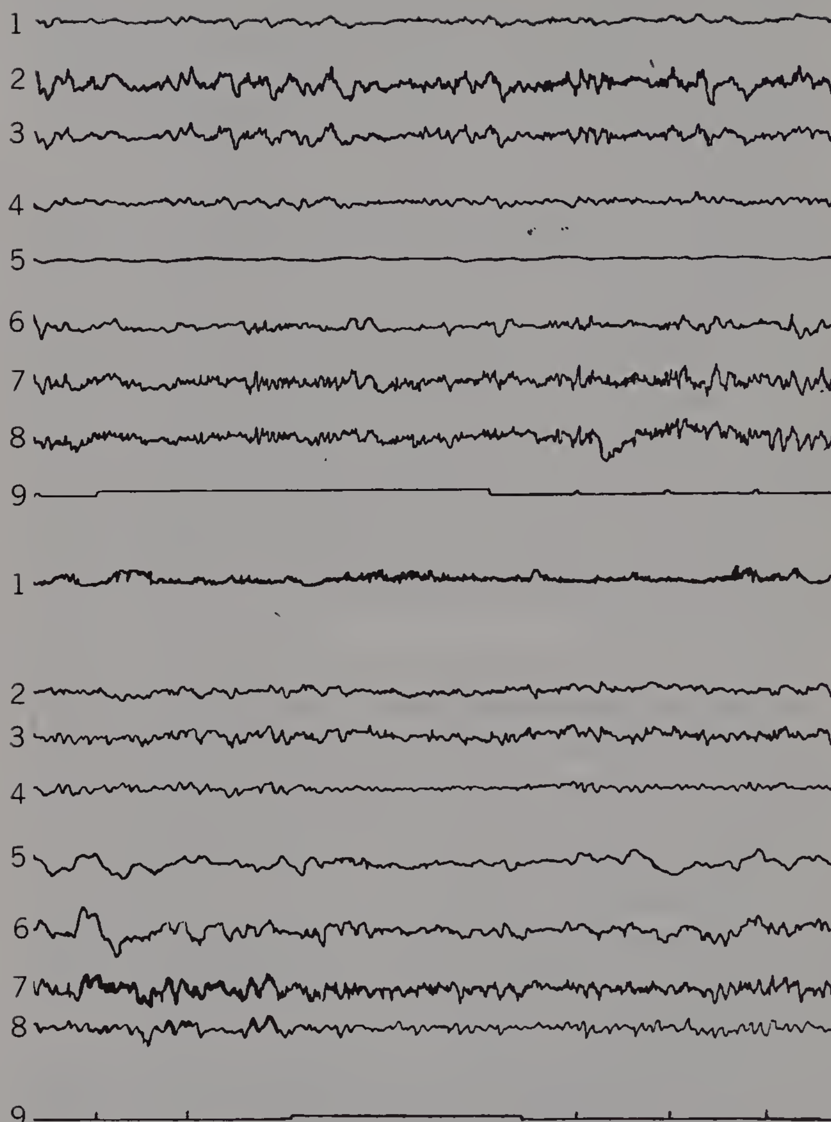
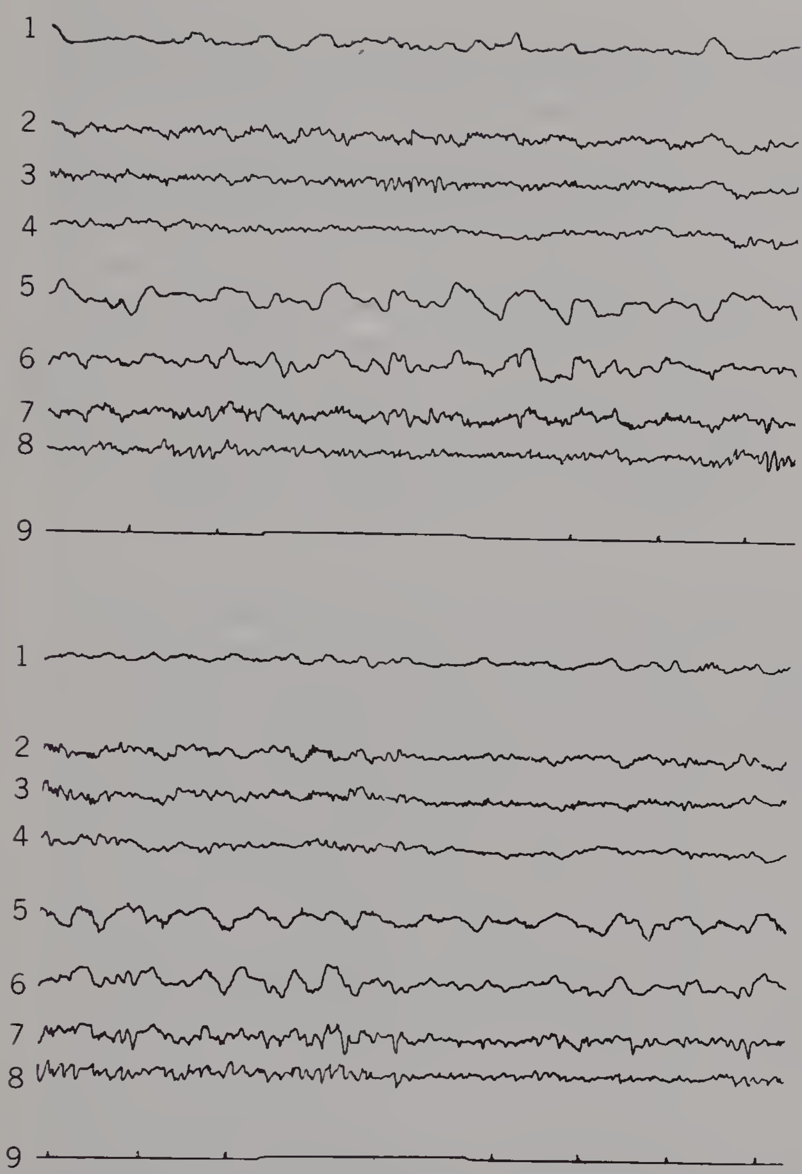


Figure 3. Dynamics of slow focal activity during the performance of conditioned reflex reactions. (a) Dynamics of the EEG during a positive conditioned reaction; (b) during a differentiated conditioned reaction. The conditioned reactions were carried out in response to sound, by the motor method with the vocal reinforcement of A. G. Ivanov-Smolensky. *Top,* increased intensity of the



focal slow waves during the reaction; *bottom,* a decreased intensity is shown. Bipolar leads were used. 1, Anterofrontal, left; 2, frontotemporal, left; 3, parietotemporal, left; 4, occipital, left; 5, anterofrontal, right; 6, frontotemporal, right; 7, parietotemporal, right; 8, occipital, right; 9, time scale (1 second) and stimuli.

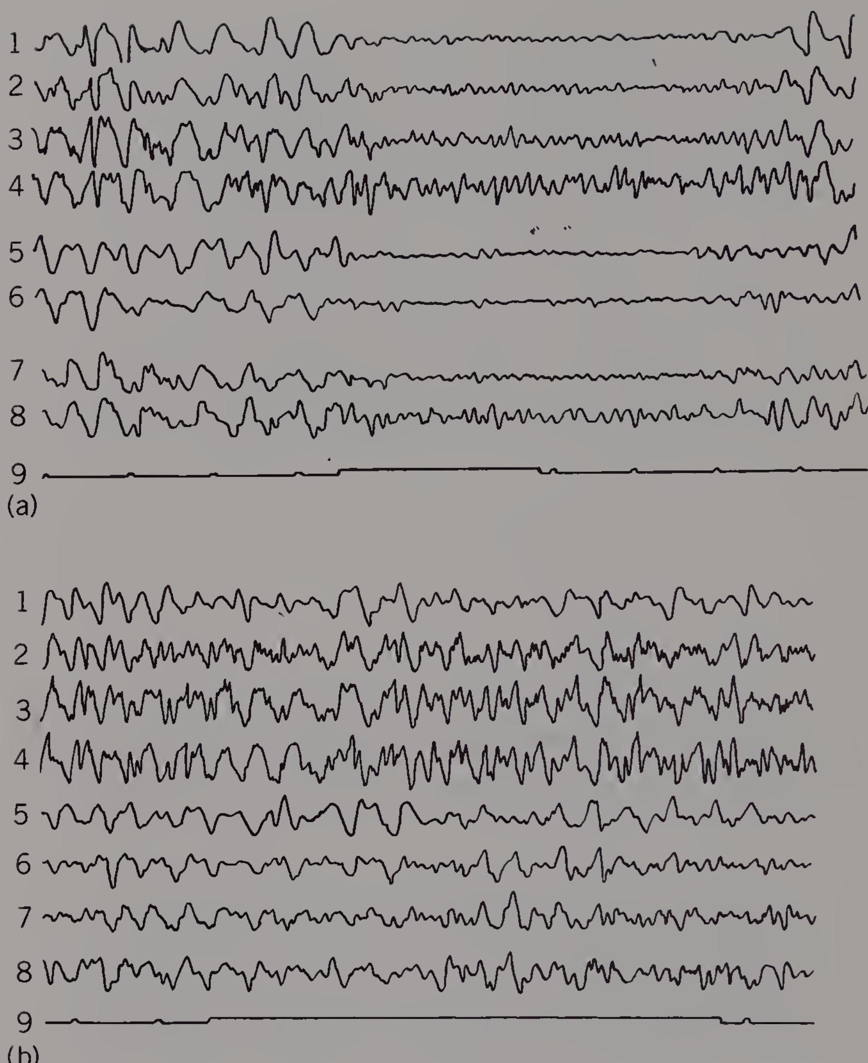


Figure 4. Electroencephalographic dynamics of paroxysmal activity during the performance of conditioned-reflex reactions. The conditioned reactions were developed in response to sound, by the motor method with the vocal reinforcement of A. G. Ivanov-Smolensky. (a) During the performance of a positive conditioned reaction, there was a distinct depression of the paroxysmal activity; (b) during the performance of a differentiated reaction, no depression was detected. See Fig. 3 for key to numbers.

focus thus led to a greater polymorphism in the reactions and suggested that these EEG shifts are purely cortical under these conditions.

Desynchronization as a distant reaction during positive conditioned reflexes was observed in patients with pathological processes in the region of the median structures of the brain and was accompanied by exaggerated paroxysmal activity. In this case, an internal inhibition was associated with slow waves in the brain and especially in the cortex; the cortical activity was the result of events at the brain-stem level. Thus, in the case of brain injuries, despite all the limitations of data of this type, it was possible to carry out a more complete study of the role of both local and general (distant) effects in the origin of EEG patterns during the performance of conditioned reactions than could have been done under normal conditions.

By combining the "physiological and pathological" in EEG studies of patients with focal brain injuries (Bechtereva, 1961), it was also possible to obtain more information on the role of local and general factors, and a somewhat more precise definition of the physiological significance of the electrographic dynamics observed during conditioned reflex activity. Investigations carried out under these conditions once again emphasized the importance of general and local factors in the cortical electrographic pattern as related to conditioned reflex activity and the fallacy of interpreting EEG dynamics as reflecting both exclusively ascending or exclusively cortical rearrangements. Continuing our argument with Gastaut, the EEG data presented could be used both to confirm some of his concepts regarding the subcortical genesis of the bioelectric shifts during conditioned reflex activity and also to refute the fundamental lines of his analysis of the data on the physiological significance of this subcortical level.

The EEGs recorded during conditioned reflex reactions convincingly indicate the fallacy of the assertion that the bioelectric phenomena of the brain can be equated with fundamental neural processes. The local and generalized changes in the EEG during conditioned reflex reactions depend on the initial bioelectric background and thus on the functional state of the brain. From all the observations presented we can logically infer that the chief nodal points in the brain responsible for the bioelectric rearrangement cannot be identified with the locus of the fundamental, determining closure of the conditioned connection. It is important to emphasize that although the source of the overall shifts in bioelectric activity recorded in the EEG during conditioned reflex reactions are phenomena that evidently take place at the mesencephalic and diencephalic levels, this does not constitute evidence either for or against the closing of the conditioned connection at these levels.

It would be a mistake, however, to go to the opposite extreme and neglect the data on changes in bioelectric patterns of the brain during conditioned reflex reactions. When the initial bioelectric background is considered, these data can be used to evaluate the conditions which develop as the brain interacts with the environment for the optimum course of conditioned reflex activity. The bioelectric phenomena indicate that huge areas of the brain are involved in the preparation for this activity. It should always be remembered that such phrases as "the whole cortex" or "the whole brain" in this context imply only the possibility of activity. The specific activity has its own much more restricted mechanisms. That the EEG primarily reflects "readiness for functioning," is also noted by Kogan (1967). Yoshii, Matsumoto, Ogura, Simokoti, Yamaguchi, and Yamasaki (1962) and others relate the EEG patterns during conditioned reflex activity not to the activity of the brain formations (centers) actually responsible for the reaction, and not to the dynamics of the neural processes, but to the dynamics of the background activity of the brain.

The changes in the EEG reported in the mid- to late-1950s were observed in large areas of the cortex. At the time, microelectrode studies on conditioned reflex reactions were already being performed (Jasper and Rasmussen, 1958; Jasper, Ricci, and Doane, 1962; and others), and these showed the extremely local nature of the neural phenomena at the cellular level. An understanding of these quite complex phenomena on the cellular level in a conditioned reflex situation became possible only considerably later, after the method was refined by Vasilevsky (1965–1968). It should be emphasized that the correspondence between what was observed on the neuronal level and in the EEG proved to be (and, to a great extent, still remains) very complicated, but the microelectrode and EEG studies were complementary, not contradictory.

Is it possible at the present time to accept any point or points of view on the relationship between neural processes and bioelectric phenomena? Evidently, certain aspects of this problem may be understood on the basis of the concepts of Rusinov (1953) concerning the importance of the direction of the changes in bioelectric activity. According to these concepts, the predominance of the inhibition that develops in the brain and the shift in its direction may be reflected in the EEG by synchronization and retardation of the activity, whereas a shift in the direction of a predominance of excitation increases the frequency of bioelectric activity and its desynchronization, the clearest form of which is a blocking of the alpha-rhythm when this is initially present in the EEG. However, this very limited scheme, which applies when a number of conditions (initial background, etc.) obtained covers only one aspect of the problem—that type of relationship in which EEG changes follow a change in the underlying bioelectric processes.

Observation of the EEG under different physiological and pathological conditions requires, with equal probability, the consideration of still another possibility: that changes in the EEG, particularly those related to conditioned reflex activity, may be not only secondary but also primary, either facilitating or complicating these dynamics. This thesis was advanced by Livanov (1957, 1962a,b), who postulated that the initial bioelectric dynamics represent a background which may facilitate the propagation of neural activity. The concepts of John (1967), who assumed that synchronization in the EEG facilitates "computation" mechanisms, differ mainly in form from Livanov's theory, presented above.

It may be said, in an even more general way, that phenomena observed in the EEG not only reflect what is taking place in the brain but also determine its current functional state and provide the optimal functional level for the occurrence of any given activity (Livanov, 1962b; Sokolov, 1962; Bechtereva, 1966). However, in analyzing these phenomena more deeply, investigators are running into ever-increasing difficulties. There is convincing evidence from neurophysiological experiments in animals (Anokhin, 1968; Vartanyan, 1966, 1970; and others) that radiation of inhibition in the brain does not occur, at least as interpreted by Pavlov. Data on the physiological nature of activating and inhibiting responses in the brain are also being obtained from direct observations of humans (Bechtereva, Bondarchuk, and Smirnov, 1969). Even if we do not object to the assumption that, on the basis of the EEG, one can speak not only about prerequisites for the radiation of neural activity but also about their propagation as correlated with that of some form of biopotential, it should be acknowledged that a great deal of what is used as evidence for such propagation can be questioned on methodological grounds.

In an investigation of this problem, one of the most important factors in studying propagation of biopotentials must be the accuracy of the calculations of the maximally monomorphic form of bioelectric activity, and the careful observation of the phase shift of waves in many adjacent regions of the brain. Research of this kind has been conducted satisfactorily only by certain workers, particularly Dubikaitis (1964, 1968) and Petsche (1967, 1968). Petsche, applying his own well-known variation of toposcopy to the activity of the peak wave, showed that positive waves occur in the cortex during bursts of bioelectric activity. However, Petsche and Dubikaitis showed little interest in the relationship between bioelectric dynamics and the dynamics of neural processes.

The electrographic dynamics of the phenomena can also be considered from a slightly different aspect. Desynchronization in positive conditioned reactions—and especially generalized desynchronization—could reflect an initially very uneconomic mechanism of involvement in activity and in the readiness of most brain regions for such activity, when there is a significant overall increase in the level of excitability of the cortex (Kogan, 1962; Chang, 1962; Livanov, 1962a,b). The limitation of the reaction during repeated exposure to the stimuli is an external manifestation of a decrease in the number of structures ready for activity, a change that results from a familiarity with the situation, that is, a sharp decrease in its novelty.

From this point of view, synchronization of the biopotentials during inhibition reactions reflects a reduction in the number of zones which are in a state of activity, or in an optimum state of readiness for involvement in the reaction. This state may develop, in principle, from a disconnection of the activating effects for such reactions or from a stimulation of synchronized effects at any level. However, inclusion of these mechanisms in the simplest conditioned reflex reaction at the "nodal" levels may be biologically advantageous (economical). Thus, realization of a positive conditioned connection, particularly initially, brings vast regions of the brain into an active state (at least before a decrease in the novelty of the situation occurs). Inhibition reactions may occur during the simplest model conditions on the basis of significantly more economical mechanisms.

Furthermore, if the desynchronization reaction, which is bioelectrically monotonic in the EEG and, to judge from the data from direct observations of the brain and from electrocorticography (ECoG), not really unequivocal, can be considered to reflect an optimization of the functional state of the brain for activity, then what is the significance of the synchronization of cortical biopotentials in the performance of inhibition reactions?

In a healthy human being with a well-expressed alpha-rhythm, the EEG picture during the performance of inhibition reactions is frequently indistinguishable from that at rest, or appears to be an intensification of the resting pattern, with an increase in the amplitude of the waves and (sometimes) a retardation of their period. Studies of human EEGs over a number of years (Bechtereva et al., 1958–1965; and others) have shown that relationships between the EEG waves and the dynamics of excitability in the brain are not always simple (Brazier, 1962). However, if we do not attempt to extrapolate from what is visible in the EEG, it must be recognized that during the simple conditioned reactions in question, excitability waves arise or are intensified in an "inhibition" situation and decrease sharply in an "excitation-desynchronization" situation. These states of synchronization may be due to the development of inhibition in the region of the diencephalic and mesencephalic activating structures, to an activation of inhibiting subcortical mechanisms, or to the interaction of these mechanisms. Inhibition, under the conditions of the investigation, may also develop at the level of the cerebral cortex; this can be traced under special conditions and may be assumed to be involved in localized mechanisms of complex mental activity. Changes in functional patterns of this type, which develop at different levels of the median structures of the brain, may, as shown above, entail not only diffuse but also local functional changes in the cerebral cortex that are related to the stimulus being applied and to local brain conditions (e.g., a pathological focus). Normally, however, EEG changes are most likely to develop in comparatively large areas of the cortex and to represent altered activity in the underlying structures rather than inhibition. These concepts are not very far removed from those of Adrian (1954) and others concerning the possibility that in certain cases the flow of information is blocked at different levels of the nervous system. Such a possibility would not contradict the views of Anokhin (1968), who postulated a pacemaker type of organization of functional systems. The excitability waves in the cortex in this type of organization represent an optimum state for the restoration of its potentialities while preserving its readiness for activity as a whole, and not for any specific activity as in an "excitation" situation. Rhythmic changes from one state to another follow one of the most general biological principles, that is, these rhythmic changes are concerned with preservation or restoration of the potentialities of an organ and of the organism as a whole. Hence, what is frequently observed in the EEG of healthy humans during inhibition of simple conditioned reactions, and analogous states, is probably conditioned by a distantly developed inhibition or an activation of the "inhibiting" mechanism, a state of rest that benefits the organism and that allows the restoration of its potentialities to proceed with the preservation of its readiness for engaging in discrete activity.

A number of objections can undoubtedly be raised against such interpretations. Thus in a number of persons, a synchronous alpha-rhythm is not detected, either at rest or in an "inhibition" situation; in some physiological states (e.g., falling asleep) a specifically positive conditioned reaction is observed with a synchronized EEG. In the first case it can be assumed that the excitability may be related not only to the alpha-rhythm but also to more frequent waves; however, the dynamics of these rhythms are difficult to observe in the EEG. The second case confirms rather than refutes the concepts in question: judging from the EEG, the first phase of emergence from a state of drowsiness (or sleep) is one of distinct fluctuations in cortical excitability (it is well known that when stimuli are intensified or frequently repeated "waking" takes place).

The generalized synchronization of the biopotentials, as indicated above, may be understood as a blocking of the activating effects of the ascending reticular formation and/or an activation of brain-stem structures involved in synchronizing activity (Morruzzi, 1962). However, data have already been obtained directly from human subjects on higher level inhibitory mechanisms. Their significance must be taken into account in understanding local synchronization reactions. These phenomena in humans may be related in particular to the activity of the median center of the optic thalamus, the nucleus caudatus, and possibly other structures (Bechtereva, Moiseeva, Orlova, and Smirnov, 1964; Bechtereva, Bondarchuk, and Smirnov, 1969).

In evaluating all these phenomena, we should not forget that primarily cortical synchronization mechanisms can also occur (Livanov, 1962a,b), though they are a somewhat less probable explanation for the case in question. At the same time it is extremely important to consider the role of corticofugal effects (Morruzzi, 1962) in the actual appearance of desynchronization mediated by the brain stem or other subcortical structures.

The explanations of the interaction between synchronization and inhibition given above do not exclude a direct relationship between these phenomena, that is, direct development of inhibition in the zone of synchronous waves in the cortex. They only show that such a direct relationship need not be postulated.

Of course, the experimental study of EEGs in humans confirms that synchronous activity during inhibiting reactions need not occur. But the appearance of synchronous activity and the intensification of the rhythmic waves of excitability associated with it, if not an essential reaction, evidently is at least one of the most beneficial reactions for the organism, a protective response that contributes to the preservation or restoration of the working potential of the brain.

It should be remembered that the most serious shortcoming in all the observations reviewed above, in terms of their value as physiological data, is that brain states have been assessed in these studies on the basis of a single parameter, the EEG, and furthermore, that the possibility of considerable distortion is inherent in this indirect method of observation, with a lead through the tegmentum.

The Electroencephalogram during Psychological Tests

Changes in the human EEG have been observed not only for the simplest model of mental activity—conditioned reflex reactions—but also during alterations in consciousness and psychological tests, in which the personality of the subject must be considered.

In terms of the neurophysiological aspects of mental activity, our greatest interest is in the dynamics of the EEG during various psychological tests. The conditioned reflex principle remains the basis of all human mental phenomena. However, in our study of the neurophysiological aspects of mental phenomena, it was necessary to use, in combination with neurophysiological methods, not only the most common and simplest conditioned reflex tests, but also the methods offered by psychological research. Only in this way could we address that state which represents a gigantic leap forward in biology—human mental activity.

Berger (1933) had already made an attempt to correlate

EEGs with mental phenomena. Changes in the EEG were later observed by using psychological tests of varying complexity as stimuli and, in particular, by using verbal signals. These studies showed in particular that the amplitude of EEG waves in response to verbal stimuli depends on the meaning of the words and on the state of the subject during the test. During light conversation usually only a small decrease in the amplitude of the alpha waves was recorded (self-observations, Adrian and Matthews, 1934). Travis and Egan (1938) observed a small increase in frequency of the alpha-rhythm (from 10.15 to 10.75) while the subject listened to a text being read aloud. On the whole, this effect was so small that Gastaut (1957) felt it was possible to disregard reactions to a verbal stimulus in evaluating the conditioned reflex changes in the EEG in investigations where this was included in the complex of stimuli.

At the same time a verbal stimulus could determine a reaction in the EEG to some concrete stimulus (Mushkina, 1956) or, depending on its meaning, it could produce the effect of a concrete stimulus (Lur'e and Rusinov, 1952). When the verbal stimulus (the word "block" in the studies of Shagass, 1952) was reinforced by a concrete stimulus, the verbal stimulus alone will then elicit the reaction characteristic of the reinforcement used.

The emotional significance of verbal stimuli plays a very important role in the EEG response to them. If the word has emotional meaning for the test subject, the depression of the alpha-rhythm is pronounced and long-lasting (Roitbak and Savanelli, 1953; Bagchi, Howell, and Schmall, 1945; and others). In patients the response might be the appearance or intensification of pathological bioelectric activity in the EEG (Peimer, 1954; Yakovleva, 1952, 1956). However, the repetition of emotion-generating words usually led to the extinction of EEG reactions to these words.

The reaction to a verbal stimulus has also been studied during the process of falling asleep and during hypnosis. When a person is falling asleep, a verbal stimulus elicits an activation reaction; alpha and beta waves appear in the EEG, and the slow waves decrease (Jung, 1954). Investigations in which hypnotic suggestion was used revealed the possibility of both increasing and decreasing the EEG effect produced by verbal stimuli (Livanov, Strel'chuk, and Melikhova, 1953; Nevsky, 1954; Loomis, Harvey, and Hobart, 1936a,b).

EEG changes in the form of a depression of the alpha-rhythm have been observed when illustrations were shown to subjects (Jasper and Shagass, 1941; Williams, 1939; Golla, Hutton, and Walter, 1943) and during the mental reproduction of these pictures (Walter and Yeager, 1956). A mental reproduction of movement blocked the rolandic rhythm (Gastaut, 1952; Magnus, 1954). A decrease in the amplitude of the EEG waves was observed during the memorization of numbers (Novikova, 1955).

A depression of the alpha-rhythm has been observed in very different situations, such as the viewing of a motion picture (Gastaut and Bert, 1954; Faure and Cohen-Seat, 1954; Lelord, 1957; Verdeaux and Verdeaux, 1955) and during the reproduction of one of the components of an artificially produced mental association (Laufberger, 1950). When a rolandic rhythm was initially recorded in the EEG of the test subjects viewing a motion picture while the behavior of the actors on the screen was very dynamic, it was possible to observe not only a suppression but also an intensification of this rhythm.

There have been many studies of the EEG during mental calculation and the solution of arithmetical problems (Mundy-Castle, 1957; Peimer, 1960; Genkin, 1963; Livanov, 1962; Gavrilova and Aslanov, 1966; Glass, 1964, 1965; Artem'eva and Khomskaya, 1966; Volavka et al., 1967; Vogel et al., 1968; and others). The most persistent observation has been a depression of the alpha-rhythm. A direct relationship between the difficulty of the task being performed and the magnitude of depression of the alpha-rhythm has often, but not always, been noted (Peimer, 1960). An investigation of the EEG in healthy persons and in patients during the process of identifying images with different durations of exposure confirmed that changes in the EEG depend on the degree of concentration and on emotional and mental stress (Zhirmunskaya, Beyn, and Volkov, 1969).

Under conditions of mental stress, an increase in the intensity of the beta waves has frequently been noted (Mundy-Castle, 1957; Beyn et al., 1967; Volavka et al., 1967) or, conversely, a decrease in the beta index. In many investigations, intensification of the theta waves during intellectual activity has been observed (Arellano and Schwab, 1950; Brazier and Casby, 1952; Mundy-Castle, 1957; Peimer and Fadeeva, 1957; Lin-Schih-yih et al., 1964; Brendsted, 1966; Beyn et al., 1967; Vogel et al., 1968; and others), as well as the appearance of a "kappa rhythm" (Kennedy, Gottsdanker, Armington, and Gray, 1948; Lin-Schih-yih et al., 1964). At the same time, several studies have shown that certain changes in the EEG during intellectual activity may, to a significant degree, be determined by artifacts, and many investigators have noted that in some persons engaged in intellectual activity there is no apparent change in the EEG (Artem'eva and Khomskaya, 1966; and many others). However, in all cases where changes in the EEG have been observed during psychological tests, the changes were widespread, although they might have been particularly pronounced in specific regions (Adey, 1969).

Much attention has been paid to changes not only in the normal resting EEG but also in evoked potentials recorded during mental activity (Peimer, Egorov, Modin, Bondarev, Govorova, and Vasil'eva, 1966; Chapman, 1966; Shagass and Canter, 1966; and others). Changes in these evoked potentials, according to the relation between the stimulus and one of the forms of intellectual activity, have been demonstrated in a particularly convincing manner by Chapman. In his work the response to meaningful stimuli was much more distinct than the response to meaningless stimuli. Gray Walter (1967), who recorded these potentials from different regions of the human brain by means of implanted electrodes, emphasized that the number of zones of nonspecific response indicates the involvement of vast regions of the brain in the process of higher integration.

Many EEG investigations during mental activity, like the EEG studies of conditioned reflex reactions, have involved only visual analysis. In some studies, however, mathematical and instrumental analysis was used to obtain data on the quantitative aspects of the EEG changes, to reveal changes not found by visual analysis, and to define more precisely the regions where primary changes occurred (Shipton and Walter, 1957; Mundy-Castle, 1957; Kennard, 1953; Kennard et al., 1955).

Storm van Leeuwen and associates (1963) made a multidisciplinary analysis of the biopotentials of the human brain during an associative experiment involving the solution of arithmetical problems and performance of the Rorschach, Crepelin, Bourdon, and other tests. The subjective reaction of the person examined was taken into account when the EEG data were evaluated. This study, however, cannot be compared with subsequent studies by Storm van Leeuwen et al. (1963) on the behavioral and EEG reactions of dogs, which practically exhausted this subject.

These methods of analyzing brain biopotentials, which involve a frequency or frequency-amplitude treatment of the EEG without any attempt to extract special information from the recording, made it possible to evaluate not only the qualitative but also the quantitative aspect of the dynamics of biopotentials (Creutzfeldt, 1969). Creutzfeldt's study did not contribute anything essentially new to our understanding of the relationship of EEG dynamics and neural processes during conditioned reflex reactions and psychological testing.

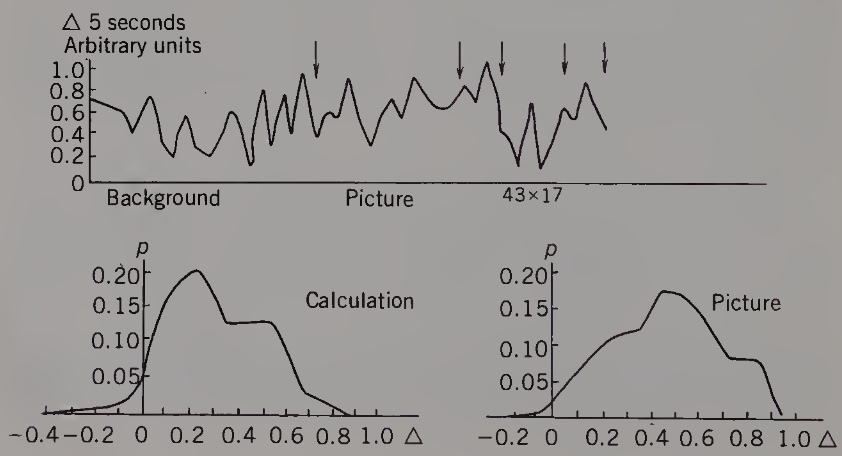
With data gathered by these methods, which could not have been obtained by visual analysis of the EEG, biopotentials in different regions of the brain during mental activity could be correlated. This cross-correlation (Walter, 1953; Darrow, Wilson, Vieth, and Malle, 1960), showed that during arithmetical calculation the phase synchronization of the EEG biopotentials of the central and parietal regions is higher than the phase synchronization of the parietal and occipital regions. At rest, the reverse was true. Of special interest in this regard are the studies carried out by cross-correlation analysis of the biopotentials of 50 leads or more (Livanov, 1962b; Livanov, Gavrilov, and Aslanov, 1966). These investigations demonstrated the occurrence of general and local changes in the phase synchronization of the biopotentials of healthy persons engaged in intellectual activity. The dynamics of the biopotentials in the frontal lobes under these conditions and the special characteristics of the relationship between the biopotentials at rest, during delirium, and during intellectual activity in mental patients were studied, and the functional changes of large regions of the brain were characterized. Summing up many years of work, Livanov (1972) has shown that in a healthy human subject at rest, 50% of the cortical points studied operate independently, 45% are weakly synchronized, and 2.2% are highly synchronized, with adjacent areas of the brain operating in synchronization in the latter case. During intellectual and physical work, a sharp increase in the number of synchronized regions is observed, while the number of unsynchronized regions decreases. Not only is there an overall increase in the number of strong and weakly synchronized regions during work, but also a redistribution of the correlations depending on the complexity of the task. When Aminazine is administered, there is a decrease in the number of correlations and an increase in the time taken to solve a problem. In the neuroses, the number of correlations is higher than normal; the "stimulation of a diseased point" (presentation of an emotion-producing word) generally increases the number of correlations but may also decrease them. These data create the impression that the development of emotional states plays a significant part in the increase, or change, in correlations. Livanov again emphasizes that the correlative relationships do not reflect neural connections but rather the condition that makes possible their realization. On the basis of his own by now very numerous data on the neurophysiology of healthy and diseased human subjects, Livanov has stressed the concept that numerous cortical points interact in the cerebral maintenance of functions.

Efforts have been made to extract from the EEG information concerning changes during psychological tests in the cortical areas where higher functions are represented. Studies by Genkin (1961, 1964, 1966) and by Artem'eva and Khomskaya (1966), who used the method of EEG analysis proposed by Genkin, revealed the possibility of documenting changes in the correlations between the ascending and descending phases of the biopotentials of a frequently "specific spatial and time pattern" in individuals, which are apparently characteristic for a given form of mental activity (Fig. 5). Changes in brain wave patterns were detected in an especially convincing manner not simply by analyzing the phase relationships, but by calculating the coefficient of the interaction of phases and constructing the phase duration vectors.

These data may be compared with the observations presented above concerning the interaction as reflected in the EEG between distant effects and the local functional state of the brain (e.g., a pathological focus) during conditioned reflex activity.

Apparently it was also possible to observe specific changes in the EEG during mental activity by using the method of synchronous detection (Voitinsky and Pryanishnikov, 1966). Adey and co-workers (Adey, Dunlop, and Hendrix, 1960) insist that information can be obtained from the EEG during conditioned reflex activity which, if not specific, is closely related to this mental activity. In particular, Adey and his coworkers showed that a cross-correlation of electrical processes

Figure 5. Dynamics of the relationship between the ascending and descending phases of the biopotentials during mental activity in humans (according to A. A. Genkin). *Top,* data of this dynamic in the parieto-occipital lobe; *bottom,* distribution of asymmetries during different forms of mental activity.



in the cortex and hippocampus with electrical processes at different points in the hippocampus makes it possible to detect specific phenomena in the brain during the formation of temporary conditioned connections.

However, it may be noted that after many years of special approaches to the analysis of the EEG, including the use of some very precise methods, there has been a gradual shift in emphasis from local to general changes in the biopotentials with local changes now being assigned a more modest role (Genkin, 1966; Artem'eva and Khomskaya, 1966).

Current methods of analysis have made possible a quite subtle differentiation between brain states in humans by means of the EEG (Adey, 1970; Berkhout, Walter, and Adey, 1969; Beyn, Zhirmunskaya, and Volkov, 1971). Instrumental and special mathematical analyses have confirmed the occurrence of EEG changes in human beings during mental activity, which underscores the prevalence and regularity of EEG changes in large areas of the cortex not only during simple conditioned reflex reactions but also during psychological tests. On the neurophysiological level, most of what has been said about the nature of the changes in the EEG during conditioned reflex activity is also true of EEG changes during psychological tests. A well-known difference is the great discontinuity and polymorphism of the changes in the EEG during tests that are strictly psychological. However, results from instrumental and mathematical analyses have emphasized that although local changes in the EEG can be noted during psychological tests, the development of these local changes is always a part of the general modification of bioelectric activity. Thus, EEG changes during mental activity reflect not so much the active state of individual structures as they reflect general changes in the brain, which evidently optimize the conditions for activity.

This thesis seems to have been based not only on the typical characteristics of the activity being studied but also on the properties of the physiological parameter selected, brain waves as shown in the EEG.

We cannot completely exclude another mechanism that could underly the extensive nature of the changes in the EEG, and consequently also the changes in the functional state of the brain. This dynamic pattern could be explained if, in fact, one of the "languages of the brain" (Pribram, 1971), in particular the language of long-term memory, were based on principles comparable to those of holography.

The Electrosubcorticogram during Psychological Tests. The Significance of its Changes during Mental Activity

An analysis of data obtained with a direct EEG lead from the surface of the human brain during psychological tests has been carried out in individual investigations (Genkin, 1964; Chapman, 1966).

A systematic study of the dynamics of the electrosubcorticogram during human mental activity, with a direct lead from the brain, became possible when the implanted electrode method was introduced into clinical practice after almost one hundred years of animal experiments (Simonov, 1866). The use of implanted electrodes for the diagnosis and treatment of hyperkinesis, epilepsy, mental diseases, and certain other diseases now has a history over two decades long (Bickford et al., 1953, 1958; Heath, 1954; Meyers et al., 1950; Bates, 1961; Sem-Jacobsen, 1961, 1968; Walter and Crow, 1961; Bechtereva, Grachev, Orlova, and Yatsuk, 1963; Bechtereva, Bondarchuk, Smirnov, and Trokhachev, 1967; Bechtereva, 1972; Bechtereva, Bondarchuk, Smirnov, Meliutcheva, and Shandurina, 1975; and many others).

In recent years it has been possible not only to explore the vast potentialities of the use of implanted electrodes in clinical practice, which were already well known from experiments, but also to determine the limitations of the method. The special requirements of clinical practice served to stimulate substantial improvements in the method itself. These improvements proved to be most significant in two ways; by making the calculations of the coordinates of placement of the electrodes during the operation itself easier, faster, and more precise [this was accomplished by using electronic computers (Ivannikov and Usov, 1967)] and by providing a more precise operative definition of structural-functional relationships within the brain (Bechtereva, Bondarchuk, Smirnov, and Trokhachev, 1967). The possibilities of elucidating these relationships increased considerably when it was learned how to achieve the desired result not only by means of electrical stimulation via implanted electrodes, but also by a more subtle and significantly more sparing means—the investigation of different parameters of vital activity in the brain during appropriate functional tests.

Variations in the electrosubcorticogram of the slow electrical processes (SEP), sometimes designated the steady potential, reflect the dynamics of the constant potential and resistence in brain tissue and the process of polarization of gold electrodes, the available oxygen, and the impulse activity (IA) during passive and active movements. The electrosubcorticogram proved exceptionally effective in defining more precisely the relationship between the different structures and the brain system for organizing movements (Grechin, 1966; Trokhachev, 1965, 1966). The most favorable parameters for solving this problem proved to be the slow electric processes, the available oxygen, and the impulse activity. When these indices were recorded during repeated motor tests, reproducible dynamics of the developing reactions were observed, which showed up very distinctly when a number of consecutive segments of the curves were superposed. (The comparison of the impulse activity reaction was performed after appropriate processing.)

With an approach identical in principle, it was also possible to study the connection between different brain formations and mental activity. Various physiological characteristics proved valuable in relation to different aspects of the phenomena being studied.

Thus, observations on changes in the vital activity of the brain and of the organism as a whole during electrical stimulation of the brain through implanted electrodes and an analysis of the brain processes recorded by means of the same electrodes were combined in a complex method, which is diagrammed in Fig. 2.

Most studies in this area are carried out by recording the electrosubcorticogram during psychological tests and during the development of spontaneous and evoked mental and psychopathological phenomena. Spikes deep within the frontal lobe during excitation and hallucinations and spikes in the hypothalamus during excitation were observed by Sem-Jacobsen and co-workers (1953, 1956), Hodes and co-workers (1954), and others. Sem-Jacobsen also found a suppression of certain specific patterns, similar to the alpha-rhythm, while the subject was reading a book. Penfield and Jasper (1954) observed the development of amnesia during an epileptic discharge in one of the amygdalae. Brazier (1966) reported a correlation of bioelectric effects in the region of the uncus with the development of a confused state of consciousness. Chapman (1966) carried out a computer analysis of the electrical phenomena of the human cortex, olfactory region, and basal ganglia. The electrocorticogram and electrosubcorticogram were studied during training, emotional experiences, memory tests, and other tests in patients with epileptic hyperkinesis who were also suffering from chronic psychoses.

Kamp, Schriger, and Storm van Leeuwen (1972) observed flashes of beta-rhythm activity in the lower layers of the frontal cortex in patients with implanted electrodes; the flashes became more intense in situations where the patient had to "predict" some event or events. The investigators hypothesized that these flashes of beta-rhythm reflected a sudden, transient removal of stress.

In contrast to investigations with a "psychological slant," in which the variety of psychological tests made it difficult to compare and analyze the data, the focus in our studies was the analysis of physiological characteristics. The number of psychological tests we used was limited, and their performance was taken into consideration only as necessary to analyze the dynamics of the physiological parameters.

Among the psychological tests we used was a basic test for short-term operative memory of the Binet type. The physiological dynamics of the brain (electrosubcorticogram, slow electrical processes, available oxygen, and impulse activity) were recorded before the test, during presentation of a series of known or unknown words, quasi-words, or trigrams, during the time of their retention in memory, during repetition of the problem (in response to the command "repeat"), and during the period of aftereffect. In some cases, the test was made more complex by using the variation of V. M. Smirnov (1968); simple numbers were pronounced, the patient subtracted or added these mentally, and only the final result of a series of such operations was reproduced (after the same 10–30 ± 2–3 seconds). Less frequently, the task involved adding mentally an odd simple number (e.g., 3) to some given number, with the requirement that only an even (or odd) result was to be spoken aloud. The brain mechanisms of emotional reactions were studied by a method which was identical in principle but which involved special emotion-producing tests (V. M. Smirnov, 1963–1968). The basic tests included the presentation of emotion-generating words or Rorschach cards and the reproduction of emotionally significant situations.

By using standard psychological tests for operative memory, it was possible to disengage our studies from the purely psychological aspects of the investigation at any given stage.

Changes in the frequency and amplitude of components of the electrosubcorticogram during psychological tests were more or less distinct at different stages of the tests. These changes were sometimes very significant, which gave the impression that the dynamics of the electrosubcorticogram revealed the brain formations in question to be of paramount importance in the type of activity tested. In other brain formations practically no changes in the electrosubcorticogram during psychological tests were detected visually, which could mean that no relationship existed between these formations and mental activity (Fig. 6).

As with the EEG, it was found in electrosubcorticogram studies that the intensity of the changes in any region were much more frequently related to the state of the structure than to the test used.

It is, of course, widely assumed in clinical electroencephalography that the most diverse functional tests can assist in the detection by EEG of a focal pathological process, irrespective of localization. This does not deny or depreciate the selectively local diagnostic value of some functional tests.

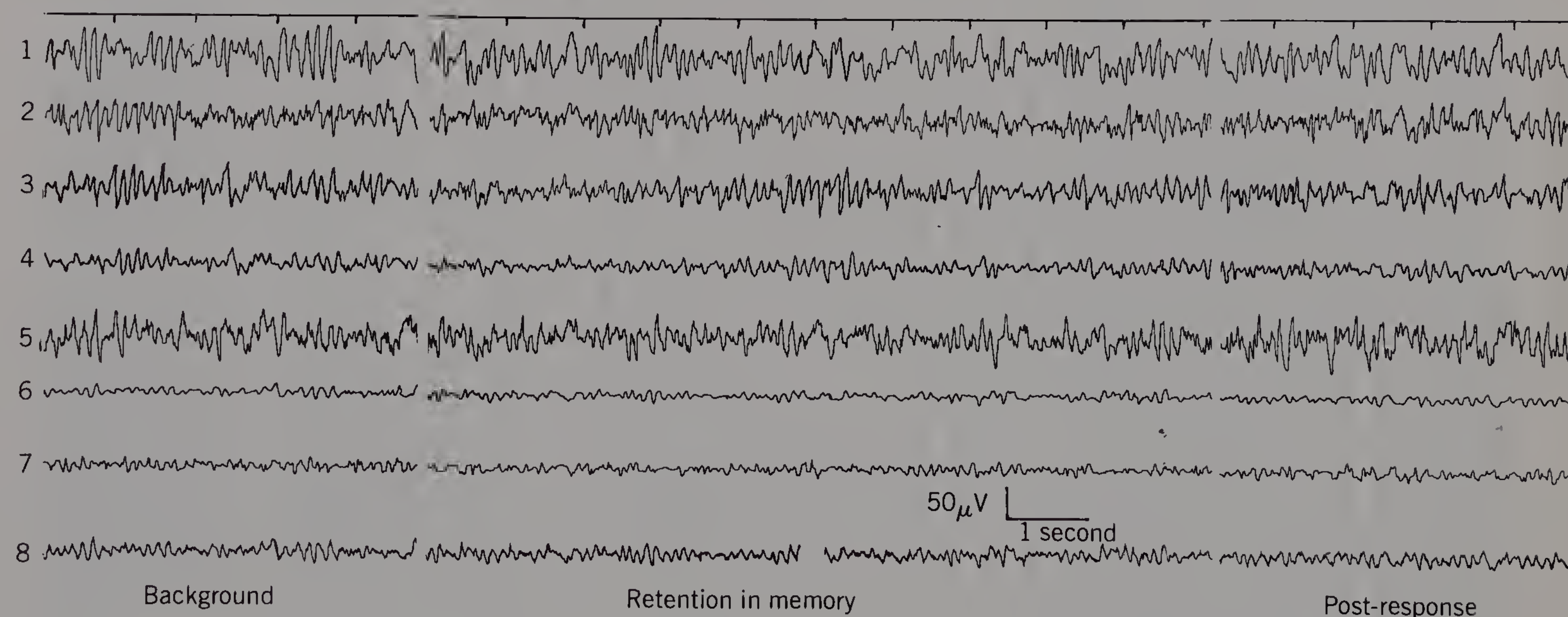


Figure 6. Electrosubcorticogram during a psychological test for operative memory.

A comparison of the electrosubcorticograms obtained during the administration of different functional tests showed that a change in the electrosubcorticogram could occur without having a direct relationship to the nature of the stimulus and without necessarily being most pronounced during psychological tests. The electrosubcorticogram pattern during a psychological test was directly related to the initial electrosubcorticogram and did not reappear during repetition of the tests—it could not be reliably reproduced. Genkin's mathematical treatment of the data, in which the relative duration of the ascending and descending phases of the waves was measured (Bechtereva, Genkin, Moiseeva, and Smirnov, 1965), confirmed the difference between the electrosubcorticogram recorded before and during the performance of psychological tests. Artificially created conditions—the selection of persons with similar EEGs in an investigation of the dynamics of the EEG during conditioned reflex reactions (Gastaut et al., 1957)—thus led to a particularly significant result.

Computer analysis of the electrosubcorticogram, a method that is increasingly being used (Moiseeva and Orlov, 1965), has demonstrated changes in the electrosubcorticogram during psychological testing even in those leads where inspection of the electrosubcorticogram alone showed no distinctive dynamics. Shifts in the electrosubcorticogram pattern of bioelectric activity were observed in different nuclear formations, within the limits of the whole spectrum of biopotentials. Moreover, depending on the initial background, very distinct differences in the electrosubcorticogram pattern could be seen during presentation of the test and during the response time. In the amygdala-putamen lead, for example, a significant increase in delta activity might take place during presentation of the test, whereas the alpha activity became dominant during the response. With other quantitative correlations between the changes in the electrosubcorticogram, the same picture, in principle, was seen in the hippocampal region. When a problem had to be solved mentally, without saying the answer aloud, the increase in beta activity could also be characteristic of the structures cited above. In the case of an incorrect solution, the theta activity became more pronounced in these same structures.

A statistical treatment of the electrosubcorticogram showed that although each specific pattern differed with the form of psychological test used (e.g., with the addition of an odd number of any initial number, with only even or odd answers being said aloud), the overall tendency of the changes in the electrosubcorticogram could reflect distinct differences, depending on the nature of the response, on whether it was said aloud or not. This is noteworthy in view of the relation between the nature of the changes in other physiological indices of the brain (Bechtereva and Trokhachev, 1966b) and the quality of the response, although naturally the differences may also be related to other phenomena, such as the nature of the physiological mechanisms which are the basis for the performance of different forms of the tests and the presence or absence of a motor component in the reaction.

As indicated above, the specific pattern of the changes in the electrosubcorticogram was not reproducible in subsequent tests. Repetition of the psychological test led, with great constancy, to changes in the electrosubcorticogram, which is easy to understand since there was always an element of novelty in the test to engage the patient's attention (this latter assumption in no way distinguishes the tests used from other human mental activities, of which so many, if not all, contain this element of novelty). Such regular development of changes has also been observed frequently in EEGs taken during psychological tests, with a direct lead from the brain and a suitable treatment of the data. This then assumes the status of a principle, and its physiological significance should then be considered.

Such a consideration seems advisable for a number of fundamental reasons. That the changes in the electrosubcorticogram, in this case, depend on the initial background is yet another confirmation of the fact that the bioelectric phenomena recorded in the EEG apparently not only (and not so much) reflect what is going on in the brain, but also serve to maintain a specific functional state of the brain and possibly control this functional state (as discussed above), establishing and then maintaining it at the level necessary for the performance of any given activity, though perhaps not on a strictly specific level (Bechtereva and Zontov, 1961). It is natural, given such a point of view, to consider the data obtained by statistical treatment of the changes in the electrosubcorticogram during the administration of a psychological test as reflecting a quantitative shift that characterizes the optimal function of the brain for that test.

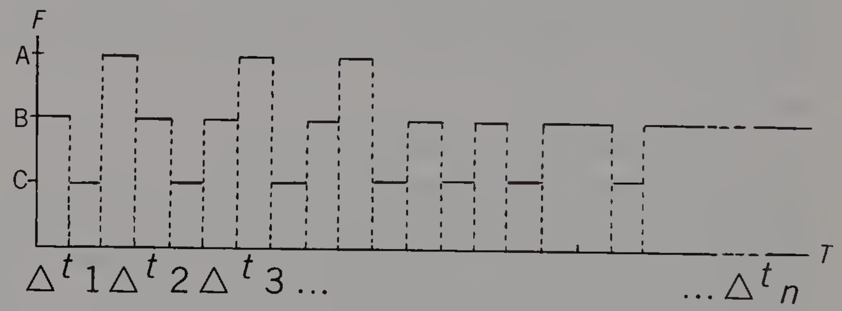
The interpretation presented above remains tentative, although very probable. A more detailed mathematical treatment of the electrosubcorticogram is essential, both for very different and for similar activities, and new methods of analyzing the electrosubcorticogram are needed to permit a comparison of the results of investigations on different patients, with a correction for the background electrosubcorticogram.

In a general way, however, this interpretation is not new, as it is another example of the familiar thesis that requires specific functional states of the central nervous system for different types of activity. Thus, if we consider the problem in terms of the development during mental activity of a specific functional state which is optimal for the activity in question under the given initial conditions and is reflected in the electrosubcorticogram, these concepts take on a familiar, or "acceptable," form.

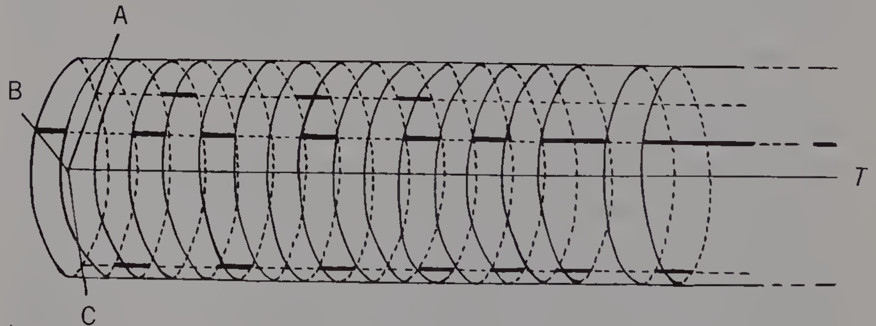
What will take place in the brain if another, new activity is necessary? It would be natural to answer that in this case the functional state of the brain (as reflected in the electrosubcorticogram) must change. Following this line of reasoning, there is scarcely any basis for objecting to the assumption that in any given minimal time interval, when the brain is attuned to one mental activity and many of its structures are involved in this activity, while others are ready to ensure that its development (and specifically this development!) proceeds, another complex mental activity is impossible. That is, only one complex mental activity can take place in the brain at one time. The phenomenon, known as far back as the days of Julius Caesar, of the simultaneous accomplishment of a number of activities is a real one, but this does not mean that all of these activities are performed simultaneously. At any given moment, only one of these activities is being carried out; their apparently simultaneous occurrence is accomplished by rapid switching from one activity to another with minimal loss of information. In the Pavlovian sense, this type of switching can apparently take place in persons with an active and powerful type of higher nervous activity. These concepts are illustrated in Fig. 7.

Levels of the functional state of the brain are shown in an arbitrary manner in Figure 7(a). These levels, in fact, represent integral quantities, the elements of which are the states of all of the brain structures participating in the activity (and probably of those ready to participate as well). Therefore, the levels A, B, and C can only be considered schematically in

Figure 7. Diagram illustrating the dynamics of change in functional states of the brain optimal for different forms of activity. (a) Process represented in a two-dimensional coordinate system; (b) process represented in a cylindrical system. A, B, and C, different activities. Horizontal axes, the dynamics of the processes in time; vertical axes (a) and the surface of the cylinder (b) arbitrarily represent the levels of the functional state of the brain.



(a)



(b)

the form represented on the vertical axis. In this schematic presentation, time is represented by one of the ordinates and the activity related to the state is represented by the others. An attempt to represent this situation diagrammatically in a form less far removed from reality is made in Fig. 7(b).

The assumptions stated above concerning the simultaneity of one activity with another can easily be verified by anyone under the condition that one of the activities being carried out takes place in connection with events developing objectively, independently of the subject, and that the constancy of the relationship between the subject and these events can later be checked by himself or by any other person. Examples of this type of activity, which is rigidly "tied" to events developing outside the subject, might be the brain activity arising in connection with viewing a film or listening to a radio broadcast.

In the interests of motor road builders, and not for the purpose of studying the principles of the physiological maintenance of mental activity, the following experiment was carried out some years ago in England: at a specific time, when an interesting program was being broadcast over the radio, the reactions of drivers along one of the difficult sections of the road were checked. The overwhelming majority of the drivers were convinced that their attention had not been distracted from listening to the text even for one second. However, all those who correctly solved the road problems, which could not be solved by automatic reactions, had completely "lost" portions of the text coming over the radio during those moments. Those who did not prove fully adequate in a difficult road situation were able to reproduce significantly more of the text. (These findings were communicated to me in 1967 in Bristol by Gray Walter, Ray Cooper and others during a discussion of the question of simultaneous performance of different mental activities.) This experiment evidently indicates the danger of listening to interesting radio programs while driving a car; it also illustrates one of the special characteristics of the performance of mental activity by the brain.

But how can we explain the fact that an interrupted (objectively interrupted) mental activity may be perceived subjectively as uninterrupted? An understanding of this phenomenon can probably be derived from statements by the mathematician Kolmogorov (1969) concerning the discreteness of thought. A thought that is initially always discrete, interpreted subjectively as a continuous process, is a fundamental prerequisite for such a subjective evaluation during the alternating performance of two or more activities. (The idea of the discreteness of mental processes is supported indirectly by Stevens' findings (1968) on the discreteness of the release of neural mediators.) Although the possibility of the simultaneous occurrence of many activities is being investigated, (Gomes, 1966), such investigations do not exclude the possibility of the occurrence of only one complex activity at one time; and their methods are not comparable to ours.

An investigation of the dynamics of other indices of the brain's vital activity has also confirmed that changes occur in the functional state of different brain structures during mental activity; changes in the levels of slow electrical processes, available oxygen, and impulse activity have been detected. An understanding of the overall changes in the brain was furthered by these data; on the whole, however, the basic data for determining the functional state of the brain during mental activity were obtained by the electrosubcorticogram in a more dynamic manner than by slow electrical processes and available oxygen indices. A further analysis of the dynamics of impulse activity, itself a dynamic indicator, may prove extremely fruitful in evaluating the nature of the overall changes in the brain.

Investigations in which EEGs were recorded from the cranial skin and directly from the brain during simple (conditioned reactions) and more complex (psychological tests) measures of the conditioned reflex activity complemented each other. The spectrum of these investigations elucidated certain neurophysiological aspects of mental activity under extremely simple model conditions and under increasingly more complex study conditions. Many of the conclusions drawn from the physiological analysis of the simpler mental phenomena may also be related to the more complex phenomena. At the same time, the increased complexity of the study conditions and the collection of valuable physiological data by recording biopotentials directly from the brain have made it possible to go beyond a consideration of only the most general aspects of the problem.

This line of investigation has established the EEG as an acceptable, and apparently adequate neurophysiological parameter to indicate the overall changes in the brain, which develop more or less as a mosaic, depending on the initial background and the activity being carried out. At the present stage of our investigation, and this is especially the case regarding the non-reproducibility of the polymorphic EEG pattern obtained with a direct lead during repetition of psychological tests, we must recommend maximum caution in drawing conclusions about the structural-functional organization of the activity studied by EEG. Mathematical analyses, which at first often confirm the occurrence of local changes in the brain, have as a rule, when the investigations were continued, reliably demonstrated the involvement of these local changes in general rearrangements and thus have also underlined the value of the EEG in the study of neurophysiological background.

The functional background of the brain is partially a manifestation of general homeostasis, in which the "constancy" of the internal environment of the organism, which varies within relatively narrow limits, is the basis for carrying out all behavioral reactions–from those ensuring the existence of the species to the most complex mental reactions related to man's individual life in a social environment.

The Cerebral Maintenance of Mental Activity

Principles of the Investigation of Elements of the System of Cerebral Maintenance of Mental Activity

Observation of the dynamics of the manifestations of spontaneous and assigned activity of the organism during local electrical stimulation of the brain has long been a method for the experimental study of subtle structural-functional relationships of the brain. By such observations, the central control of different functions has been studied and attempts have been made to elucidate the cerebral control of emotional reactions in animals under acute and chronic experimental conditions as well as, with improved biotelemetry in recent years, under normal conditions.

Local electrical stimulation of the human brain is used in neurosurgical practice mainly to define more exactly epileptogenic foci and regions of assumed disturbances in hyperkinesis. It is also used in prolonged observation of patients undergoing treatment, by means of multiple implanted electrodes. The data obtained during local electrical stimulation of the human brain have added greater detail and depth to the data obtained by analyzing disturbances of higher mental function in patients with pathological foci. Electrical stimulation of the brain has made it possible to obtain a large amount of information on the structures involved in the cerebral organization of emotional control.

It is well known that the findings of Olds and Milner (1954, 1966) for many years remained only an extremely interesting collection of data, which interpretation was, at best, hypothetical. An understanding of the subjective significance of "zones of punishment," "zones of encouragement," and so on, became possible only when emotional reactions could be observed during stimulation of the human brain; these reactions included those accompanied by the development of an "inclination" for the reception of repeated stimuli (Smirnov, 1967), which sometimes served as a basis for complex behavioral changes (Bechtereva, Grachev, Orlova, and Yatsuk, 1963; Smirnov, 1967).

The development of emotional reactions during electrical stimulation of the deep structures of the human brain has been described by Heath (1954, 1963); Peacock (1954); Monroe and Heath (1954); King et al. (1954); Heath and Mickle (1960); Sem-Jacobsen and Torkilden (1960); Angeleri, Ferro-Milone, and Parigi (1961); Spiegel and Wycis (1961); Delgado (1963, 1970); Delgado and Hamlin (1962); Sem-Jacobsen (1964, 1968); Bechtereva, Grachev, Orlova, and Yatsuk (1963); Van Buren (1963); Smirnov (1963–1969); Walter, Chapman, Porter, Crandal, and Rand (1964); Chapman (1966); and Umbach (1966). In a review, Sem-Jacobsen (1968) divided these changes in emotional state into nine types:

1. The patient is calm and has a feeling of "well-being." Moreover, he may be somewhat drowsy—a positive reaction of degree I.

2. The patient's state is distinctly altered. He is in a good mood, with a feeling of well-being. He is calm, satisfied with himself, and smiles frequently. Moreover, a slight euphoria is observed, but his behavior remains within normal limits. He wants a repetition of the stimulation—a positive reaction of degree II.

3. The euphoria has clearly gone beyond normal limits. The patient laughs loudly and is quite satisfied with himself. He

likes the stimulation very much and wants it repeated—a positive reaction of degree III.

4. The patient becomes restless, tense, or sad—a negative reaction of degree I.

5. The patient is irritable and may be depressed. He feels unhappy and is uncomfortable—a negative reaction of degree II.

6. The patient is depressed, irritable, or even angry. He is afraid and sometimes is offended; he sometimes cries—a negative reaction of degree III.

7. Sudden emotional outbursts of a positive or negative type occur.

8. The patient is ambivalent, sometimes liking the stimulation and sometimes disliking it.

9. In a reaction of an orgasmic type, with corresponding changes in mood, the patient initially reacts positively to the stimulation, and then suddenly is satisfied. This satisfaction is so complete that he refuses stimulation for a while. Continuation of the stimulation during this period is definitely unpleasant.

Sem-Jacobsen emphasizes the necessity of also analyzing behavioral reactions, since the patient's verbal response is far from reliable in all cases. A strong desire for repeated stimulation was considered particularly important.

The emotional reactions observed under these conditions have been studied in systematic detail by Smirnov in our laboratory. On the basis of his observations, it has already proved possible to construct model charts of the structural-functional organization of emotional control in humans (Fig. 8).

Analysis of the results of these investigations has shown that emotional reactions develop during electrical stimulation of specific brain structures when there is a basis for assuming that a shift in the constant potential of the stimulated region (frequent electrical stimulation, polarization) has occurred. This was confirmed by direct measurements of the constant potential of the brain after such electrical stimulation (Abramov, 1965).

In complete agreement with Sem-Jacobsen's findings, Smir-

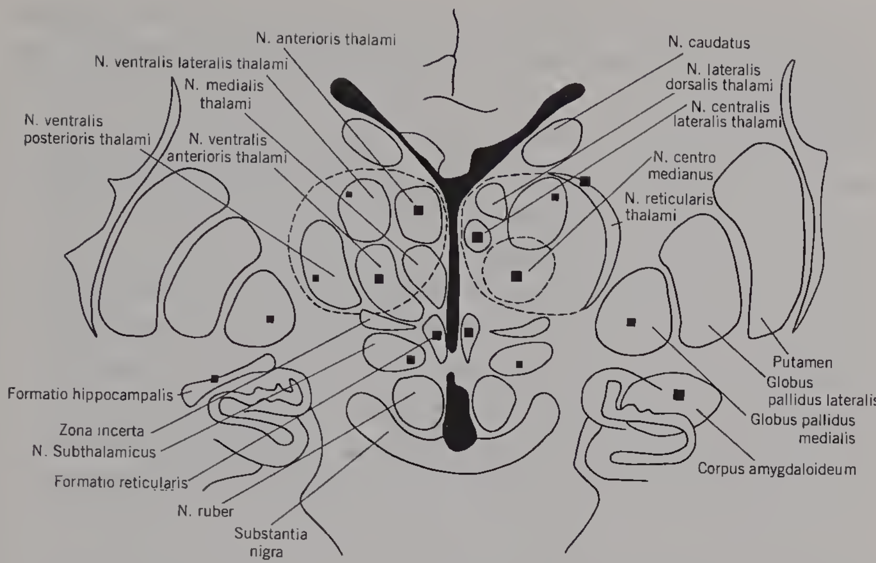


Figure 8. Diagram of the brain. Black squares, zones in which stimulation produced emotional reactions: Larger squares, regions in which stimulation produced emotional reactions of greater intensity and greater constancy; smaller squares, regions in which stimulation produced less distinct and less constant emotional reactions.

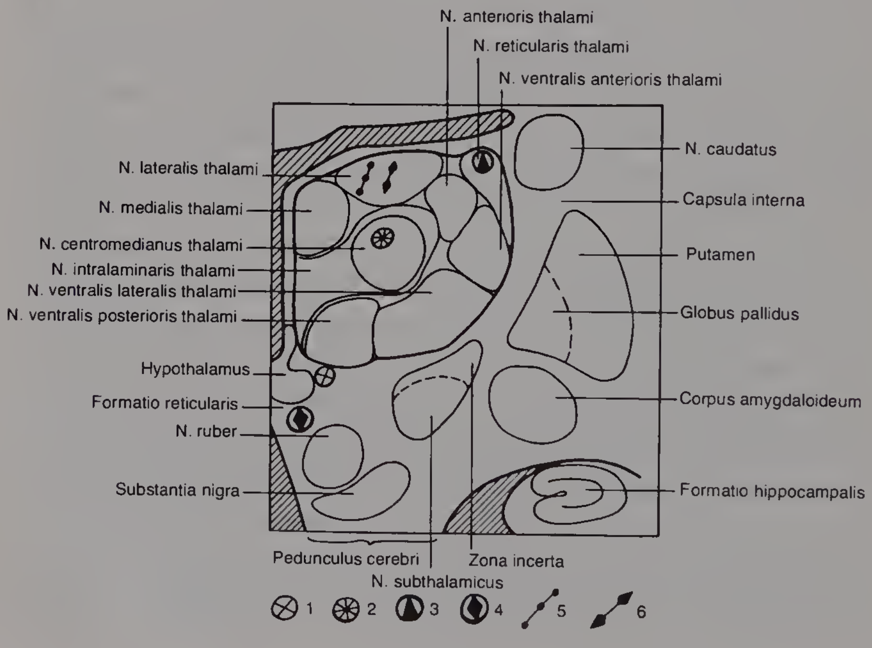
nov (1970) and others noted that different emotional reactions appeared during stimulation of the deep structures, with more or less stable behavioral reactions developing in individual cases. The accumulation of data on symptoms correlated with stimulation of the deep structures of the brain (Smirnov) has made possible the suppression of emotional states that arise in the course of diagnostic procedures involving stimulation through implanted electrodes. Thus, for example, a feeling of fear arising during electrical stimulation of the zone at the boundary between the ventromedial thalamus and the rostral brain stem led to the development of a stable phobia. The phobia was completely dispelled by subsequent stimulation of a zone in the region of the centrum medianum of the thalamus. The development of this phobia may be regarded as the appearance of a stable pathological state (Bechtereva and

 Bondarchuk, 1968), which can be rapidly overcome by disrupting the function of the brain system that mediated its appearance.

By stimulating the deep structures of the brain, it is also possible to disrupt the systems that mediate the behavioral/emotional reactions arising in "natural pathology." Thus, therapeutic electrical stimulation in the region of the pulvinar thalami caused the fragmentation, "fading," and subsequent disappearance of a phantom-limb syndrome that a patient had suffered for several decades (Smirnov, cited by Bechtereva, Bondarchuk, Melyucheva, and Smirnov, 1972) (Fig. 9).

Electrical stimulation of a number of subcortical structures—the centrum medianum, anterior ventral nucleus, reticular nu-

Figure 9. Schematic representation of the subcortical structures in which electrostimulation produced stable emotional reactions or disrupted the function of the systems producing behavioral reactions. 1, appearance of a phobia during electrostimulation; 2, disappearance of the phobia; 3, appearance of obsessive laughter; 4, elimination of obsessive laughter; 5, disappearance of phantom limb and defragmentation of the phantom; 6, extinction of the phantom.



cleus of the thalamus, subthalamic region, fornix cerebri, mesial globus pallidus, and other formations—has produced results which the investigators evaluated as changes in the level of wakefulness and changes in consciousness (Jung, 1954; Hassler, 1961; Umbach, 1961; Smirnov, 1967; Bondarchuk and Smirnov, 1969). Following these observations it was possible to demonstrate that stimulation of some subcortical structures (elements of the nucleus caudatus—Van Buren, 1963; Bechtereva, Moiseeva, Orlova, and Smirnov, 1964, 1966; and the centrum medianum of the thalamus—Smirnov, 1967; Bondarchuk and Smirnov, 1969) often reduced the ability to perform some forms of intellectual activity. Thus, stimulation of the nucleus caudatus, as observed by Van Buren, caused inhibition of speech, difficulties in perception, and even clouding of consciousness. Stimulation of the nucleus caudatus, and of some structures of the anterior nuclear group of the thalamus, can also increase the number of errors in the performance of psychological tests (Bechtereva et al., 1964). On the other hand, depressing electrical activity (by frequent electrical stimulation, polarization) in the region of the centrum medianum, and also in the ventrolateral nucleus, can raise the threshold for distinguishing between pictures with different characteristics which could be distinguished statistically (Gorelik, Smirnov, and Tonkonogy, 1969). Smirnov has described different degrees of this increase in the "level of wakefulness" during electrical stimulation of deep structures —right up to the development of a transient hypomania.

Changes in speech during electrical stimulation have been observed as one of the elements in a change in the level of wakefulness. During electrical stimulation of deep structures (different thalamic nuclei, the mesencephalic brain stem, the nucleus caudatus, and other formations), such phenomena as cessation, retardation, and acceleration of speech, changes in voice characteristics, or aphasia have also been observed (Sem-Jacobsen, 1965, 1968; Ojemann et al., 1968b; Smirnov and Shandurina, 1969; Delgado, 1970). Stimulation of the deep structures of the left hemisphere in Sem-Jacobsen's studies also elicited agraphia (disturbances in writing).

Sem-Jacobsen (1968) produced vocalization by stimulating a region located 1.5 cm from the median line, near the frontal corpus callosum.

Penfield related activation of memory he observed during stimulation of the supralateral temporal lobe to involvement of the hippocampus in the reaction. This relation was confirmed by Gray Walter and Crow (1964), who observed that reproduction of pictures from an earlier experiment occurred during stimulation of the amygdala and the hippocampus. Studies by Mahl and Delgado (cited by Sperry, 1966) demonstrated that these induced experiences may be modified by changes in the external environment. Despite the fact that a relationship between the phenomena observed—or, at least, the ease with which they appear—and a morbid brain state cannot be excluded, it is difficult to dispute the fact that, whether they derive from the normal potential of the cortex or from a morbid state, these phenomena seem to involve cerebral mechanisms of memory. Significant disturbances in short-term verbal memory during stimulation of the lateral thalamus, the parietal and temporal regions, and the nucleus posterior thalami on the left side were observed by Ojemann and Fedio (1968).

A great deal of information has accumulated on both the activation and the depression of memory during stimulation of subcortical structures. Gerard (1961), Sem-Jacobsen (1965), Brazier (1966), Chapman (1966), and Smirnov (1968) have demonstrated that electrical stimulation of the tegmentum of the mesencephalon, certain nuclei of the thalamus, the medial basal temporal lobe, and other formations may produce a more or less prolonged amnesia.

By stimulating deep structures of the brain, Sem-Jacobsen (1968) elicited two types of reactions described by Penfield: a reproduction of pictures of the past and a sudden "transport to the past." These phenomena thus acquired a more general significance since in this case they cannot be attributed to an epileptic aura—Sem-Jacobsen's subjects were parkinsonian patients.

Many psychopathological phenomena can also be observed during electrical stimulation of deep structures of the brain. Illusions, hallucinations, delirium, aggressive reactions, outbursts or rage, and phenomena of the *déjà-vu* type have all been reported during stimulation and polarization of such structures (Umbach, 1961; Chapman, 1966; Jasper and Rasmussen, 1958; Smirnov, 1967; Delgado, 1970; and others).

The results of therapeutic electrical stimulation of deep brain structures presented above are impossible to understand without taking into account the role of memory in the development and maintenance of stable pathological states and in the modulation of both short-term and long-term memory during the stimulation of deep structures. The disappearance of phobias, phantom-limb syndromes, and other states apparently occurs through an effect of stimulation on long-term memory, primarily.

Smirnov (1967) and Smirnov and Shandurina (1969) directed special attention to disorders of the body image during stimulation of subcortical nuclei. The temporary disorders of the body image that were observed, such as certain illusions, apparently could be best understood as temporary disturbances in the functional state of "error detecting mechanisms."

Of great interest are the data presented by Albe-Fessard (1954); Spiegel, Wycis, Orchinick, and Freed (1956); Penfield (1958); Chapman (1958); Bickford, Mulder, Dodge, Svien, and Rome (1958); and Smirnov (1969), whose results can be interpreted as a change in and disturbance of the "time scale" during electrical stimulation of the brain. Such a disturbance in the time scale was manifested most frequently by the development of a more or less prolonged disorientation in time, but an abrupt acceleration and retardation of different activities were also observed. This was demonstrated very graphically in the form of an acceleration in speaking aloud series of numbers during stimulation of the medial basal temporal lobe (observation by Smirnov; see Bechtereva, Bondarchuk, and Smirnov, 1969) and by an acceleration of speech during stimulation of the frontal lobe (Sem-Jacobsen, 1968).

These data illustrate the cerebral control of mental functions, including the development of phenomena in time. They also indicate that the brain may maintain not one but many different time scales.

The possibility that the brain may operate in different time systems, and that mental phenomena may proceed within a time system different from the everyday one, is demonstrated not only by the observations presented here, which, although objective, are still isolated nor by the subjectively known capability of our memory in complex life "stress" situations to "run through" short segments of time in retracting a long journey nor finally by similar phenomena in dreams. The last two instances can always be criticized on the grounds of the selective, fragmentary nature of memory in such cases and the use of traces representing not a complete chain of events but a chain of representative "sections," so that the mental operation could correspond with the usual time scale.

A more convincing possibility of transition to other time systems is represented by the exceptional ability of some individuals to multiply in their heads multiple-digit (six-digit!) numbers, to extract square roots of nine-digit numbers, etc., within minutes or even seconds. In cases where this is in no way connected with skillful charlatanism, it lends itself to only one explanation—that the calculation is carried out in accordance with the usual laws of mathematical operations, but within a different time system. Numerous eyewitness reports, including those of medical specialists, indicating that Arago (18 ? –1949), who was well known for such abilities, became tired after short (half-hour) sessions of such calculations, provide some evidence for the assumption that during these moments not only the brain structure providing for the calculations, but the whole brain and perhaps the whole organism, were experiencing a different time scale. The calculations involved in these numerical operations show that "Arago's half-hour" was, at peak performance, equivalent to many hours of continuous ordinary work.

An ability of this kind to "go beyond the framework of the ordinary time scale," seems to be real and to carry a biological danger, when the whole brain or organism is involved in an accelerated (or a retarded) program, so that evidently the ability is usually firmly restrained. Its disinhibition is possible by electrical stimulation of the brain and also probably by pharmacological means. Of interest in the solution of this problem is the possibility of accelerating time in one or two functional systems episodically. When the problem is approached intelligently, this may not prove as dangerous as an overall acceleration or retardation of the brain's reading of time during life under ordinary conditions. (It is understood that overall acceleration may lead to rapid wear, in particular, of particular low-stability systems, and that retardation may sharply lower the social adaptability of a human being.)

The data presented (and many analogous data) confirm the very important role of subcortical structures in the maintenance of normal emotional and mental reactions and the significance of changes in these reactions in different types of mental disturbances, a role already emphasized in those works based on data from cases of focal injuries to the brain (Nielsen, 1958; Roberts, 1958; and others).

With regard to studying the brain mechanisms of emotional and mental reactions, electrical stimulation of the brain has produced (1) a relatively large, though hardly complete, body of data on the areas of the brain related to the central control of emotions; (2) evidence of the presence in the brain of structures that change the potential for the performance of mental activity; and (3) some very interesting observations of different mental phenomena and their variability. This last type of information, however, is still available only as individual observations rather than data of the type from which even very approximate maps of the cerebral control of mental functions could be constructed.

On the whole, however, data obtained by electrical stimulation of the brain have substantially broadened our concepts of the structural-functional organization of the brain. These data have served as a basis for significantly more precise investigations in which the neurodynamics of the brain have been evaluated during the performance of appropriate types of activity.

In more recent electrical stimulation studies of the central mechanisms of emotional and more differentiated mental reactions, much more has been learned about the mechanisms of emotional control. However, it appears that the more complex the mental activity, the less the amount of data on its organization obtained during electrical stimulation of the brain locally.

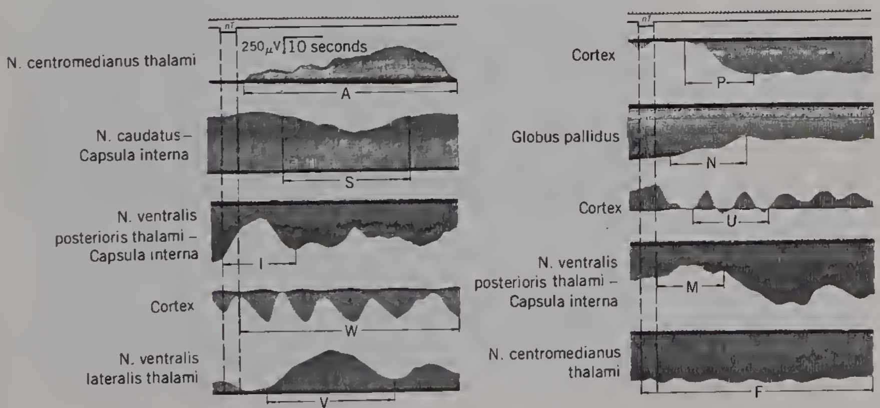
The study of the structures, the "points" of the brain most closely related to the performance of mental functions, along with continuing studies of the cerebral control of emotional and mental reactions, led to possible methods for investigating neurophysiological indices during repeated performances of psychological tests (including emotion-producing tests). Because of the special characteristics of the electrosubcorticogram and the current lack of methods for analyzing reactions in which the initial background can be corrected for, and thus the impossibility of obtaining comparable results, data on the dynamics of the slow electrical processes (SEP or the so-called steady potential), on the available oxygen (O_2a), and on the impulse activity (IA) were used in this investigation. Multi-channel recordings of these indices offered special possibilities. These investigations showed that the SEP and O_2a indices are very useful in tracing the development of emotional states (Smirnov, 1967; Grechin and Smirnov, 1967). An analysis of the SEP and O_2a values obtained during emotion-producing tests (the reproduction of emotion-producing situations by means of emotion-producing words, questions, the presentation of Rorschach cards, etc.) showed two fundamental types of changes.

First, certain changes developed 0.3 second after termination of the stimulus and lasted about 10 to 15 seconds. They were characterized by a change in the pattern of the variations of the SEP observed during calm wakefulness and sometimes by a moderate shift in the SEP level. These changes were not intrinsically related to the development of an emotional state, but rather reflected an activation of attention preceding the development of emotions. They were observed primarily in the nonspecific nuclei of the thalamus (anterior and medial nuclei, centrum medianum), in the amygdala and hippocampus, and less distinctly, in the ventrolateral nucleus, the globus pallidus, the nucleus ruber, and in some areas of the cortex. When no emotions developed, these changes disappeared. But when strong emotions developed, the second type of change appeared; here, in the majority of cases, the direction of the shift in the SEP could be "correlated" with the emotional coloring of the reaction: a positive shift in the SEP was observed during negative emotions and a negative shift during positive emotions, although in a number of structures, negative emotions were accompanied by a negative shift in the SEP. These shifts proved to be most distinct in the nonspecific nuclei of the thalamus (anterior and medial nuclei, centrum medianum), certain parts of the ventrolateral nucleus, the subthalamic region, hippocampus, amygdala, globus pallidus, nucleus caudatus, and cellular formations of the brain pedicles, and in some areas of the cortex (Smirnov and Speransky, 1970).

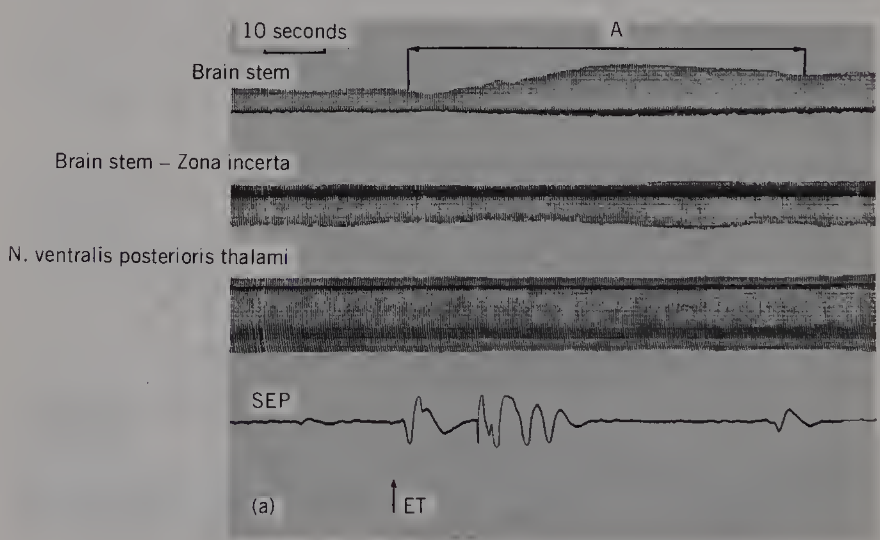
The dynamic changes in the SEP during emotion-producing tests could not always be reproduced. When repeated, a test might lose its effectiveness, and presentations of different emotion-producing tests could produce results that were not entirely comparable. In these investigations one can usually speak of reproducibility of the results in principle, based on the level of the shifts in the SEP and their direction.

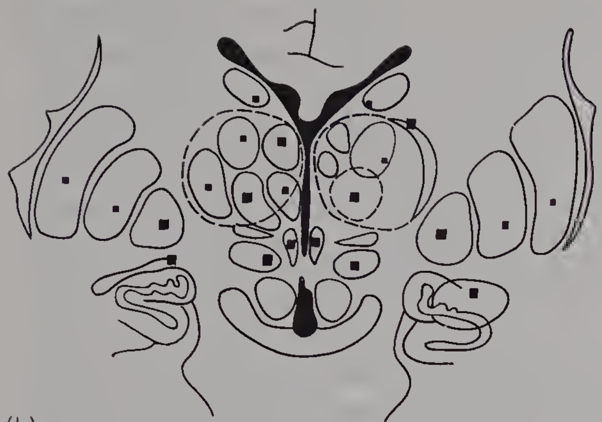
However, an analysis of data obtained over many years of observations on slow electrical processes, and their form and amplitude, enabled Smirnov and Speransky (1970) to create an original "alphabet of emotions" from the dynamics of the SEP (Fig. 10).

Figure 10. Typical components of SEP responses during psychological tests activating attention and emotional behavior. High-amplitude complex components of the wave: A, application wave; S, sellar wave; I, I-wave; W, W-wave; V, V-wave. High-amplitude, non-complex components of the shift: P, positive; N, negative shift in the SEP. Low-amplitude, non-complex components: U, undulation waves; M, monotonic waves (fluctuations); F, background activity.



Shifts in the SEP during emotion-producing tests are of special interest when they are compared with the emotional reactions developing during a shift in the SEP in the brain caused by external electrical stimulation. Recordings of the physiological indices during emotion-producing tests provided more complete data on the brain structures related to the development of an emotional reaction. The zone of the greatest shifts in the SEP during emotion-producing tests coincided with the region in which an electrical stimulation elicited the development of an emotional reaction. Thus the method of electrical stimulation used, and studies of the physiological indices of the brain, made it possible to obtain consistent data for a structural-functional outline of emotional reactions (Fig. 11). An analysis of the direction of the shifts in the SEP during emotional reactions in brain structures participating in these reactions (thalamus, temporal limbic system, etc.) provided the basis for reevaluating an emotionally neutral state as corresponding to an average physiological state of these formations, characterized by a specific level and fluctuating within narrow limits. Measurements of O_2a during emotion-producing tests (Grechin and Smirnov, 1967) also made possible the detection of distinct changes in the level and sometimes the dynamics of the oxygen requirement by the subcortical structures, with not only the general characteristics fundamental to





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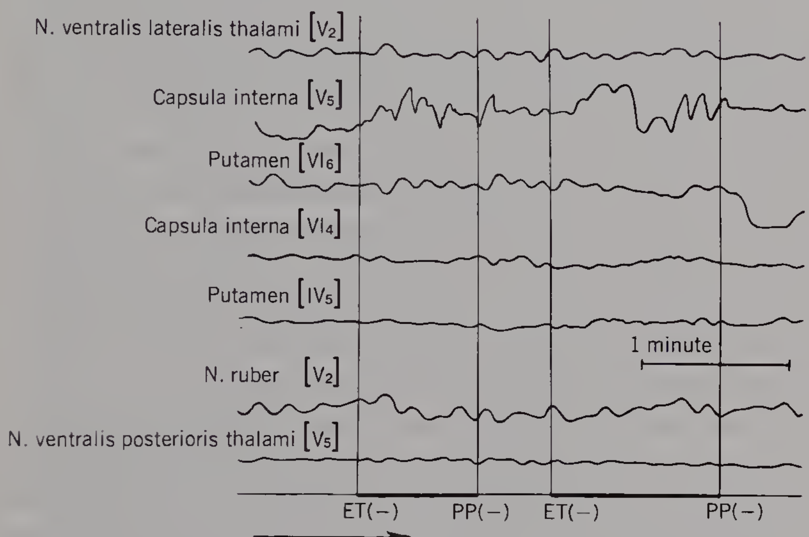


(c)

Figure 11. Investigation of the emotion-producing zones of the brain. (a) Change in the slow electrical processes during emotion-producing tests; ET, emotional test. (b) Diagram of the brain. Black squares, zones in which changes in the slow electrical processes were observed during emotion-producing tests: Larger squares, regions in which changes in the slow electrical processes were observed with greater intensity and higher frequency; smaller squares, regions in which changes in the slow electrical processes were observed with less intensity and lower frequency; structures, see Fig. 8. (c) Dynamics of the available oxygen during emotion-producing tests. Roman numerals, clusters of electrodes; Arabic numerals, the number of electrodes in each cluster, respectively.

these shifts but also the characteristics related to the region of the lead being specified. Thus, the appearance of "sinusoidal" vibrations or less frequently, aperiodic, multi-phase vibrations of relatively short duration, and most frequently, of a consistent pattern during negative and positive emotions, was characteristic of the ventral, posterolateral, and ventrolateral nuclei of the thalamus. Changes in O_2a in the dorsomesial nucleus were observed with a longer latent period and only in the most meaningful emotion-producing tests.

Changes in O_2a in the thalamic nuclei were observed when the tests were repeated. But in the nucleus ruber, the substantia nigra, and the tegmentum, the reactions during repetition of the tests became less distinct in a number of cases. A difference in the direction of shifts in O_2a or their dynamics (pattern), depending on the sign of the emotional reaction, was noted in the tegmentum, hippocampus, amygdala, and the nucleus caudatus.

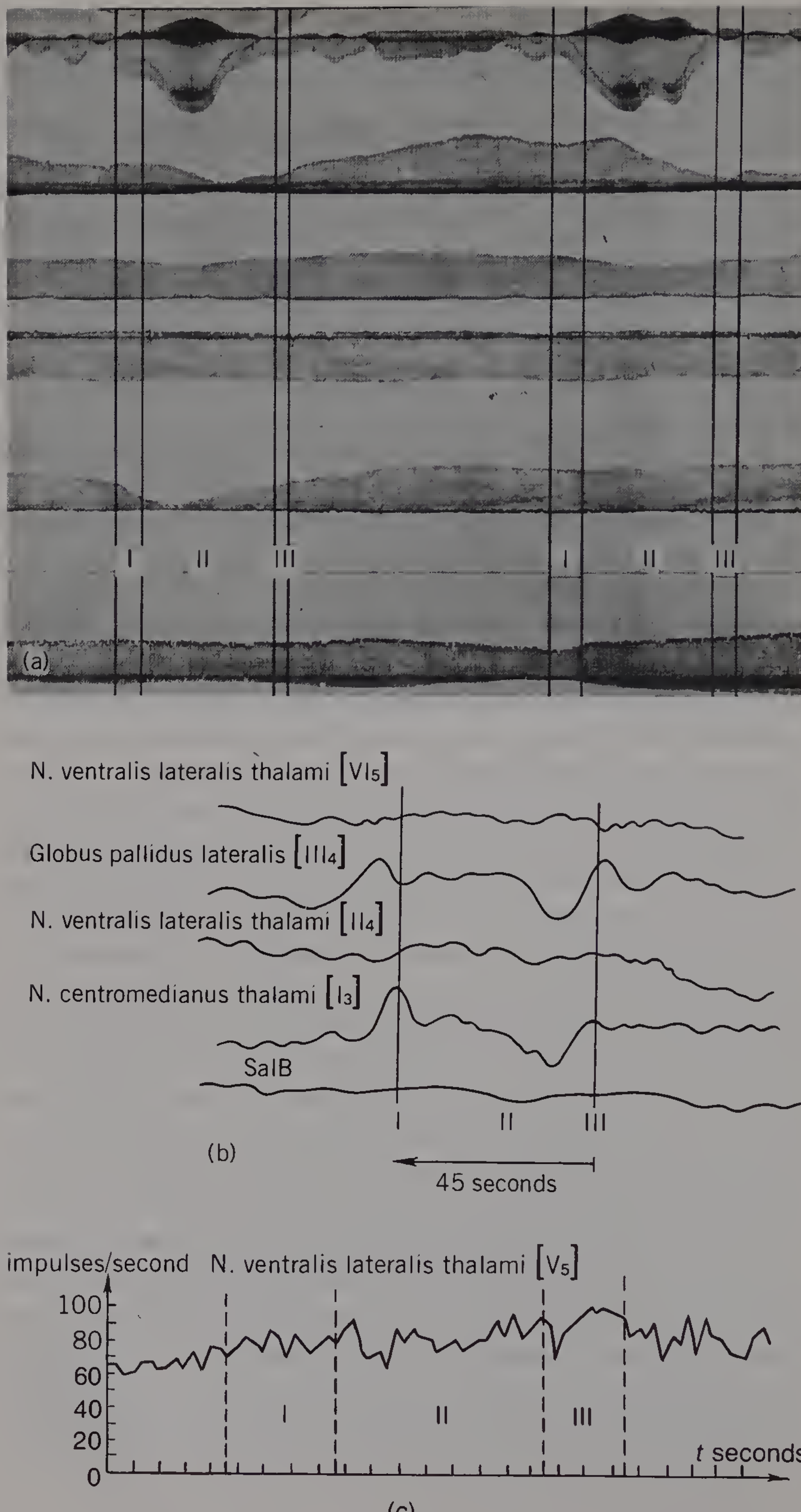
The neurophysiological mechanisms underlying these changes in the brain, like the mechanisms by which emotional reactions develop in response to changes in the external and internal environments of the organism, are evidently best understood when the polyfunctionality of the neuronal populations, and, hence, the large number of "afferent drives" to different subcortical structures, is taken into account.

Variations in the SEP and O_2a during testing with the Binet and other types of psychological tests could almost always be investigated by a superimposition of sections of the curves, that is, by studying the reproducibility of the reactions. The comparability of the data on impulse activity was analyzed on the basis of integrator functions (Matveev, 1971), after a preliminary calculation and correlation of the frequency of the impulses in different phases of the test with the background (Bechtereva and Trokhachev, 1967) and also on the basis of graphs constructed by computer analysis (Orlov) of the number of impulses during specific time intervals (0.3, 0.9, 1 second, etc.) and other more complex analyzes of these processes. The treatment of data of this type is at present being done with an analog-digital computer.

The use of tests for operative memory had the fundamental advantage that tests of basically the same type could be repeated several times during a particular investigation, with the conditions of observation arbitrarily varied. More or less significant deviations of the physiological indices from their initial state were noted in various deep structures (and at the cortical points studied). Recordings of the SEP, O_2a, and IA during repeated performances of the psychological tests showed that the dynamics of these indices at many points in the brain were reproduced very closely, and sometimes almost exactly.

The reproducibility of these dynamics under specific conditions was considered to confirm the relation between the brain formations in question and the mental activity studied. For the sake of convenience in describing the structural-functional relationships detected, during the performance of emotion-producing tests, for instance, one must generally speak of the anatomical formations in which these physiological indices could be reproduced. This reproducibility was observed in different nuclei of the thalamus and in the globus pallidus, the nucleus caudatus, the hippocampus, and a number of other structures (Fig. 12). However, it must be emphasized that such reproducibility was almost never observed throughout the structure as a whole, but was detected only at one, or less frequently at several, of its points. At the same time, it is precisely investigations at this level that have confirmed the polyfunctionality not only of the brain formations ("nuclei") investigated but also of the cell populations. As in the case of electrical stimulation (not to speak of focal pathological processes!), in recording the dynamics of the physiological indices, it was found that many cell populations have more than one function and hence may respond with a reproducible pattern to not only one but several stimuli. That is, these cell groups could be associated, for example, with both mental and motor activity. Moreover, the "sets" of functions, associated with individual points of the brain varied. Characteristic reactions of impulse activity from the centrum medianum of the thalamus were detected, for example, in response to psychological tests, to bending the arms at the elbows, and so on (Fig. 13).

The polyfunctionality of brain cell populations, noted in



(a)
I
II
III
I
II
III
N. ventralis lateralis thalami [VI5]
Globus pallidus lateralis [III4]
N. ventralis lateralis thalami [II4]
N. centromedianus thalami [I3]
SalB
I
II
III
(b)
45 seconds
impulses/second
N. ventralis lateralis thalami [V5]
100
80
60
40
20
0
I
II
III
t seconds
(c)

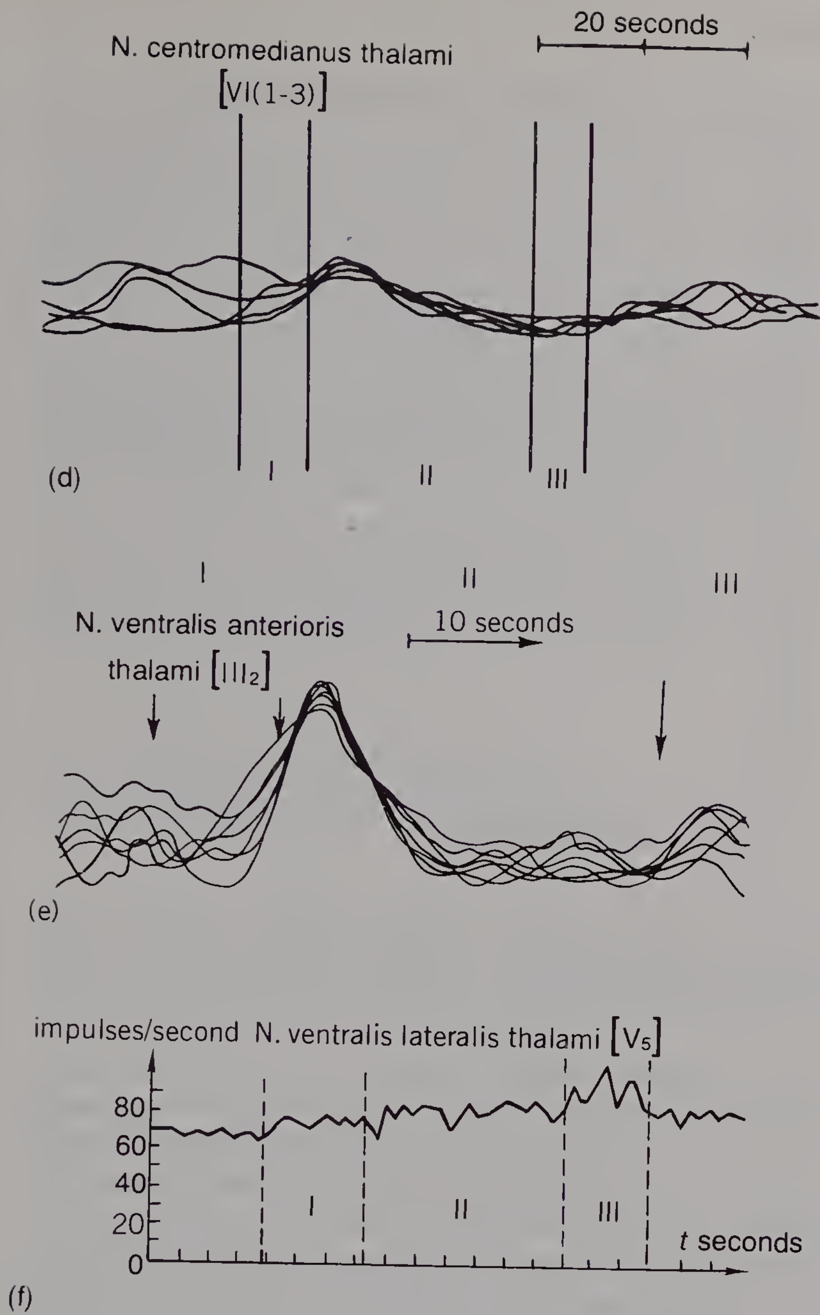


Figure 12. Changes in the slow electrical activity. (a) Available oxygen; (b) impulse activity; (c) test for operative memory. I, presentation of test; II, retention in memory; III, response. *Left:* Data from one test. *Right:* (d) and (e) Superimposition of the data from several tests; (f) averaging of six tests. Roman numerals and Arabic numerals, number of clusters and number of electrodes in each cluster, respectively.

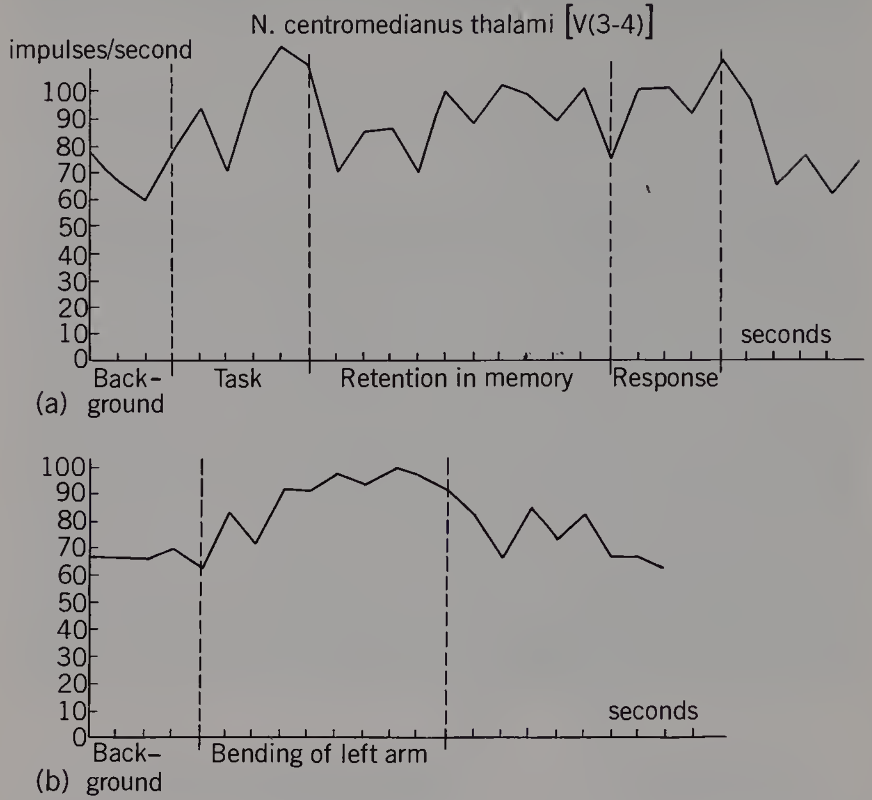


Figure 13. Dynamics of the impulse activity in the region of the N. centromedianus thalami (a) during a test for operative memory and (b) during a motor test.

papers by Luriya (1962) and many others, is a prerequisite for optimal interaction of the organism with its environment.

A precise investigation, recording many indices of the vital activity of the brain and using various functional tests, indicates that the brain is organized according to principles that fall between the two most extreme views: the concept of centers of functions and the concept of the equivalence of different areas of the brain.

A very large number of "points" in the most diverse brain formations are involved in the performance of complex mental functions, but these "points" do not have the same functional characteristics. A multiple-link organization of a system of initially polyfunctional links gives the system both reliability and adequacy in its operation. By maintaining the mental activity of the healthy organism in a stable normal state, this system ensures that the most complex tasks can be performed.

And at the same time, it is precisely the multiple-link, complex nature of this system, that may determine the complexity of the reaction elicited by a number of pathological processes and characterized by the development of a stable pathological state (Bechtereva and Bondarchuk, 1968). In this case, the whole range of reactions that maintain the stable state is reversed to produce and maintain a stable pathological state. Compensatory reactions, mediated by the large number of links of any regulatory system in the central nervous system—which is very important in maintaining a stable state of health—may also act adversely, although only in part, during the development of a chronic disease or during the shift from a stable normal state to a stable pathological state.

The Physiological Significance and Special Characteristics of the Links in the System for Cerebral Maintenance of Mental Functions

The role of the different brain formations of the system that maintains mental activity must be studied in order to understand the principles and specific mechanisms underlying the performance of mental activity in the organism's changing external environment and the internal environment of the brain. Study is also necessary to understand how the mechanisms that maintain mental activity are optimized.

The role of the external environment was investigated as follows: psychological tests were presented under conditions that limited stimuli (other than the basic stimulus) when the subject's eyes were closed, when his eyes were open and the illumination moderate, and against the background of "noise"—non-rhythmic, random, or "trigger" photostimulation (Bechtereva, 1965).

The reproducibility of the pattern of indices measured at rest at some "points" in the brain was lost against a background of noise. On the other hand, against this background, reproducible patterns appeared at points in the brain where

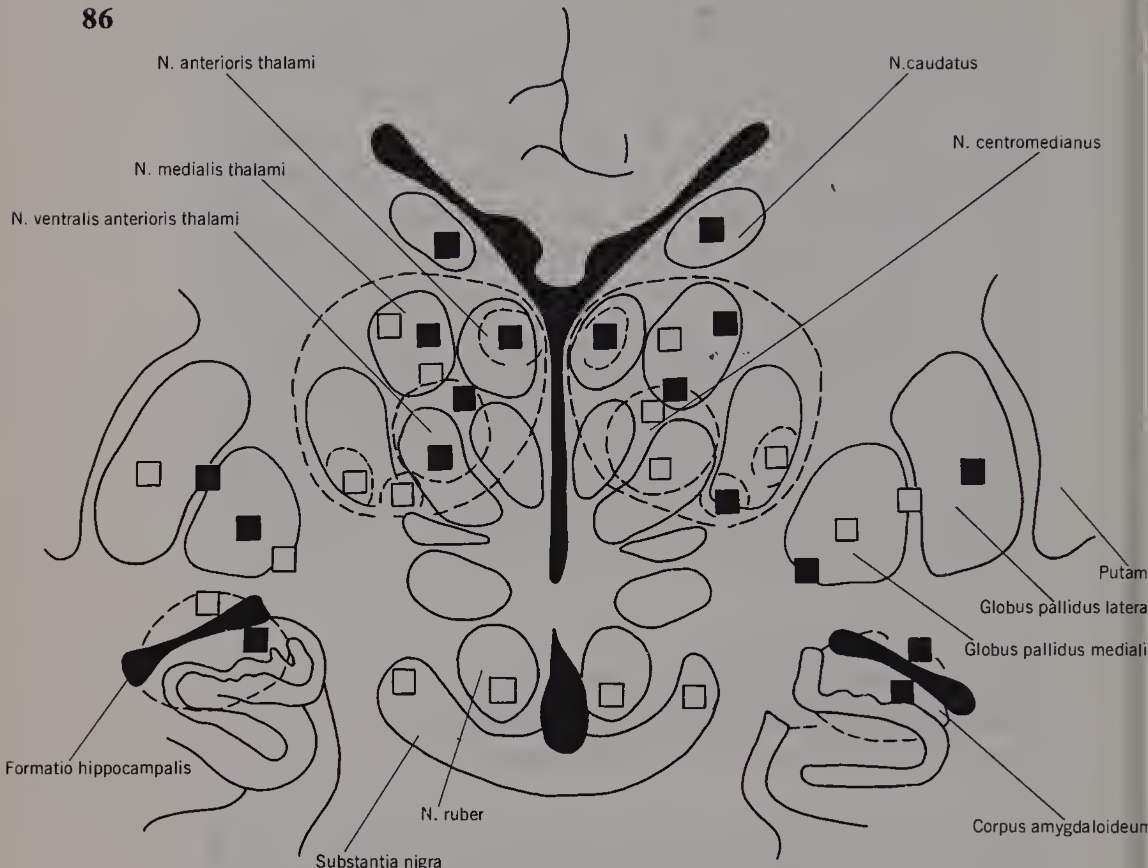


Figure 14. Diagram of the brain. Black squares, regions of the brain in which reproducible changes in available oxygen were detected. *Left,* test presented at rest; *right,* test presented against background noise.

they had not previously been observed (Fig. 14). Moreover, these new "points," which were reproducible, could appear within the same structure (nucleus). This may be related not only to known relationships but also to the fact that exploration of the brain during therapeutic stimulation with implanted electrodes cannot be complete. When points with a reproducible pattern disappear from one structure and appear in another, the mechanism is not the "disconnection" of one nucleus and the "connection" of another. Rather, on the one hand, it is a question of the "disconnection" of one zone in the nucleus and the absence of electrodes in another part of the same nucleus which could be "connected" to the activity on the one hand, and on the other hand, the placement of an electrode in another brain formation. Accumulating evidence attests to this and also to the vast complexity of the structural-functional relationships of the brain, which cannot be forced to fit the procrustean bed of an artificial differentiation of the brain into nuclei (a model that varies with different investigators in any case).

At first, for example, the reproducible changes in the physiological indices of the hippocampus were detected primarly during the performance of a psychological test without a background of noise, whereas, in the amygdala they were observed against a background of noise. Later, however, with a somewhat different arrangement of the electrodes within the same structures, a "connection-disconnection" of the active sections was seen when the environmental conditions were changed. These new findings do not contradict the original data, but only supplement them. Naturally, the "intranuclear" as well as the "internuclear" dynamics may also vary.

Of paramount importance is the fact that some links are constant and others inconstant in their activity within the structural-functional system of the brain that maintains mental activity under the changing conditions of the external environment. This suggests that certain brain formations in the system are required for the activity in question, operating independently of changes in the external environment (at least within certain limits), and thus may be considered rigid links, while other links are flexible, being required for the activity only under certain specific external conditions.

The term "rigid" is not used here in the sense of a rigid closure of a reaction through one neuron. And within the flexible and rigid links of the system, the activity of a neuronal population occurs according to statistical probability (Kogan, 1962). It is this type of connection between the rigid links (or probably, more accurately, the relatively rigid links) and the flexible links that ensures the economy, exceptional flexibility, and adequacy of the brain system maintaining mental activity.

Experience in clinical neurosurgery, including stereotaxic surgery, shows that the destruction of many brain structures, particularly those in which a connection with mental activity has been demonstrated, does not always lead to observable mental disturbances. This may be related to the psychological investigations themselves–if the conditions under which a psychological investigation is carried out are not sufficiently varied, they might fail to reveal a deficit that has developed.

Such an absence of mental disturbance, however, is more likely to be related to the vast compensatory resources of the brain and to the assumption of a function by another system, including the corresponding formation in the intact hemisphere. In observations on human subjects, this thesis is supported by an increase in the frequency of mental complications following bilateral operations on subcortical brain structures. It can be imagined that bilateral destruction of the rigid links of the system for the physiological maintenance of mental functions would be particularly damaging.

The phenomena investigated have a number of other aspects. As has been pointed out, the performance of mental activity against a background of noise requires not only the activity of additional brain formations, but also the "disconnection" of some points that are active in a state of rest. In other words, external noise in some way complicates the system (acting as "interference"), but in a way also simplifies it (by acting as a source of necessary "tonus"?). Hence, the values of the SEP, O_2a, and IA indices may also be used to further expand the thesis of an optimal background for activity–these values show that the same activity, carried out under different conditions, corresponds to a specific functional state of the brain, which arises from the functional state of its different structures. The background state of the brain against which an activity, particularly a mental activity, is carried out integrates the functional state of the individual structures involved in maintaining that activity.

How can one visualize the mechanisms that connect and disconnect some of the elements of the structural-functional system that maintains mental activity? An understanding of these mechanisms is possible when one takes into account the polyfunctionality of the neuronal populations related to mental activity.

Changes in impulse activity associated with changes in the external environment may "connect" some elements of the system (brain structures) and "disconnect" others. On the other hand, elimination of some external stimuli is optimal for the activity of other brain structures, and of structures within the system, ensuring the performance of mental activity in the absence of specific stimuli (or number of stimuli). This does not, however, exclude the possibility that variations in the activity of brain structures (flexible links) also reflects the maintenance of mental activity under changed environmental conditions by reserves of the brain.

These assumptions were supported indirectly by studies of the physiological organization of mental activity when the brain's internal environment had been altered by the application of neurotropic drugs. The drugs used in these studies acted on different types of synaptic transfer in the brain—adrenergic, cholinergic, and serotoninergic (Anichkov, 1968; Kambarova, 1969; Chernysheva, 1971). The drugs changed not only the background of the brain's physiological indices, but also its dynamics during the performance of mental activity, in particular the SEP patterns and the cellular activity during psychological tests. The administration of Deseril led to the disappearance of reproducible SEP changes in the region of the thalamic nucleus centralis during psychological tests. "Pediphen" had a similar effect in the nucleus ruber and globus pallidus medialis. Methyldiazil, however, significantly increased the reproducible SEP changes in the nucleus ruber and globus pallidus medialis during psychological tests (Ilyukhina, 1972).

The changes in impulse activity following the administration of neurotropic agents (Bechtereva, Kambarova, and Matveev, 1970) were of particular interest. Recordings of impulse activity at rest and during the performance of psychological and motor tests made it possible to follow both the general changes that were initiated at a distance and the changes that occurred in the region of the recordings. The general changes appeared as changes in the level of neuronal activity; moreover, the dynamic pattern of the changes in impulse activity during the corresponding tests also changed. The direct action of neurotropic drugs in the region of the impulse activity leads was manifested by a distinct change in the dynamics of the impulse activity during specific tests. It thus proved possible not only to differentiate between local and general changes, but also to detect phase changes in the brain. For example, administration of Deseril initially increased the background impulses (activity) in the thalamic centrum medianum, which was probably caused by distant activating influences. The dynamic pattern of these impulses during a psychological test differed only slightly from the initial pattern. After one hour, the background impulse activity returned to its initial level; there were more pronounced changes in the dynamics of the discharges during a psychological test presented at this time. The pattern changed even more significantly after two hours, with a considerable decrease in the background impulse activity (Fig. 15). Observations of this type indicate that a rearrangement of the neurophysiological system which maintains mental activity with a change in the links of this system may result not only from changes in the external environment of the organism, but also from changes in the internal environment of the brain. In the latter case, the rearrangements may reflect changes in specific synaptic activity, whether adrenergic, cholinergic, or serotoninergic. Hence, these observations support the view that the neurophysiological system for maintaining mental functions contains links which respond to different chemical substances. The suppression of any form of neurochemical transmission—at least to the extent to which this can be judged from the indices measured—disconnects the neuronal population in question as a link in this system [although we know that in many cells synapses of different types are available (Jung, 1963; Bradley, 1965; Anokhin, 1968; and others), without even considering the possibility of different neurotransmitters within overall cell population].

Naturally, before any definite conclusions can be drawn, these studies should be extended. If the findings are confirmed, they will not only open up an avenue for further neurophysiological analyses of the links of the system, but they also may

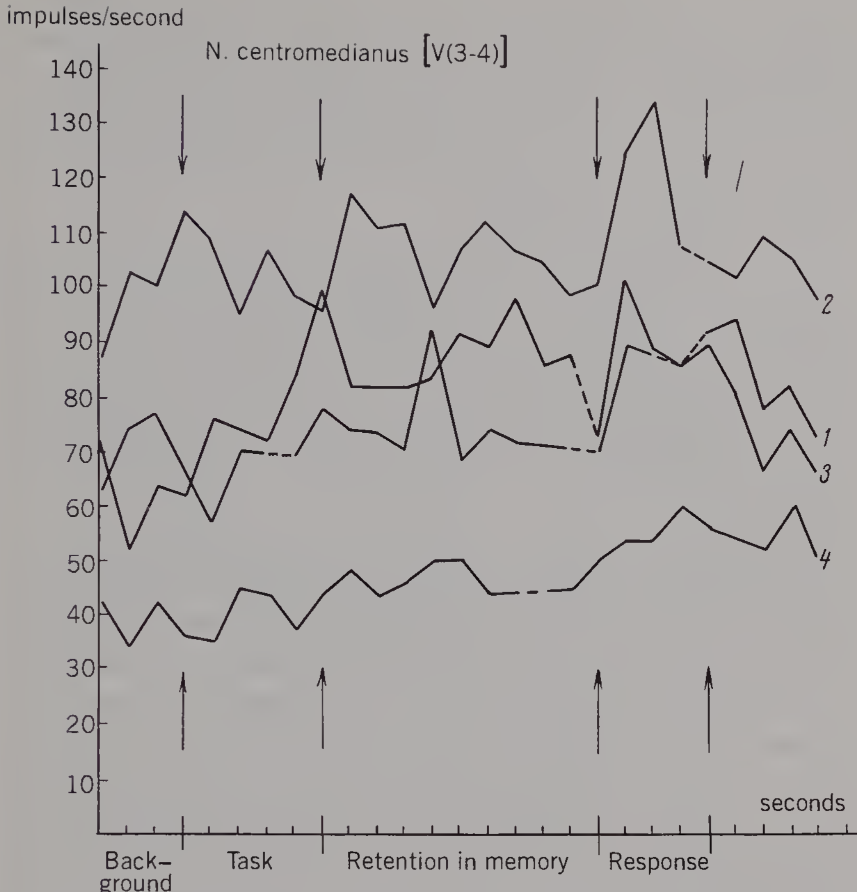


Figure 15. Dynamics of the impulse activity of the N. centromedianus in tests for operative memory carried out at rest (1), 15 minutes (2), 1 hour (3), and 2 hours (4) after the administration of Deseril.

have clinical application. It should be possible to disconnect certain links of the system, selectively and quantitatively, without essentially changing the conditions for the activity of other elements of the system or the activity of the same brain structures as links of other functional systems.

The data obtained are important in at least one other respect. Deseril has proved to be highly active with respect to changes in the links in the system maintaining mental functions, and one administration site has been the centrum medianum of the thalamus, a structure which when stimulated electrically significantly changes the conditions of performance of mental activity (Smirnov, 1967; Bondarchuk and Smirnov, 1969). These observations may be of use in determining the anatomical basis for the activity of such serotoninotropic psychomimetic agents as LSD-25.

In our studies, factors "from without" or "from within" that affect the physiological basis of mental activity were taken into consideration to the degree to which such changes can be detected during a neurophysiological investigation. It was found that the potential for performing a given mental activity usually was not fundamentally affected by these changes. However, some tests could not be reproduced at rest or under other test conditions.

It was of interest to examine the special characteristics of the neurophysiological system that maintains a mental activity as a function of the quality of performance of that mental activity itself. From changes in the physiological indices which occurred as a function of the correctness or incorrectness of test performance, it was possible to characterize three types of structures or, more correctly, "points" in the brain. In the first type, the reproducible dynamics of the physiological indices (available oxygen) did not depend on the quality of the test performance (Fig. 16). Such points were detected in the hippocampus, the amygdaloid complex, and the ventral, posterolateral, and the central thalamic nuclei. In the second type, there were reproducible changes in the physiological indices which differed during correct and incorrect test performances (Fig. 17). In the third type, reproducible changes in the physiological indices were detected only during incorrect performances of the test (Grechin, 1968) (Fig. 18). Such points were found in the nucleus caudatus and the centrum medianum and other nuclei of the thalamus.

These findings are also of interest as evidence of a greater or lesser differentiation of the links in the physiological system under study, if it is assumed that the brain mechanisms of mental activity closely approximate analogous mechanisms of other forms of activity of the organism.

In terms of optimizing mental activity, the points at which

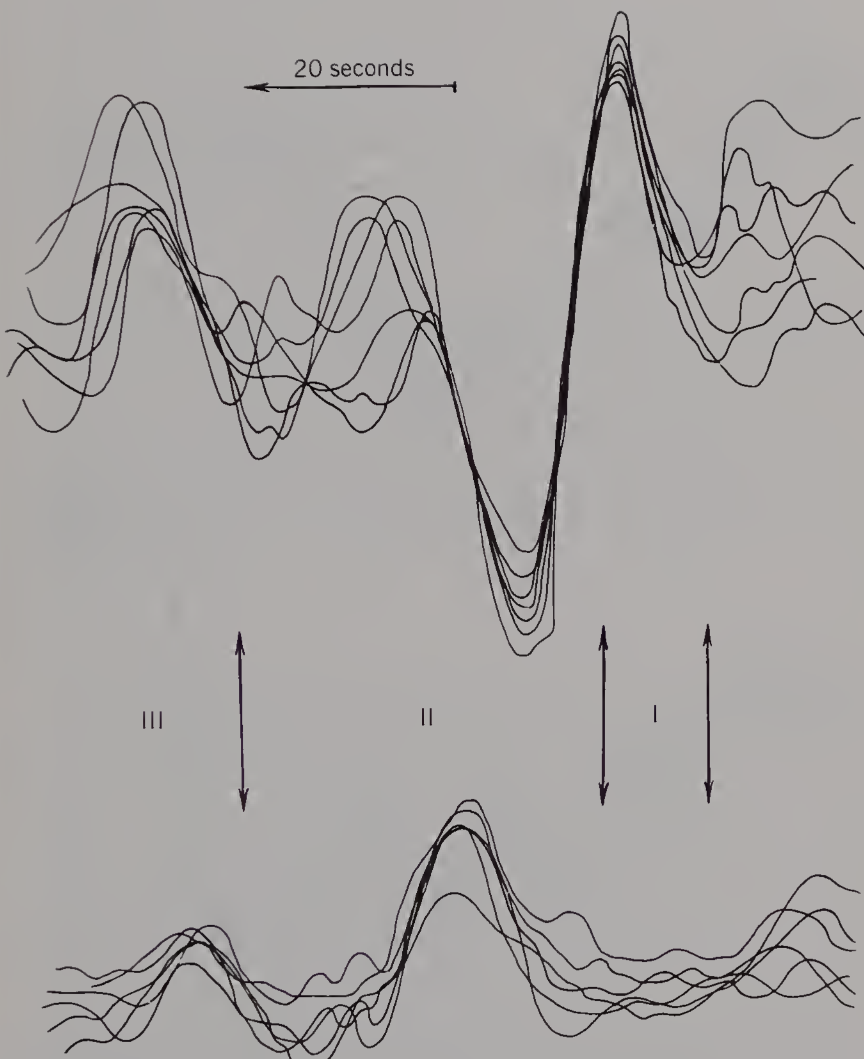


Figure 16. Similar reproducible indices of available oxygen during the correct and incorrect performance of psychological tests. I, presentation of the test; II, retention of the test in the memory; III, response. *Top:* N. centralis thalami; *bottom,* N. ventralis lateralis thalami.

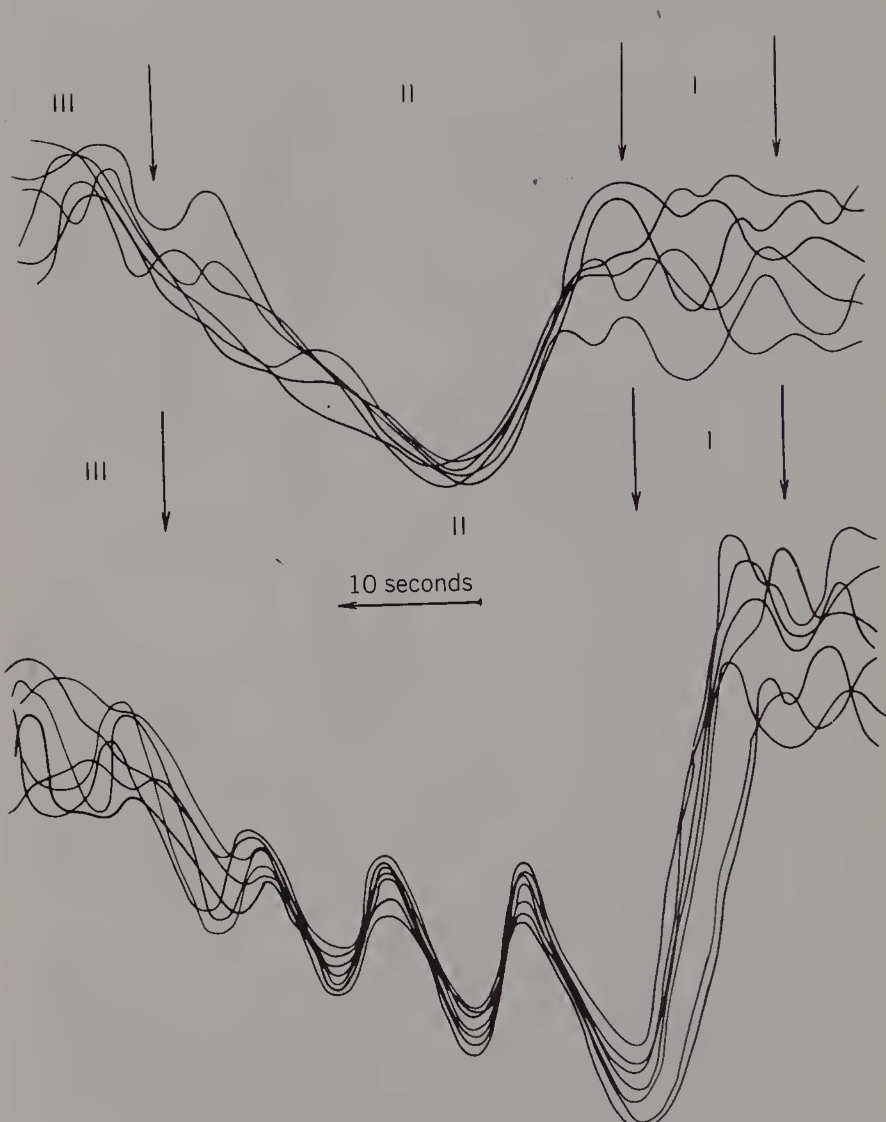


Figure 17. Different reproducible dynamics of the available oxygen during the correct (*bottom*) and incorrect (*top*) performance of psychological tests. I, presentation of test; II, retention in memory; III, response. As in Fig. 16 (*bottom*), the recording was made from the N. ventralis lateralis thalami, but different leads were used.

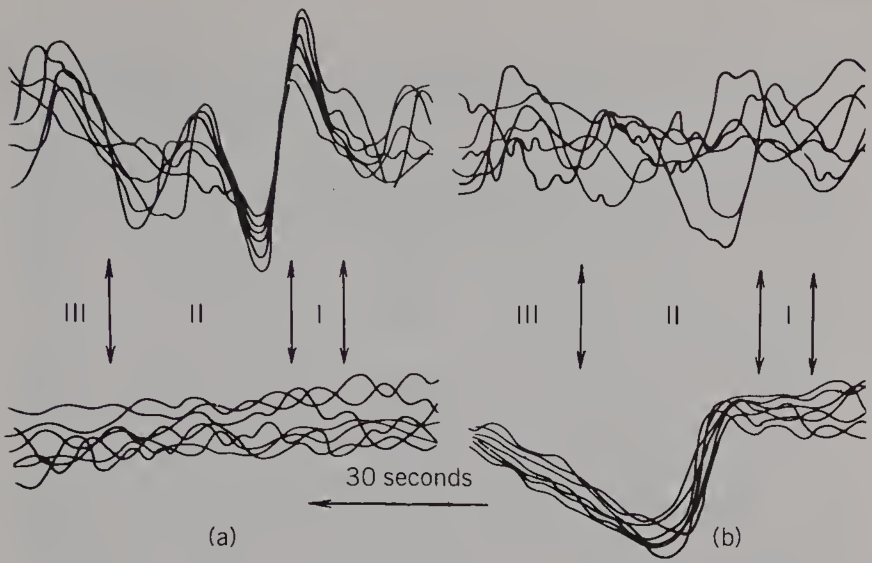


Figure 18. Dynamics of the available oxygen during correctly and incorrectly performed tests. (a) The presence of reproducible changes in the available oxygen during a correctly performed psychological test and the absence of reproducible changes in the region of the N. medialis dorsalis thalami during errors. (b) The absence of a reproducible change in the available oxygen during the correct performance of psychological tests and the presence of a reproducible change during an incorrect performance of the tests in the N. caudatus.

reproducible changes occur during the incorrect performance of a test are naturally of most interest. It would be very tempting to assume that these points represent a sort of "error detector," an analyzer of the correctness of actions that would participate in the "action acceptor" of Anokhin (1968). This view is supported by complementary findings. If reproducible changes are detected in the nucleus caudatus during an incorrect test performance, then stimulation of that structure may lead to an increase in the number of errors (Bechtereva, Moiseeva, Orlova, and Smirnov, 1964; Bechtereva, Genkin, Moiseeva, and Smirnov, 1965; and others).

Many experiments, despite the ambiguity of the general conclusions to be drawn from them, have provided clear-cut evidence of the inhibiting role of the nucleus caudatus with respect to different types of activity. What is the mechanism for the development of reproducible changes in the physiological parameters for the nucleus caudatus and other structures where errors occur? How is the "connection" between these formations made? Superficially, the impression might arise that "the brain is more intelligent than the man," that the brain "knows" about the error even when the man does not. This is not the actual situation, of course. The following is offered as one probable explanation.

At least short-term (and probably also long-term) memory is based on a complete "remembering," on the retaining of a trace of the whole event that has taken place—in the present case, on complete retention of the test presented. However, with the process of remembering, a "forgetting" mechanism is simultaneously, and in the overwhelming majority of cases expediently, connected; this represents not "obliteration" but retardation: the trace is translated to a form in which a "reading" becomes more difficult.

A premature or an inadequate connection of this second mechanism may itself cause a reaction of some element of the action acceptor. It is more probable, however, that an inadequate connection for the retardation produces a dissociation between the traces present and allows for their reproduction, which results in the connection of a structure recording such a dissociation, a mismatch with all the possible consequences of a general, emotionally determined activation.

The continuing accumulation of observations might lead one to assume that "error detectors" have actually been found, but the solution of this problem, or at least the analysis of the physiological indices, requires a study of the role of emotional factors, which is particularly significant in the case of an incorrect response. In collecting these additional data, however, one must realize that these two points of view—an initial connection of the structure (1) with an error or (2) with an emotional reaction—are in no way contradictory; rather, the second view (if it were substantiated) would supplement the first. It is important to consider the latent period, the form of the reaction, and the dynamics of the secondary reaction, since these parameters most frequently differ in reactions to psychological tests of the operative-memory and emotion-producing type.

It is interesting to note that the use of neurotropic drugs has made it possible to identify certain neurophysiological mechanisms which determine that the neuronal populations will react only to incorrect responses during psychological tests. Thus, when Deseril was applied to individual points of the brain (in the region of the centrum medianum and the ventral nucleus of the thalamus), a previously unobserved, reproducible pattern, a unique "generalization of effect," appeared during psychological tests; that is, a characteristic pattern appeared even during positive performances of the test in cases in which, before drug administration, the reaction was observed only when errors were made (Fig. 19). It may be noted in passing that after the introduction of Deseril, characteristic changes in the impulse activity at the same point began to appear not only during movements of the contralateral extremities (as was observed before drug administration) but also during movements of ipsilateral extremities. However, the application of Deseril at other points in the brain led to the appearance of "specific" properties: the neuronal population, which previously had revealed a characteristic pattern for both correct and incorrect performances of the tests, started to react only during incorrect performances. These data testify to the neurophysiological properties of neuronal populations and to the paramount role of different biochemical mediators in the manifestation of these properties.

A hypothesis advanced in 1966 by Bechtereva with respect to the maintenance of human mental activity by a cortical-subcortical, structural-functional system with links of different degrees of rigidity is receiving increasing support and thus offers a basis for interpretation of the physiological mechanisms of mental phenomena, particularly the structural-functional aspect of their maintenance. Our investigations have shown that flexible links predominate in the system of cerebral control of mental activity; that is apparently one of the fundamental features distinguishing it from other systems for the central control of functions. The correlation between rigid and

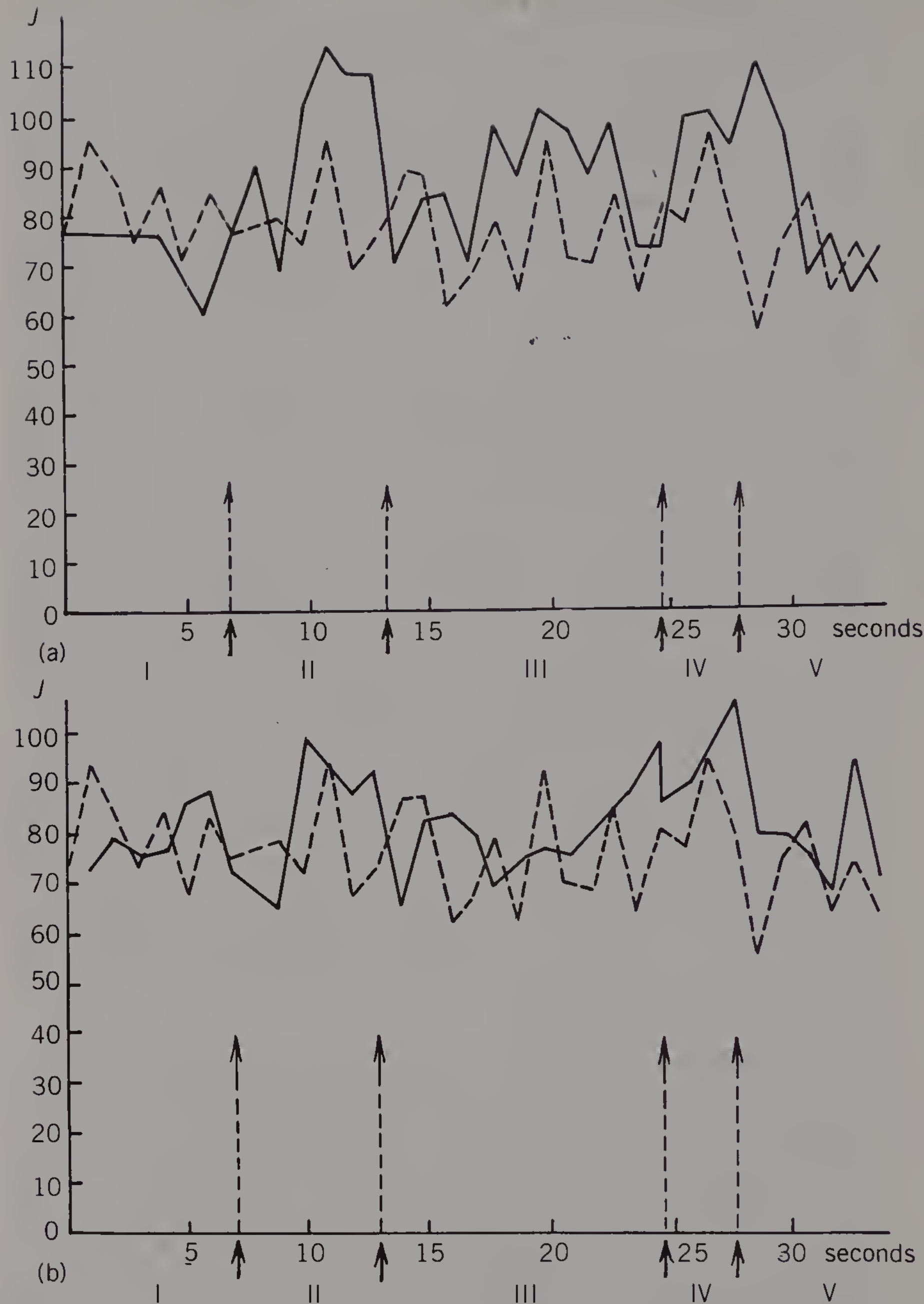


Figure 19. A graphic representation of changes in the frequency of impulse activity in the region of the one of the neuronal populations of the N. centromedianus during a psychological test. (a) Broken line, dynamics of impulse activity during a correct performance of test; solid line, dynamics during an incorrect perfor-

flexible links in such systems could be regarded as an essential criterion of their complexity—the complexity of the systems is based on both an absolute and a relative increase in the number of flexible links.

This correlation should be considered in interpreting the data obtained by electrical stimulation of the brain. Rigid links in any system may be detected by observing neurodynamic indices during electrical stimulation of the brain and during the presentation of appropriate tests. An investigation of the flexible links is practicable only when the neurodynamics of the brain are studied during the presentation of functional tests and under varying conditions of observation.

The investigation of physiological characteristics of the brain's vital activity during psychological tests has proved a more subtle method of study than the observation of changes in mental activity associated with focal pathological processes, local surgical destruction, and electrical stimulation of the brain. It has permitted a more complete study of the structural-functional basis of mental activity and has made it possible to show that those formations which might, as a result of specific disconnection and stimulations, be mistaken for "silent" zones, also participate in mental activity.

Thus, it was decided that a study of the most complex brain systems, in particular the system for maintaining mental functions, requires a combination of electrical and pharmacological

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mance. The characteristic dynamics of the impulse activity are found only during an incorrect performance of the test. (b) Broken line, the dynamics of the impulse activity during a correct performance of the test before the administration of Deseril; solid line, dynamics after the administration of Deseril. A correct performance of the test after the administration of Deseril produces a characteristic pattern of impulse activity, similar to the pattern for an incorrect performance of the test before the administration of Deseril. Vertical axis: *J*, number of impulses. Horizontal axis: Arabic numerals, time (seconds); Roman numerals, background and phase of psychological test. I, initial background; II, presentation of tests; III, retention of test in memory; IV, vocal response by patient; V, background after test performance.

The arrows mark the beginning and end of the test presentation (II) and of the response by the paticnt (IV).

stimulation of the brain with direct observation of the dynamics of function.

The Neurophysiological Nature of Certain Changes Developing in Links in the System for the Cerebral Maintenance of Mental Activity

One of the most intriguing problems in this area concerns the nature of the changes that occur in different brain formations during the maintenance of mental activity. Two questions may be asked: (1) What physiological changes occur in the elements of the system maintaining mental activity during the performance of this activity? (2) Which changes ensure the specific character of each mental activity? In other words, is it possible to find in some form of physiological activity a pattern characteristic of a specific word, sentence, etc.?

An answer to the first question can be given at this time.

The active state of the structures participating in mental activity is related to change in all the physiological indices of brain activity. The levels of the slow electrical processes (SEP) and the available oxygen (O_2a) change. Moreover, changes in SEP levels not only occur during connection of the structure into an activity, but conversely, a change in the level of the SEP (probably the steady potential primarily) may "connect" the structure into an activity, at least an emotional activity. Furthermore, activity that arises from a change in the SEP (again the steady potential probably) in specific brain formations may be the basis of complex and very stable behavioral reactions (Bechtereva, Grachev, Orlova, and Yatsuk, 1963; Smirnov, 1967). Phenomena of this type have been studied experimentally in the greatest detail by Rusinov (1957); other workers later investigated the process of temporal connection during the creation of artificial foci in the brain by weak polarization. These studies clearly indicate the very important role of changes in the SEP, and in particular, the steady potential, in brain function.

The O_2a level may reflect changes in both the consumption and the supply of oxygen to tissues. A decrease may therefore indicate an increase in the consumption, a decrease in the supply, or both. If we consider the conditions under which activity takes place and the special characteristics of the brain vessels, a decrease in the oxygen supply to active brain structures (and this can be determined from other physiological parameters) is improbable. Although it is generally known that hypoxia of the brain may occur in Parkinson's disease, decreases in the level of O_2a varied in different structures under the conditions of the investigation: a significant decrease occurred in the ventrolateral nucleus, in the centrum medianum and in the dorsomesial nucleus of the thalamus; a less significant decrease occurred in the medial globus pallidus and the nucleus caudatus; decreases were rare in the hippocampus and the amygdaloid complex.

The question is more complex when there is an increase in the level of O_2a which may be related to both a decrease in the consumption and an increase in the supply of oxygen. Again, the physiological nature of the phenomenon can be understood by comparing other physiological parameters. These parameters indicate that a decrease in oxygen consumption is improbable, and an increase in supply is more likely. An increase in the O_2a level during mental activity was occasionally observed in parts of the centrum medianum and dorsomesial nucleus of the thalamus, in the ventrolateral thalamic nucleus, and in the medial globus pallidus. Not only the region where the O_2a leads were placed but also the phase of performance of the psychological test affected the O_2a levels (Grechin, 1966). It is more difficult to evaluate changes in the electrosubcorticogram since these, as mentioned above, varied greatly, depending on the initial background. It can only be confirmed that changes in the electrosubcorticogram measured with a direct lead from the brain within the limits detected (development of slow waves, sharp waves, and other wave patterns in structures related to the maintenance of mental activity) did not affect test performance. This should be taken into consideration in assessing the data on the relationship between the electrosubcorticogram patterns and the fundamental neural processes. Again, it must be recognized that the presence of slow waves in any region of the brain does not necessarily indicate a retardation in the region, although of course it is not evidence against that possibility either. Changes in the electrosubcorticogram and SEP and O_2a indices during mental activity reflect changes in the functional state of the structures involved in that activity. Reproducible shifts in the SEP and O_2a, as shown above, are reliable indicators of the closeness of the relationship between the structure and the activity. However, an interpretation of the nature of this relationship must be based on impulse activity data. Only an analysis of the impulse activity can answer the question of what takes place in a structure during its connection into the functional activity and whether other, regularly developing physiological shifts (in SEP and O_2a) are the result of a regularly occurring connection of the structure into the activity or of an equally regularly occurring disconnection on which the activity in question depends.

The changes in impulse activity in structures in which an active state during the psychological test was revealed by other parameters differed greatly, both in the direction of the changes (an increase or a decrease in frequency of the impulse activity) and in their dynamics. The impulse activity reactions differed depending on the region ("point") of the lead, the phase of performance of the test, external factors ("interferences"—Trokhachev, 1966), and the correctness or incorrectness of the test performance.

Thus, for example, an increase in the frequency of impulses during the performance of a Binet test could be observed in different thalamic nuclei, showing up in most of the formations during the memory retention phase of the test. During the reproduction phase (vocal response), a further increase in impulse frequency, no change in impulse frequency, or even a decrease in impulse frequency, occurred. Clear-cut changes in impulse activity occurred in the upper brain stem, while at the level of the tegmentum of the pons there was a zone in which the vocal response produced an increase in the impulse frequency; thus increase was significantly more distinct than in other tests, including motor tests (Fig. 20).

As mentioned, the dynamics of these reactions differed depending not only on the structure (nucleus), but also on the

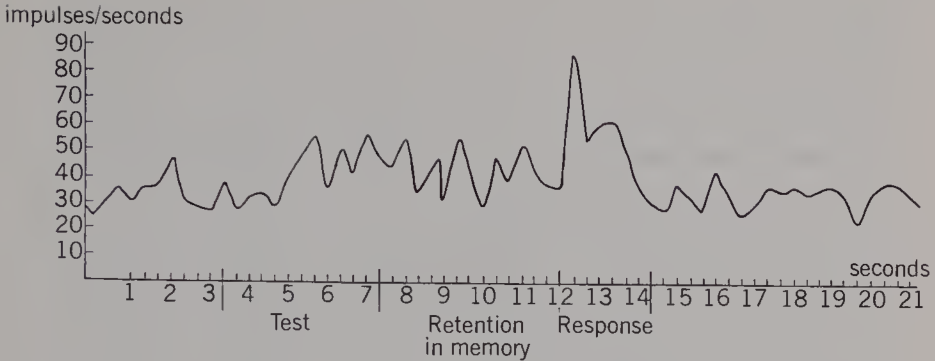

Figure 20. Dynamics of the impulse activity in the tegmentum pontis during a test for operative memory. (The recording was made with an integrator.)

location of the lead within the limits of each structure. After many investigations (Trokhachev, 1966; Bechtereva and Trokhachev, 1967; Matveev, 1971), it was possible to show that specific standard variations in these dynamics occur. This was, of course, of great interest.

Matveev (1971), taking an approach suggested by Livanov (1965), analyzed the processes that were manifested as increases in the frequency of impulse activity. The dynamics of the impulse activity during psychological tests and motor tests showed that the frequency of the discharges increases (or, to be more cautious, may increase) when the number of active neurons decreases (Fig. 21). This phenomenon could be explained essentially on the basis of lateral inhibition (Jung and Tonnies, 1950; Creutzfeldt, 1969; Baumgartner, 1961). One can imagine that elements of the neuronal population involved in control of some function could be activated on this basis and that at the same time the remaining elements of the neuronal population would be depressed. It can also be assumed that not all the elements of the neuronal population which can participate in a particular activity are connected into this activity, but only some optimal number of them. However, it is difficult to completely discount yet another assumption, which contradicts these two very tempting ideas. If we imagine that in any polyfunctional neuronal population the individual neurons

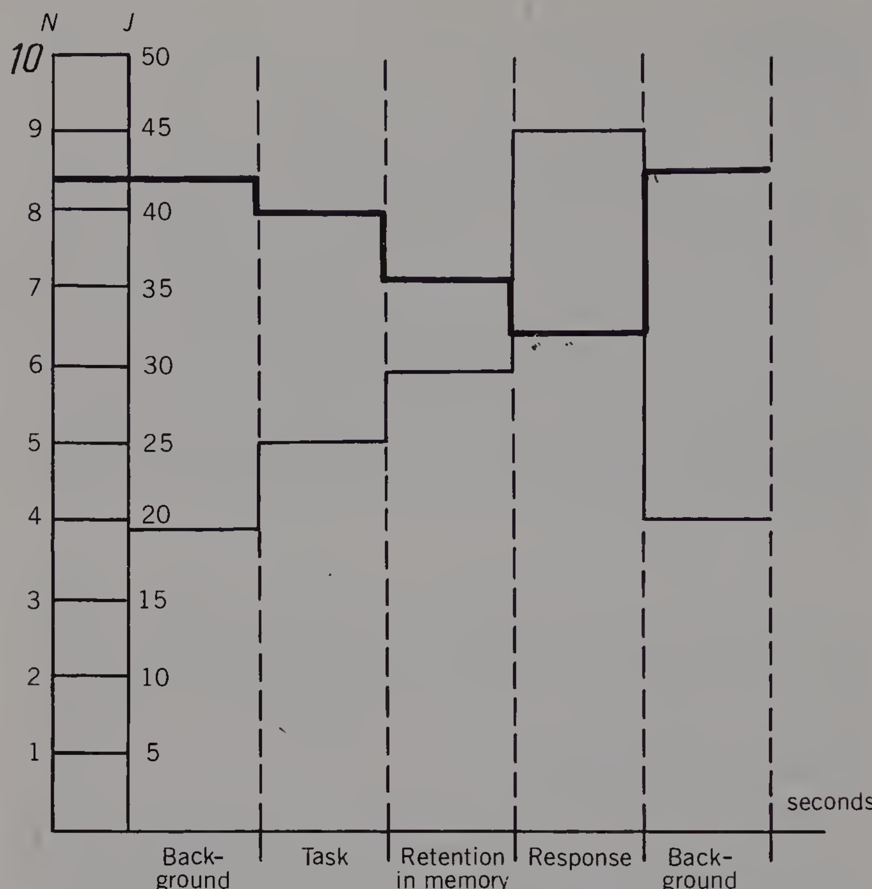

Figure 21. The impulse activity and the number of active neurons during a test for operative memory. Vertical axis: *J*, number of impulses; *N*, number of active neurons.

are also polyfunctional, then the whole process can be considered not as an activation of a certain number of specific elements, but simply as an activation of the number of polyfunctional neurons that is optimal for the activity in question. Under the first two assumptions, the impulse activity is somehow related to the specific nature of the activity. Under the third, it plays a more modest role by maintaining a specific functional state of the substrate. The data on changes in impulse frequency during incorrect test performances confirm that an optimal number of "working" neurons is involved in a given activity, but the data in no way attest to the nature of these neurons. Studies in which a single neurotropic drug changed the role of a given structure in the system for the maintenance of mental functions seem to support the first assumption, at least for certain subcortical structures. However, the polyfunctionality of many subcortical neuronal populations requires one to be cautious in drawing conclusions from these data. The role of the phenomena observed in the integrated system for the maintenance of some activity can be determined only from further analysis of much quantitative data on brain activity. Nevertheless, the investigations carried out at the neuronal level are already lifting the veil slightly from the "mysterious, as compared with the properties of a single neuron, properties of the neuronal populations" (Mountcastle, 1966), which maintain all forms of brain activity.

A very important result which is confirmed by these neurophysiological studies is that of the unity and complexity of the neurophysiological mechanisms underlying different forms of activity carried on by the brain, including mental activity. Thus, Sherrington's well-known dualistic thesis has been shaken, and the brilliant prediction of Pavlov concerning the possibility of applying "a system of non-spatial concepts of psychology to the material construction of the brain" (Pavlov, *Collected Works,* Vol. III, Moscow-Leningrad, 1951–1952, p. 203) is being realized.

As physiological techniques improve, an increasingly detailed, step-by-step approach to the question of what physiological changes occur in elements of the system maintaining mental activity during its performance will be possible. Though it is still difficult to answer this question, the denial that it can, in principle, be answered, which is essentially the position adopted in a number of physiological and philosophical papers, means limiting oneself to yesterday's data in the study of the human brain. The denial of the possibility that the physiological correlates of specific human mental phenomena can be investigated leads inevitably to a rupture between mind and matter, to a separation between mental activity and the processes occurring in the brain. It can be imagined that just as the electron microscope has made it possible to define more accurately the morphological basis of so-called functional changes in the central nervous system, progress in physiological methods will pave the way toward the solution of this very important problem in the physiology of the human brain.

During the few years that have elapsed since the publication of the first edition of this book, there had been intensive work on the correlates between impulse activity and the "external" (acoustic) and "internal" semantic characteristics of the verbal stimuli presented. The search for these correlates led to investigations on the impulse activity of nerve cells which may be regarded as one of the brain mechanisms of information transfer and coding and decoding, including that of verbal signals. Even in its electrophysiological aspect, however, impulse activity should not be considered the only such mechanism, since biochemical mechanisms of information processing and storage are very important. A search for correlates of verbal signals in the impulse activity of neuronal populations required special analytical equipment, which was developed by Bundzen himself and together with Gogolitsyn and Kaplunovsky (1972–1973). The methods of analysis applied at the First Physiological Institute of Erlangen-Nurnberg (German Federal Republic) were also used by these workers.

The multicellular activity was recorded on an MGCh-1 four-channel magnetic recorder with a speed of magnetic transport of 10.5 mm/sec. The investigator's vocal commands and the corresponding response reactions of the patients were recorded on one of the channels of the magnetic recorder.

The analysis of the multicellular activity of neuronal populations was carried out in two stages on an analog-digital complex (MN-14 automatic computer, "Promin-2" electronic digital computer, "Minsk-32" electronic digital computer) at the Institute of Experimental Medicine of the Academy of Sciences of the USSR, and on a "Link-8" electronic digital computer at the First Physiological Institute at Erlangen-Nurnberg.

The objective of the first stage of data processing was to search for characteristic changes related to the test performed in populations selected on the basis of superposition data (see above). For this purpose, a continuous amplitude discrimination of multicellular activity was used, and the output values of the useful signal were divided into several proportional intervals. In each discrimination interval (discrimination window) the function of the actual current frequency was calculated from the quantity of action potentials terminating in the discrimination window. The analysis period was 20 milliseconds. The output signals were transmitted from the discriminators to an M-168 multi-channel magnetic recorder. Later, the dynamic selective correlation method was used in the search for trace processes.

The aim of this dynamic correlation was to separate by functions the current frequency of activity patterns which, according to the distribution of the impulse discharges, are statistically similar to the space-time pattern of multicellular activity developed during the phase of test presentation or to the contours of the dynamic spectra of the verbal test-stimuli. The basis of the dynamic selective correlation method is the calculation of a cross-correlation function during a continuous unidirectional shift of the series analyzed, in order to determine the zones of correlative similarity of the reference (psychologically specific) and analyzed series. On the basis of dynamic correlation data, synchro signals were applied to the recording of multicellular activity, marking zones of significant (99.9%) correlation and thus making it possible to isolate with greater accuracy the fragments of activity containing the patterns being sought. These fragments were then subjected to mathematical processing by the "Link-8" computer.

The basis for digital processing was a program which made possible, with a quantization time of 10 milliseconds for the bioelectrical process, analysis and storage of the amplitudes of the extreme values of the process and of the intervals characterizing the spacing of the extremes in time. This program included two subprograms: one for amplitude histograms of the maxima, minima, and absolute values of the action potentials, for interval histograms of the maxima and minima of the process, and for information on the duration of the ascending and descending phases of the biopotentials; the other for amplitude-phase histograms according to the duration of the ascending and descending fronts in combination with the absolute amplitude of the spike and according to the general duration of the fronts and the absolute amplitude of the spike.

This program permitted a two-parameter separation of the action potentials according to amplitude and phase duration.

The resulting three-dimensional patterns reflected the degree of ambiguity in the process.

The resources of multifactorial analysis are being increasingly used in the analysis of the data.

Investigations carried out by Bundzen with Gogolitsyn and Kaplunovsky (1973), and later with David, which substantially supplemented earlier studies of the characteristic spectrum of the impulse activity during psychological tests, showed that impulse activity pattern in a number of neuronal populations depends on the acoustic characteristics of a verbal stimulus (type I pattern).

To conform with the tasks, some changes were made in the methods of examining patients. To patients in whom multiple gold electrodes had been implanted for diagnostic and therapeutic purposes, tests for short-term memory were presented in the form of two or three (or more) short Russian words, meaningless combinations of the letters (phonemes) making up these words, foreign words unknown to the patient, and the same foreign words whose meaning was then taught to the patient. Thus, in the first case, the patient memorized words which were previously well known to him, and the memorization process could be related to an address to the long-term memory. The second and third cases involve stimuli carrying no semantic information for the patient, but different in sound, known to have no meaning or having a meaning still unknown to the patient. The third and fourth cases involve words identical in sound, but without a meaning in one case and already having a specific meaning for the patient in the other. In the fourth case, one could again assume an address to the long-term memory, so that the test performances in the first and fourth cases could share a common neurophysiological basis. The patient repeated test items to himself and aloud at the physician's command 15 and 30 seconds after presentation, respectively. The impulse activity was recorded from 30 to 40 points in the brain, initially by means of an integrator.

By superimposing curve sections, zones of the brain connected with performance of the memory tests were detected. Reproducible changes were found in the centrum medianum, nucleus centralis lateralis thalami, nucleus dorsalis superficialis thalami, and other areas.

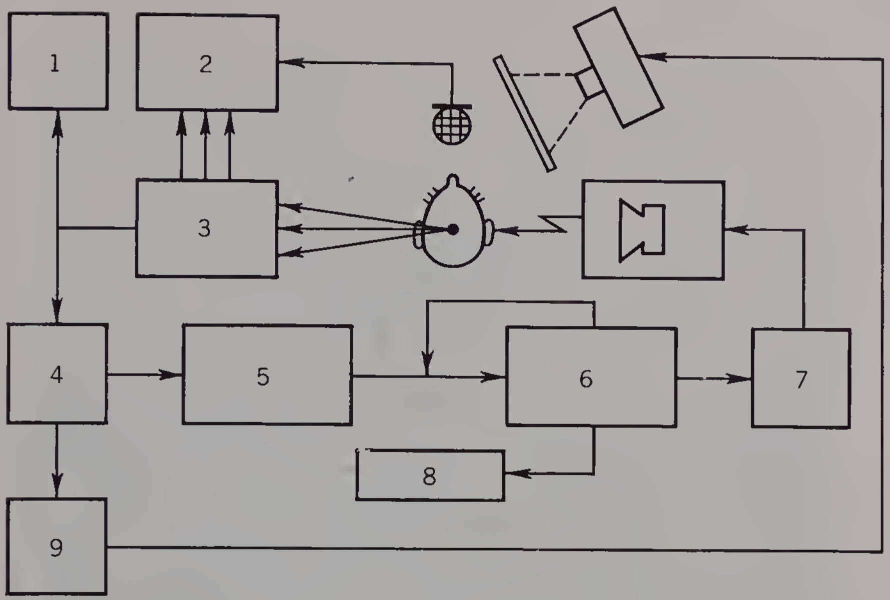

Figure 22. Generalized block diagram of a control experiment. 1, control oscillograph; 2, four-channel magnetic recorder; 3, bio-amplifiers (Disa); 4, activity arresting-forming unit; 5, MN-7 analog computer; 6, program-time unit; 7, tape recorder for phonogram reproduction; 8, control signal panel; 9, automatic recorder. *Top right:* microphone, automatic projector, and dynamic speaker.

The activity of those brain areas recorded with the four-channel magnetic recorder was investigated further (Fig. 22).

In an automated, biocontrolled experiment a number of tests were presented synchronously with a specific functional state of the neuronal population.

Reactions of both the tonic and phasic types were elicited by the verbal stimuli. The phasic component of the activity was functionally related to the amplitude-frequency characteristics of the acoustic stimuli (Fig. 23).

These neurodynamics, which were manifested as space-time patterns in the form of changes in function of the current frequency of individual groups of neurons, correspond statistically to the time structure of the maxima of the amplitude characteristics of the acoustic signal; in a number of cell groups (in the region of the nucleus ventralis lateralis thalami and the centrum medianum and in other regions), they could be cor-

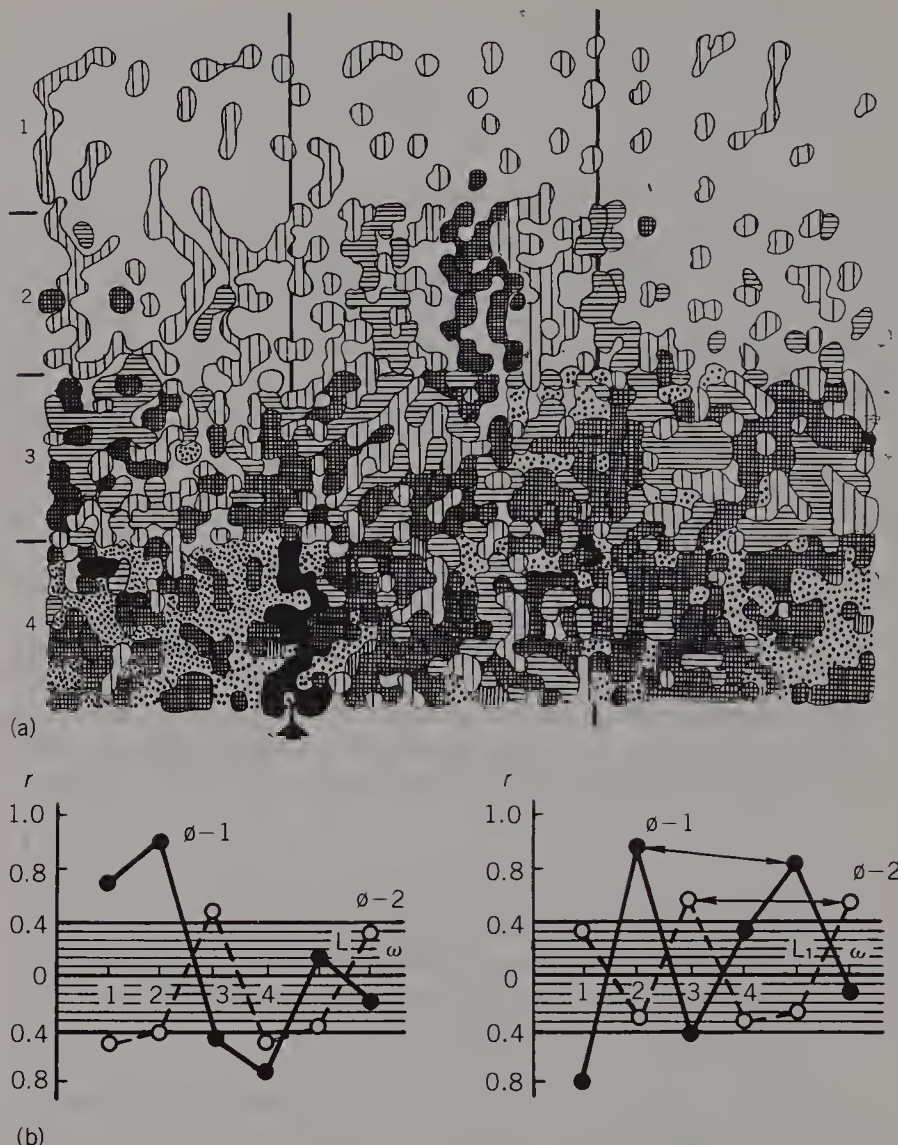

Figure 23. (a) Chronogram of the impulse activity of a neuronal population of the human brain in analog form. Horizontal axis, time (periodicity, 40 milliseconds); vertical axis, activity recorded within the limits of four discrimination windows (1–4) for a tenfold presentation of a verbal signal (the word "chorus"). Hatching: vertical, one impulse per 40 milliseconds; horizontal, two impulses per 40 milliseconds; cross-hatching, three to four impulses per 40 milliseconds. Dots, five to seven impulses per 40 milliseconds; solid area, eight to twelve impulses per 40 milliseconds. Vertical lines, beginning and end of verbal signal. (b) Results of a

related with the frequencies of the spectral maxima of the verbal stimulus. In the latter case, a kind of initial coding of the verbal signals according to their acoustic properties could be detected. This coding is probably a necessary preliminary step for an interaction with the engrams of long-term memory.

In the retention phase of memory, there is a more or less stable reproduction of the pattern formed, with a characteristic process of compression in time of its sequential elements developing within 3 to 6 seconds (from the assignment stage). The subsequent dynamics of the pattern are related to other features of the stimulus.

The pattern associated with known words is attenuated during the first few seconds, and at the moment of mental or actual reproduction of the assigned words, a new space-time pattern of impulse activity is formed, with characteristics similar to those of the output signal (the word pronounced by the patient). This pattern is found in the impulse activity of neuronal populations even before the word is pronounced by the patient (approximately 38 or more milliseconds before) and apparently can be regarded as a control signal (Fig. 24).

In response to foreign words, that is, verbal stimuli with a previously unfamiliar sound and an unknown meaning, the activity patterns formed during the assignment phase reverberate for a longer period of time—until the words are reproduced by the patient (Fig. 25). An analysis of the impulse activity during presentation of the same words after their meaning had been learned by heart, according to the methods of Gogolitsyn (1973), showed that the process of teaching new verbal stimuli leads to a regular decrease in the duration of the bioelectric

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factorial analysis of the matrices of correlated current frequency functions, isolated from the multicellular activity by the amplitude discrimination method and of the characteristics of a verbal signal with the tenfold presentation of the word "chorus." Horizontal axis, activity of discrimination level (1–4); vertical axis, correlation coefficients (r); L and ω, amplitude and function of control frequency of verbal signal; ϕ-1 and ϕ-2, significant factorial values. *Left,* control fractional analysis of background activity and characteristics of verbal signal; *right,* factorial analysis of activity at the moment of verbal signal.

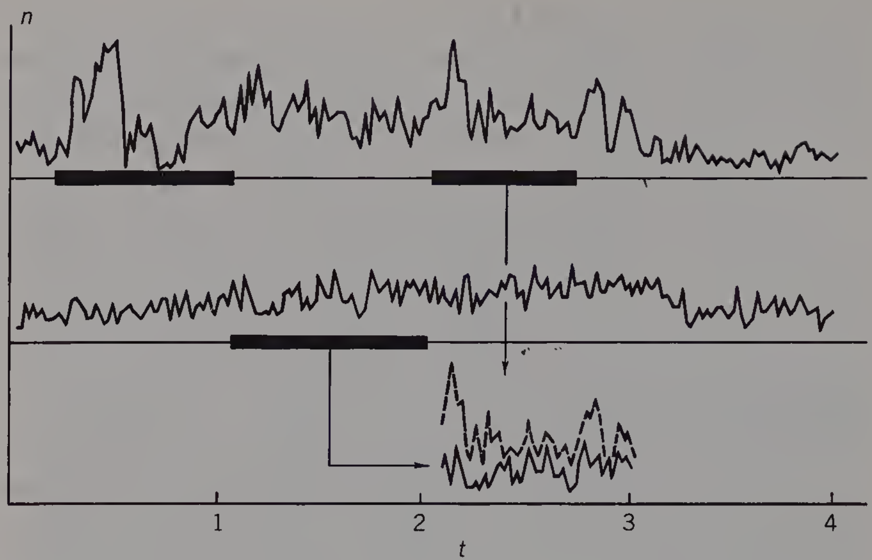

Figure 24. An example of the anticipation of a response pattern in one of the regions of the globus pallidus lateralis during analysis of the multicellular activity of a neuronal population for short-term verbal memory. The current frequency (20 milliseconds) of the mluticellular activity is shown for different regions. *Upper curve,* moment of assignment and moment of response; *lower curve,* moment anticipating pattern begins; *n,* number of impulses per 20 milliseconds; *t,* time (seconds).

pattern correlated with the stimuli. In this process, the dynamics of the impulse activity patterns are similar to those that are observed when known words are presented (Fig. 26).

A vocal response during the performance of a test for verbal memory may thus be associated with two basic variations in the neurodynamics of the brain regions where the primary code is developed: (1) a recombination of the activity pattern formed in the assignment phase and the development of a significantly different neural code (characteristic of short-term operative memory, with traces stored in long-term memory); (2) a stable maintenance of the activity pattern established during the assignment of foreign words with unfamiliar acoustics and carrying a semantic burden unknown to the subject (characteristic of short-term memory with no traces stored in long-term memory). In the latter case, a maximum mobilization of the short-term memory mechanisms probably takes place, which has been motivationally reinforced and is expressed in the high stability of the reverberation of the trace processes formed during the assignment phase.

Thus, a mathematical analysis of the dynamics of the impulse activity of neuronal aggregates demonstrated a difference in their functional organization for operative short-term memory with long-term memory base and for operative, short-term verbal memory without such a base.

Short-term memory is characterized by a stable reverberation of the trace processes. Evidently this can be considered an adaptive autoreinforcement necessary for learning, that is, for the development of stable neurochemical changes which produce an additional long-term memory base. During the short time interval of a memory test, the stable traces apparently also are the basis for the necessary response.

This view has been confirmed by studies in which previously unknown foreign words were taught to patients.

The dynamic correlation method has made it possible to isolate still another type of pattern, which was not related to the amplitude-frequency contours of verbal signals (Bechtereva, Bundzen, Keidel, and David, 1973). When verbal stimuli were presented, a new space-time pattern of impulse activity, which was more complex than patterns of the first type, appeared in the neuronal populations of the associative structures (nucleus dorsomedialis, nucleus lateralis posteriori thalami, etc.) and later became more or less stable. Words that occur with high and low frequency in speech and quasi-words were used in the tests. The dynamics of these patterns, provisionally called "autonomous" by Bundzen, depended on the probability of the occurrence of these verbal signals in human speech.

When words with a high frequency index are used in tests of short-term memory, stable autonomous patterns are observed only during the first 2 to 3 seconds of the retention of the words in memory, and where the retention ends. When words characterized by a low frequency index are memorized, significantly longer autonomous patterns were found, lasting from 18 to 30 seconds. When quasi-words were presented to the patient, there was a very stable periodic reverberation of the au-

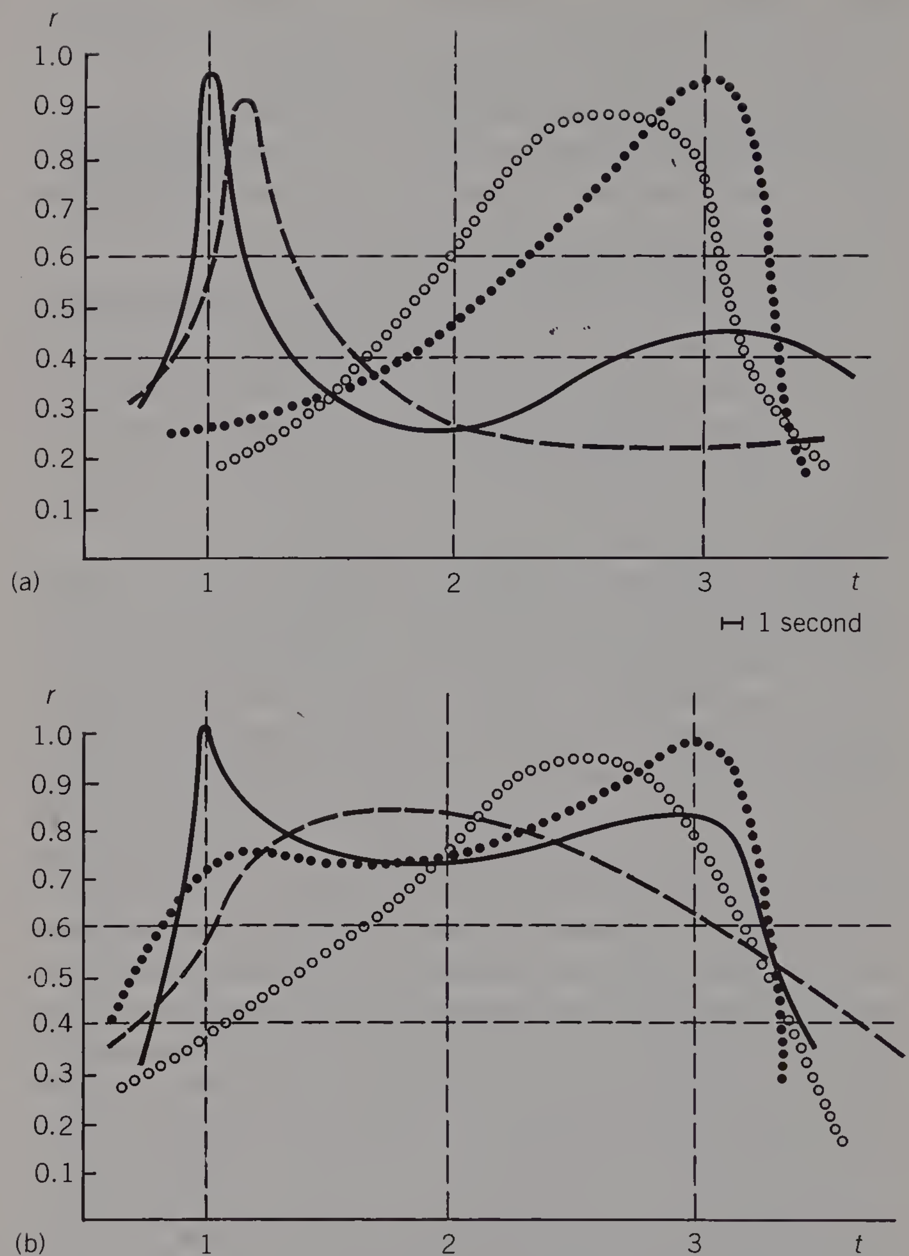

Figure 25. Averaged results of a mathematical treatment by optimal dynamic selection of the characteristic patterns of multicellular activity in tests for short-term memory. (a) Activity patterns during memorization of a set of Russian words; (b) activity patterns during memorization of a set of unknown foreign words. Horizontal axis, time (periodicity, 1.0 second); vertical axis, cor-

tonomous patterns, which, by the end of the retention phase, could be found in all the neuronal populations (Fig. 27). These dynamics may be regarded as a distant effect of the formation of long-term-memory engrams as the neuronal populations respond to acoustic stimuli.

A dynamic histogram analysis of autonomous patterns suggests that the late high-frequency components of the patterns have a bundle structure. During the period of retention of the test items in memory, the structure of the autonomous patterns changed in accordance with the frequency index of the words, apparently depending on whether or not semantic decoding occurred.

The patterns of multicellular activity during the coding of words with a high frequency index is characterized by a subtle differentiation present even in the assignment phase, which is significantly reorganized 2 to 3 seconds after that phase ends. The methods of analysis described above indicate that patterns of this type are characterized not only by a bundle structure but also by the generation of action potentials of a specific form. Activity patterns of similar structure are formed secondarily only after instructions to reproduce the test words have been given.

When words with a low frequency index are presented, the impulse changes significantly in the absence of pronounced elements of impulse flow structuring. In the initial phases of retention of the test items, there is a sharp decrease in the number of low and high amplitude action potentials and an increase in the activity of groups of neurons with medium-amplitude action potentials. To the extent that the verbal signals were retained in the memory, a gradual, negligible in-

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relation coefficients (r). Vertical broken line: 1, assignment phase; 1–2, stage of retention of verbal sequence in memory; 2–3, retention in memory; 3, vocal reproduction of test. Horizontal broken line, zone of significance, 0.95 probability. Solid line, dynamics of pattern coinciding with the neuronal activity occurring during the assignment phase; solid circles, dynamics of patterns coinciding with the neural activity occurring during the phase of vocal reproduction of the verbal signals; open circles, selection of the indicated patterns with a reduction in time.

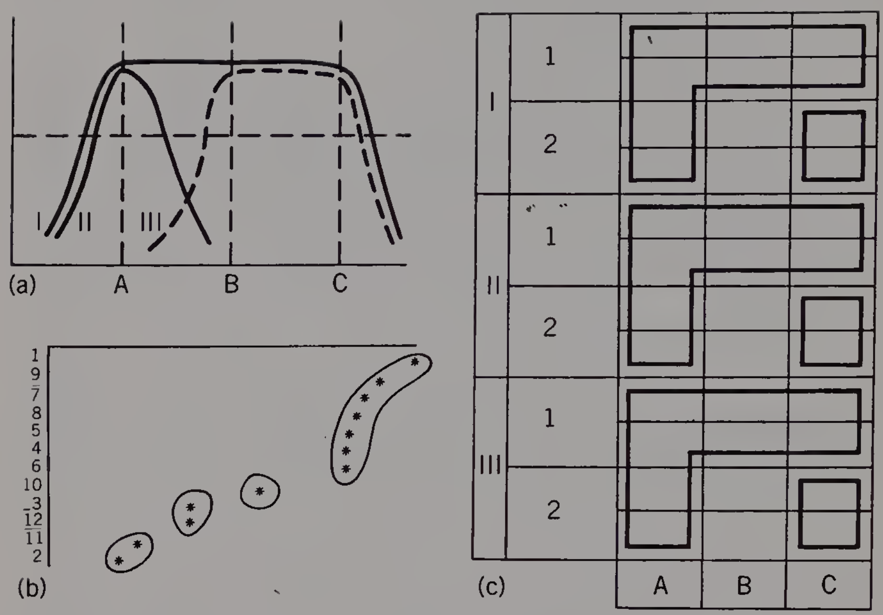

Figure 26. Classification analysis of multicellular activity patterns obtained during the teaching of new verbal signals (foreign words). (a) Diagram of pattern stability: I, ultrastable structure of the activity pattern arising at the moment of assignment during the performance of a test for memorization of unknown foreign words; II, the same pattern during assignment after the meaning of the words had been learned; III, a significantly changed pattern occurred during subsequent phases of the test. Horizontal axis, test phases: A, assignment; B, mental repetition; C, spoken repetition. Vertical axis, significance of the similarity. (b) Classification results from the electronic computer: horizontal axis, degree of similarity of patterns; vertical axis, number of fragments analyzed. (c) Table of classification results: I, II, and III, pairs of words presented twice each (1) before and (2) after teaching. The mental repetition phases after teaching were not separated into different classes, but are similar (95% reliability) to the corresponding spoken repetition phases after teaching. Horizontal axis, test phases (A, B, and C, as above). The fragments with significantly similar (99.9%) dynamics of multicellular activity are shown within the boxed areas.

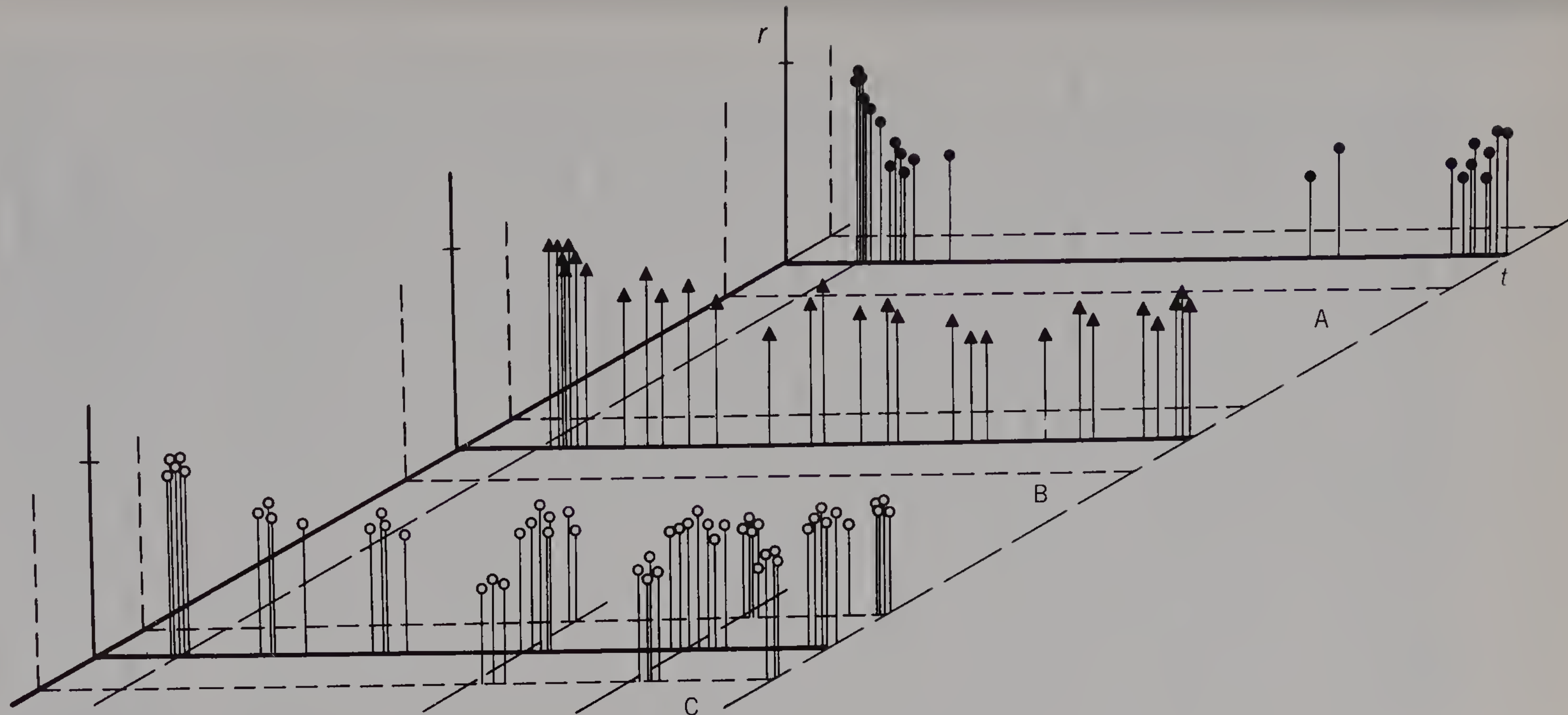

Figure 27. Dynamics of trace processes in multicellular activity during memorization of words with different frequency indices. Horizontal axis, time (t); vertical axis, correlation coefficients (r). Long dotted lines, phases of assignment and reproduction of test items; short dotted lines (parallel horizontal and vertical axes), activities of adjacent groups of neurons. Solid circles, solid triangles, and open circles, correlation coefficients (r) and their projections on time axis. A, dynamics of trace processes during coding of words with a high frequency index; B, of words with a low frequency index; C, of quasi-words.

crease in the spatial synchronization of the neurons in the group and a stabilization of the action potentials took place. Differentiation of the populations reached its maximum between the 6th and 12th seconds of retention of the words in memory.

Characteristic features of the changes in impulse activity during the presentation of quasi-words are a significant increase in high amplitude discharges and an increasing synchronization of cells in population. Differentiation of the neuronal populations can be observed only at the end of the retention phase, and the structuring of impulse flows observed during the presentation of semantically significant information is not observed when quasi-words are memorized (Fig. 28).

Multifactorial analysis thus has made it possible to isolate a highly specific form of coding of verbal signals, which is detected simultaneously with acoustic coding and in its absence as well. This code is expressed in altered patterns of interaction between adjacent and, apparently, distant groups of neurons; it represents a dynamic space-time reorganization of neuronal populations. Specific changes in the spatial relations between neuronal populations probably reflect semantic coding in the brain. The high specificity of this coding has made it possible to identify, in the impulse activity of neuronal populations, the appearance of correlates of a word even before it is pronounced by the patient, and the appearance of correlates of individual phonemes. On the basis of this type of coding, it is possible to investigate the course of the simplest thought processes, in the strict sense of the term, in the brain.

Thus, the coding of verbal signals may be characterized by changes in the current frequency of the impulse activity of neuronal populations, by the appearance of a bundle structure in the impulses, by impulses of a specific form, and by a particular spatial pattern of the relation between neuronal populations.

Dynamics of the Interaction between the Links of the Cerebral System for the Maintenance of Mental Activity

Results from electrical stimulation and the measurement of physiological indices of the brain's state during mental activity have shown that many links participate in the maintenance of this activity and that many polyfunctional cellular populations and mental functions are involved. It is logical and natural to imagine that these are not all separate, uncoordinated elements, but links within a single system. The word "system" is often used loosely in biology: the basis for postulating the presence of a system may be only the expression of an activity. A final integrated effect is thus taken as evidence for the presence of central integration.

New methods for the analysis of physiological data make it possible to investigate the organization of mental activity. One of these methods is correlation analysis, which, for more than 10 years, has been increasingly used in the study of interrelationships between different brain formations according to their bioelectric characteristics (Brazier and Barlow, 1956; Grindel, 1965; Belyaev, 1968). Brazier (1967) used correlation analysis of the electrosubcorticogram to study the dynamics of the interactions between human subcortical structures while the subject was awake and while he was falling asleep.

One may assume that if the electrosubcorticogram does reflect a state optimal for some given activity, arising from the states of many individual brain structures, then indications of the organization of individual structures into a system maintaining different forms of activity must be sought primarily in the electrosubcorticogram. This assumption is supported in the brilliant work of Livanov (1972) and his co-workers (Livanov, Gavrilova, and Aslanov, 1966), though these studies were carried out in human subjects only by analysis of EEGs recorded from the scalp.

In study of this system for maintaining mental activity, it is primarily the electrosubcorticogram with electrodes implanted directly in the brain which has been studied by the correlation analysis method.

Correlation analysis of background electrosubcorticograms (Belyaev, 1968, 1970) demonstrated characteristic regularities in the relationships between the biopotentials in different subcortical structures of the brain under conditions of calm wakefulness.

Neurotropic drugs that decrease the intensity of parkinso-

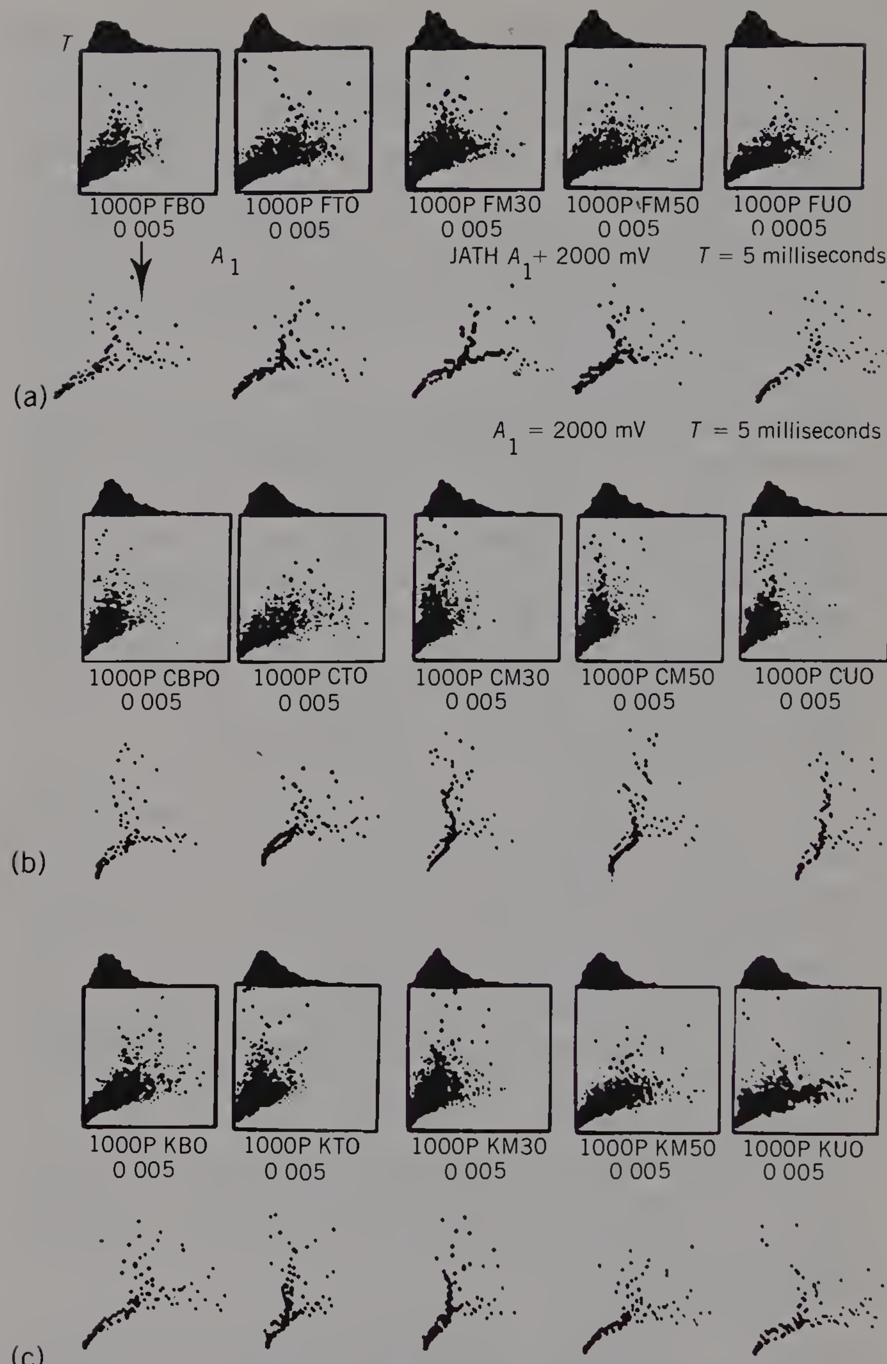

Figure 28. Patterns of multicellular activity isolated during the coding of words with different frequency indices. The upper series in (a), (b), and (c) are JATH histograms; the lower series are two-dimensional distributions of centers of JATH, calculated by

nian manifestations could change these relationships—and sometimes even reverse the biopotentials (Belyaev and Anichkov, cited by Belyaev, 1968). Even on the basis of preliminary data obtained by this method of studying mental activity, distinct changes in the interdependence of different subcortical formations can be detected. Changes in the closeness of connection in different stages of the performance of a test for operative memory were best shown by the time differences in states of high correlation between the structures, i.e., the "lag" or "advance" time of the bioelectric phenomena in one structure with respect to another (Belyaev, 1968). Here differences depending on the phase of the test, its nature, and the quality of performance could show up in both the rapid and slow components of the "cross-correlograms" (Fig. 29). Cross-correlation analysis of electrosubcorticograms thus revealed that during mental activity the interaction of the subcortical structures may change until it differs substantially from the background relationship. The synchronization during bioelectrical processes in different deep structures of the brain after both a correct and an incorrect response has attracted attention as it may be related to the connection of an emotional component ("self-evaluation") with the neurohumoral and bioelectric shifts in the brain that accompany it.

Differences in the correlation coefficient of the biopotentials among the structures investigated were on the whole small (see Fig. 29). Three basic variations were noted: (1) maintenance at a high level for all stages of the test, (2) maintenance at a low level for all stages, (3) a fall during the phase of retention in the memory followed by a rise after the response. Re-

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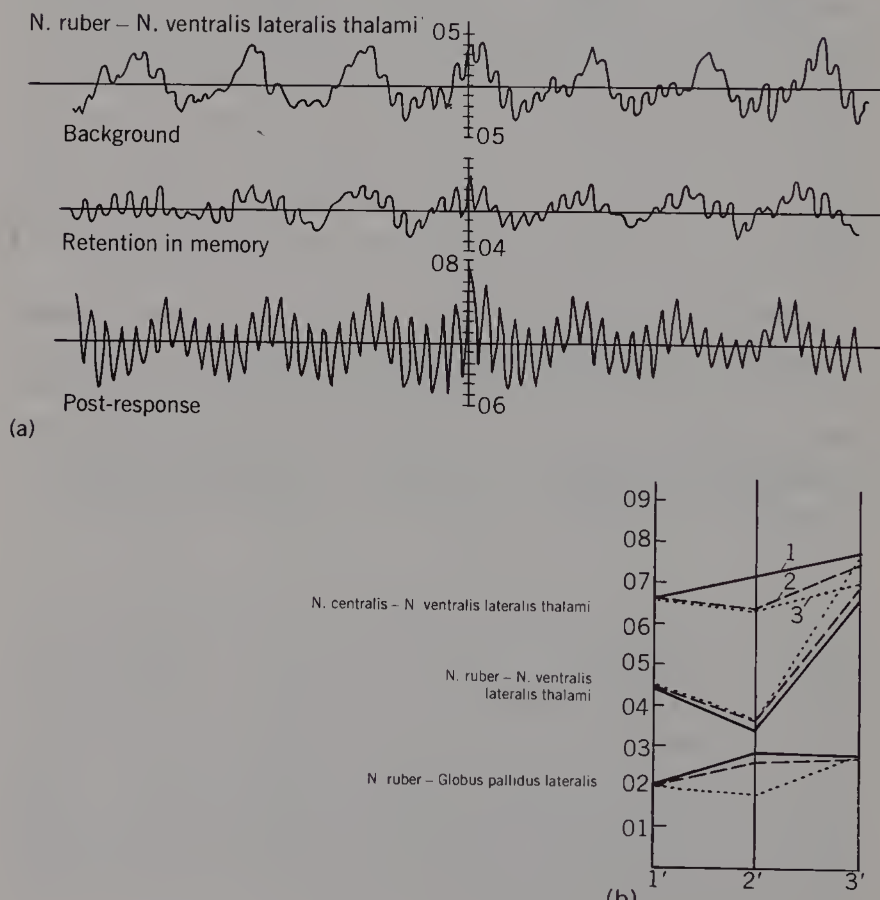
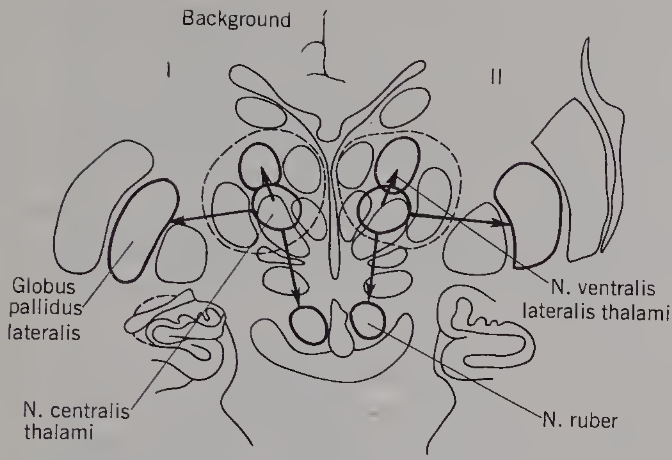
the JSCHW program (see text). Horizontal axes (histograms): A, amplitudes of spikes. Vertical axes: *t*, duration of spikes. The total number of spikes forming the histogram (P), the index of the coded verbal signals, and the scale of the vertical axis are shown under each histogram. Group F of the histograms corresponds to the coding of words with a low frequency index; group K to the coding of quasi-words. All series of dynamic histograms: BO, fragment of background activity; TO, presentation phase of verbal signals; M 30 and M 50, retention phases of verbal signals in memory; UO, reproduction phase of verbal signals.

lationships of this last type, which characterize a less close connection for the parameter in question, were observed between the nucleus ruber and the nucleus centralis of the thalamus.

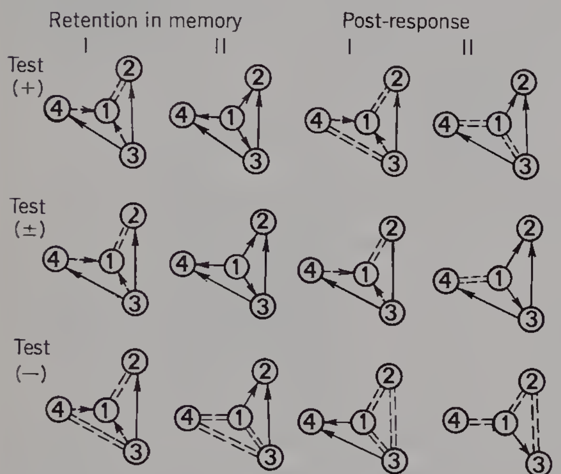
The changing relationships between elements of the neuronal population recorded from a single electrode and between different neuronal populations recorded from electrodes in areas where reproducible shifts in the physiological parameters appeared during psychological tests were defined in considerably greater detail through an analysis of the impulse activity (Bechtereva, Bundzen, Kaplunovsky, and Matveev, 1972; Bechtereva and Bundzen, 1974).

From such analyses, it was found that in a state of calm wakefulness (background), the activity of neuronal popula-





(c)



(d)

Figure 29. Dynamics of correlations during tests for operative memory. (a) Cross-correlograms, obtained from an analysis of the electrosubcorticogram during different phases of the performance of tests for operative memory. Vertical axis, correlation coefficient. (b) Typical variations in the dynamics of the cross-correlation coefficients: 1, test performed correctly; 2, test performed with a significant error; 3, test performed with a minor error; 1′, background; 2′, retention in memory; 3′, post-response. (c) Diagram of the brain. (d) Graphic representation of the dynamics of interaction with time between the subcortical structure according to the (I) rapid and (II) slow components of the cross-correlograms. The arrows go from a "leading" structure to a "lagging" structure; broken line, no shift with time.

tions is characterized by variations in the frequency, in the grouping, and in the nature of the functional organization of the impulses. It has been shown by factor analysis that during periods of the highest frequency of impulse discharge, most of the cell groups in a neuronal population operate synergistically. During periods of lowest discharge frequency, on the other hand, there is a significant differentiation among the neuronal populations. Thus, functional aggregates of different groups of neurons are formed "spontaneously" in neuronal populations (Fig. 30).

The presentation of psychological tests produces a change in "spontaneous" fluctuations: functionally united neuronal aggregates are formed according to the task being performed. Moreover, as in periods of maximal differentiation of the population, reciprocal relationships between the neurons of neighboring groups are often detected in the background activity during test performance; however, the specific organization of the neuronal populations may vary. A process of lateral inhibition (Matveev, 1971) apparently should be regarded as the physiological basis of this phenomenon.

One of the important conditions underlying the correctness of the performance of tests for short-term memory has proved to be the current frequency and the functional organization of the neuronal populations at the moment of test presentation. During periods of extreme current frequency values, and thus of maximum synergism on the one hand, or on the other, of differentiation among the neuronal populations, the performance in verbal tests declined. This decrease in the quality of test performance took the form of changes in the verbal signals, and their incorrect reproduction.

Therefore, it can be assumed that optimal starting conditions for information processing by the cerebral neuronal populations occur, in all probability, during periods when the organization of the neuronal populations is indeterminate.

A study of the dynamics of the multicellular activity of previously identified neuronal populations shows that, in the first place, during the period of retention of the verbal test items in the memory, the total number of interpopulation links is re-

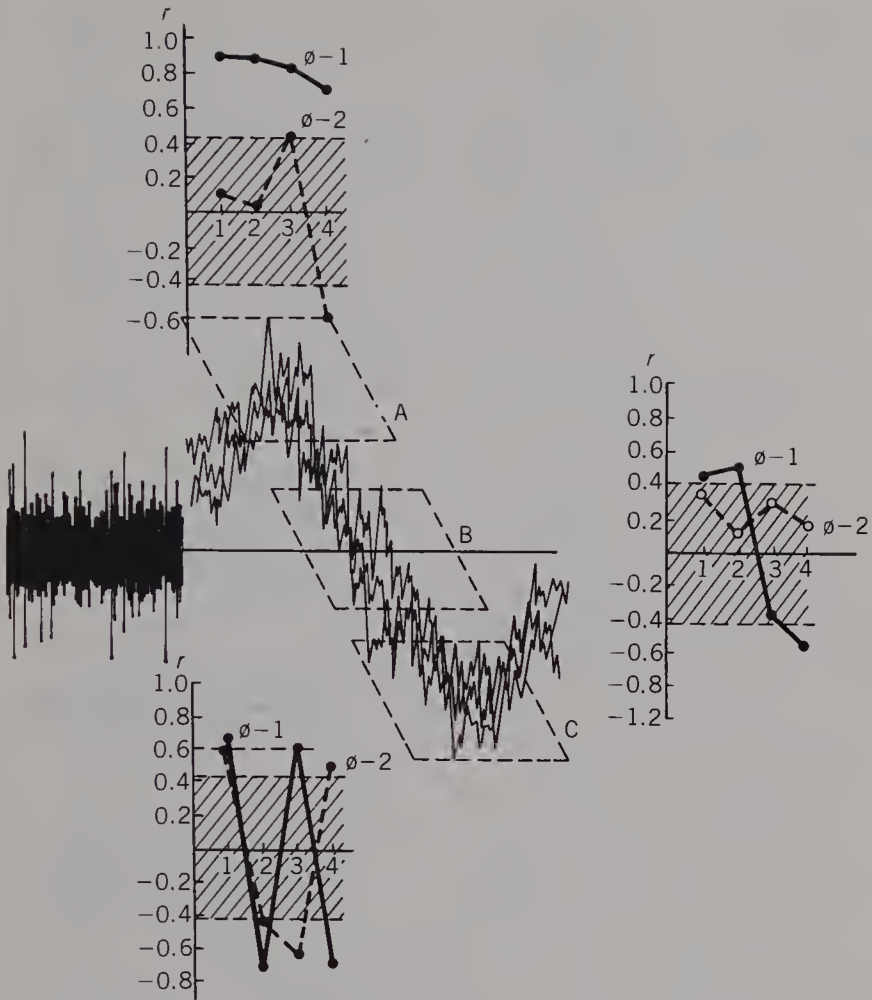


Figure 30. Nature of the changes in the structural-functional organization of the neuronal populations during a very slow cycle of background activity. Parts of the integrated multicellular activity of the neuronal populations have been provisionally designated, center. Broken lines, zones A, B, and C are the activity subsequently processed; results of a factorial analysis of the matrices of the inter-correlations between the functions of the current frequency of the neuron groups correspond to the zones A, B, and C. Horizontal axes: 1, 2, 3, and 4, activities of the neuron groups isolated by discrimination analysis; vertical axes, correlation coefficients (r). ϕ-1 and ϕ-2, factorial values. Hatched line, region of non-significant values. Part of the original recording of the multicellular activity is at left.

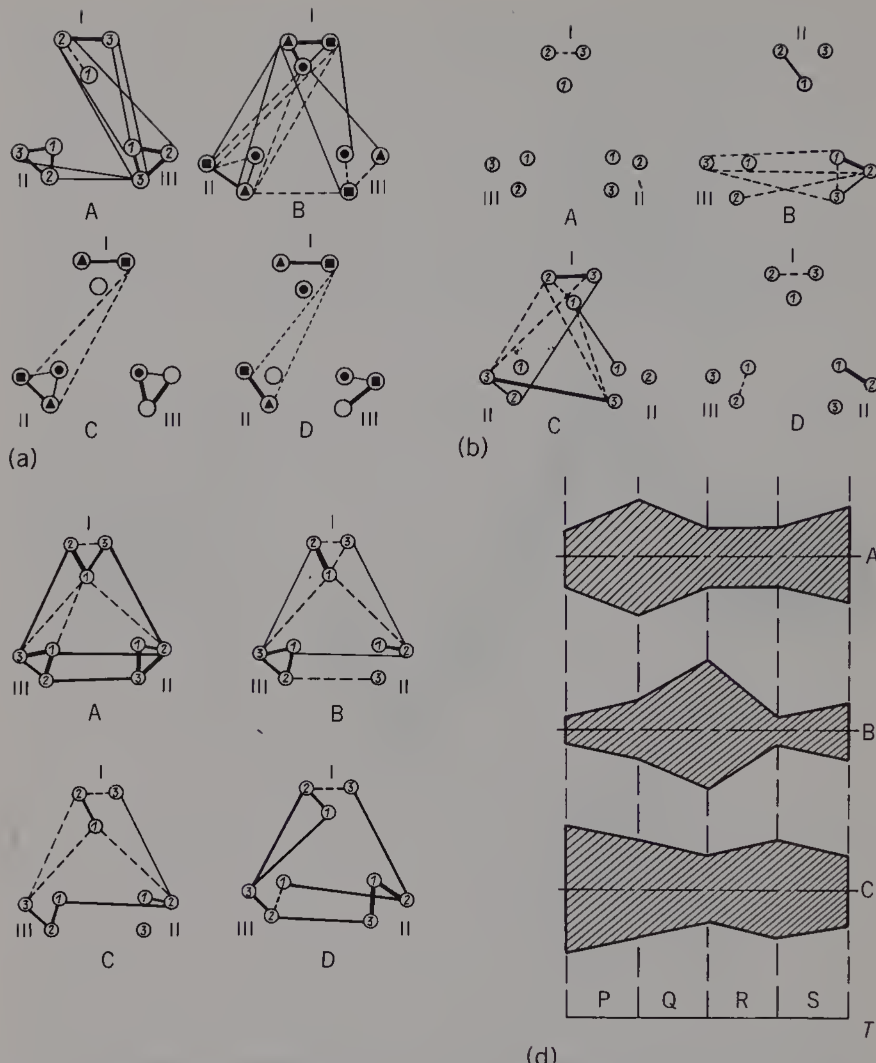


Figure 31. Cross-correlation analysis of the functions of the current frequency of the neuronal groups (1, 2, and 3) isolated within the limits of the neuronal population (I, II, and III) under conditions of (a) correct and (b, c) incorrect performances of a test for short-term verbal memory. Heavy solid line, 0.999 probability of a positive link; thin solid line, 0.99 probability; thin broken line, 0.95 probability of a negative link; heavy broken line, 0.99 probability; dotted line, 0.999 probability of a negative link.
Average dynamics of the overall magnitudes of the matrices of the intercorrelations of functions of the current frequency of the activity of neuron groups isolated from the populations by discrimination analysis at different stages of tests for short-term verbal memory. P, background phases; Q, assignment; R, mental

duced, and the links formed during the assignment phase (rigid components) still predominate. In the second place, along with a progressive decline in the impulse discharge frequency, there is an increase in the magnitude of the negative correlation links, indicating greater reciprocity of operation between the neuronal aggregates participating in the maintenance of mental activity. Moreover, a stable profile of functional relationships prevails between neuronal aggregates in which trace processes are most likely to be found (Fig. 31).

An analysis of the processes by which neuronal systems are organized while trace reactions persist indicates that during this phase there is not an overall minimization of interaction between the systems' links but rather an optimal minimization of the interaction between a functionally significant neurodynamic complex and neuronal elements that do not directly determine the result of the ongoing activity (P. V. Bundzen; see Bechtereva and Bundzen, 1974). A minimization of the possibilities for interaction between the functioning system and "extraneous factors," the "environment," probably occurs. This principle of self-organization can ensure economic operating conditions for the system, along with an increased stability of the informationally significant structural-functional complex in a "noisy" environment.

The formation of functionally determined neuronal aggregates is evidently most important in the "rearrangement" of a polyfunctional neuronal population for its participation in the maintenance of a specific type of activity. It is precisely on this basis that changes within the aggregates can be correlated not only with the phase of the psychological test but also with the characteristics of the stimuli presented.

A study of the neurophysiological mechanisms of human mental activity, carried out by analysis of physiological indices

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reproduction of the test; S, spoken reproduction of the test; T, aftereffect; A, correct; B and C, incorrect performance of the tests. Horizontal axis, stages of the tests; vertical axis, relative magnitude of the correlation links. Phases: A, background activity; B, test assignment for verbal memory; C, mental reproduction of the test; D, spoken reproduction of the test.

of the brain that were directly recorded, has provided information on certain principles of brain function. About 2,000 points in the brain were investigated. Selected physiological phenomena were studied in relation to a few relatively simple forms of mental activity (to reduce the number of unknowns in the solution of complex "equations"). The results shed light on at least some of the physiological mechanisms of human mental activity.

These investigations showed that it is possible to study how the brain is designed to ensure the adequacy of mental activity as environmental conditions are changing, what maintains its flexibility under these conditions and how maximum economy in brain function is achieved. A new experimental phase has begun: investigation of the code of mental phenomena.

Data obtained from patients cannot carry the same significance as data for the healthy brain. However, the principles established in these clinical studies apparently have general application, and we may hope that the continued accumulation of data will not only confirm these principles but will also permit the many questions concerning the mechanisms of the most complex function of the human brain–mental activity–to be gradually answered.

4 Some Fundamental Questions and Prospects

Progress in scientific research is related to the requirements of practice, to methodological possibilities, and to motivating ideas. A promising, far-ranging idea may throw light far ahead along the difficult road into the unknown. When a viable theory arises in the mind of an investigator despite inadequate information, it may be "laid aside" and initially forgotten if there is no method to obtain additional information and to verify and elaborate on the theory. Sometimes an idea may be rediscovered and thus comes to life many years later when a new method makes possible the experiment that can be used to test it.

In the physiology of higher nervous activity, a striking example of the combination of promising ideas and methods was the Pavlovian stage of its experimental study.

Studies of the physiology of human mental phenomena using model conditioned reflex reactions have confirmed that the conditioned reflex principle extends to human mental activity. However, these models have contributed relatively little to an understanding of the neurophysiological mechanisms of complex human mental phenomena. When neurophysiological data obtained in studies of conditioned reflex reactions and the performance of very simple psychological tests are compared, even though only one direct measure of the development of changes in the brain—the electroencephalogram—is analyzed, it is evident that the EEGs in these two situations, which are similar in principle, may be distinctly different.

The EEGs differ especially in the extent of the bioelectrical changes that occur and in the direct involvement of nonspecific and specific brain structures.

It followed from this that in order to study the neurophysiological mechanisms of mental phenomena, one must use not only sterotypic conditioned reflex tests but also psychological methods along with a variety of neurophysiological techniques. Thus, in studying the mechanisms of human mental phenomena, we combined the classical methods of Pavlovian physiology and those of the "old" psychology, with modern methods of neurophysiology.

Among the many different views on the physiological mechanisms of normal and pathological human mental phenomena held by psychologists and clinicians, there have undoubtedly been some valuable ideas. Thus, it is difficult even now to raise any substantial objections to some of Jackson's early views discussed earlier in the book. The fundamental concepts of the cerebral organization of mental activity developed by Filimonov (1940), which were supported and elaborated upon by Luriya (1962) and others, and which have much in common with these early views, are being confirmed by the most subtle studies of the human brain possible at this time. Advances in research on the physiology of the human brain are confirming the complexity of localization of functions and the plurality of formations at different levels of the brain which participate in the maintenance of mental activity. The multiplicity of functions of structures of the brain has not only been confirmed at the level of cell populations, but it is also the basis of the potential for performing the most complex forms of mental activity under the changing conditions of ordinary human life. The view that there are multiple links in the system that maintains mental activity, confirmed by neurophysiological studies, is also supported by the finding that disruption of a particular mental function may be associated with pathological foci in different brain areas and that often only very particular characteristics of a psychopathological syndrome will depend on where the focus develops. During the diagnosis and treatment of patients by the implanted-electrode method, and thus under conditions of direct contact with the brain, data were obtained that made it possible to investigate certain principles concerning the complex regulation of functions by brain systems as well as the maintenance of mental activity.

On the basis of past and current work, a hypothesis was advanced concerning the maintenance of human mental activity by a cortical-subcortical, structural-functional system with links of different degrees of rigidity: rigid links, which necessarily participate in the reaction and ensure economy of operation of the brain, and flexible links, which may or may not be connected depending on variations in the external environment, the internal environment of the brain, and the quality of the mental activity in progress.

The outer world, with its regularities varying within narrow limits plus a large number of random, irregularly occurring phenomena, which can dominate human interactions, is reflected in the rigid and flexible links of the system for controlling mental activity. In parallel with the views of Vavilov (1950) on how eye structure is related to characteristics of the solar spectrum, we may assume that fundamental characteristics of the environment, including the psychosocial environment, must be taken into account in an analysis of this system.

Neurological and neurosurgical practice confirms the interchangeability not only of flexible elements, but also—in the case of a unilateral injury—of rigid elements. It may be imagined that the formation of such a system, though morphologically predetermined by the evolution of the species, is always primarily the result of individual development. In human history, the structural organization of this system is primarily a manifestation of the statistical influence of species characteristics on individual characteristics.

On the other hand, this structural organization, or anatomical "predetermination," is itself the optimal experience of individuals, accumulated and consolidated during the process of evolution. How, on the basis of available data from brain research, can we most logically infer the effect of individual experience on species characteristics? What is being consolidated in the continuous process of interaction with the environment, which is becoming increasingly more complex? Is it correct to speak of the transition from conditioned reflex reactions to unconditioned reactions (at the human level), and is this transition beneficial?

Apparently, the variability of the external environment, which determines the formation of the flexible structural apparatus of brain activity (the flexible links of the system) and of the flexible physiological apparatus (conditioned reflex reactions), also determines the development of some of the most common and most important, biologically favorable reactions. In this case, it is not the reaction itself that is consolidated (or, more precisely, that may be consolidated), but the ease of its formation. The influence of individual experience on the experience of the species may thus appear as a consolidation of the underlying mechanisms of reactions, which again emphasizes the importance of flexibility in the phase of evolution in question. Ecological physiology presents convincing examples of this evolutionary path, and a similar point of view may be found in W. M. Bechterew's *General Fundamentals of Human Reflexology*.

A sharp increase in the number of flexible links in the system for the control of mental activity is the basis for the exceptionally high operating resources of this system.

This factor—the appearance of flexible links and later the large increase in the number of these links in the system—is also of fundamental importance in determining the complexities of brain systems. It may be noted in passing that when the relationship between rigid and flexible elements is considered, there are fundamental differences not only between the system for the maintenance of mental functions and, for example, the system that maintains motor functions, but also between the systems for maintaining mental and emotional reactions; this in no way rules out a very close relationship between these latter systems.

The predominance of flexible links in the system for the maintenance of mental functions also indicates why a physiological study of this system was impossible for such a long time: the investigators who attempted to study it did so by disconnection and stimulation methods (which, in humans, naturally served as methods of diagnosis and treatment). In principle, flexible links in the system could appear under conditions of brain stimulation but in practice they were seen only when a defect could be revealed. For example, a defect in some form of mental activity might be manifested when stimulation was carried out against additional background "noise," or conversely, with sensory deprivation. Studies of this type, however, have not been performed on human subjects. Furthermore, the method of electrical stimulation also has fundamental limitations in the study of the structural-functional organization of the brain, in that not only locally produced effects but also a wide range of both simple and complex distant effects may be observed.

Only a combination of information obtained from a "natural experiment"–focal brain disease–with truly miltidisciplinary investigations of neurodynamics has made it possible to show that connections and disconnections occur in the brain during the maintenance of mental activity and that they occur in a certain way.

An important result of the investigation of neuronal populations, carried out by physiological, mathematical, and pharmacological methods, has been the convincing demonstration of the common character of the neurophysiological mechanisms of the different forms of activity investigated, and the complexity of these mechanisms at the level of the system. Thus, Sherrington's well-known dualistic thesis of the fundamental differences between neural and mental phenomena has been challenged (if not refuted), and the basis for realizing the brilliant Pavlovian thesis that it is necessary to correlate the patterns of mental activity with physiological design has been established.

This, however, means only that the way is open for such an effort: every step along this path is very difficult. A definitive study of this problem is now primarily a question of technique, time, and clinical and physiological collaboration to ensure that the maximum number of brain regions at different levels is investigated. The first and foremost problem is to study the cerebral cortex, which is not only feasible, but also very important clinically in relation to some forms of epilepsy and mental disorder.

Findings on the mechanisms for the reliable maintenance of mental activity should help in approaching this problem. Among these mechanisms, a paramount part is played by (1) the multiple-link structure of the system of mental control and (2) the presence in this structure not only of fixed, rigid elements but also of variable, flexible elements.

The property of "connecting" different links in the system of mental control by specific neurotransmitters makes it possible for a polyfunctional neuronal population to function as an element of this system, but the activity of these links may be disrupted when the biochemical mediator mechanism is damaged. Biochemical mediation substantially changes the properties of the polyfunctional neuronal population, either "extinguishing" or activating its various resources, narrowing or broadening its functional range.

The differences in biochemical mediation in different links of the system that maintains control of mental functions, which preserve its capacity to function during a disturbance of any single form of biochemical mediation, are undoubtedly an important basis for its reliability. They assure that mental activity can be maintained during changes in the external environment of the organism and in the internal environment of the brain.

It is impossible to understand the mechanism for the reliable maintenance of an activity, in particular, a mental activity, without considering the mechanism for its optimization—the mechanism that reduces the overall probability of errors and determines the quality of its performance. A very important mechanism for the optimization of mental activity is the detection of errors, which is carried out in the brain by neuronal populations that selectively or exclusively react to incorrect performance of an assigned activity—in the present case, of psychological tests. A researcher in our laboratory, V. B. Grechin, has shown that at the moment of error detection, the neuronal population that functions as an error detector becomes "leading" with respect to many other neuronal populations: its physiological processes occur before the analogous physiological processes develop in the other populations (as shown by cross-correlation analysis of the dynamics of the available oxygen). In light of these findings, the concept of an error detector as a formation activating a reaction and determining the possibility of the performance of a subsequent brain activity at a higher energetic level is taking on increasing detail. A number of zones that react selectively or exclusively to the incorrect performance of a psychological task have already been detected in the human brain, which allows us to speak not only of error detectors but also of an error-detection apparatus. The possibility that this error-detection apparatus is wholly, or more probably partly, common to different activities has not been excluded.

The presence in the brain of neuronal populations that react subtly to an incorrect action, as well as the different degrees of intensity of the reactions to an error in a psychological test, leads to the assumption that the different elements of the error-detection apparatus are not equally significant and that they are arranged in a hierarchy. It is possible that this hierarchy is dynamic and is determined, to a large extent, by the nature of the activity performed; however, this problem requires further study. One can say, with a certain degree of confidence, only that in the realization of a mental activity, the error detectors of the neuronal populations of the nucleus caudatus are of great importance.

Thus, the mechanisms for the reliable maintenance of mental activity may be considered to include an error-detection apparatus, which helps optimize this activity.

However, the error-detection apparatus should be considered on still another level—the role it may play in psychopathology. The disturbances in error detection that we have observed when neurotropic drugs were administered—the appearance of identical or very similar reactions in neuronal populations during both incorrect and correct performances of psychological tests—suggest one form of pathological change. The breakdown of selective or exclusive reactions of elements of the error-detection apparatus, and thus the partial or complete disruption of the conditions for the optimization of mental activity, may be the basis for certain intrinsic mental disorders. This type of disturbance may also account for the empirically observed danger of driving an automobile after taking certain tranquilizers.

Changes in the error-detection apparatus may also develop in another way: stimulation of those structures whose neuronal populations contain elements of the error-detection apparatus leads to errors. We observed an increase in the number of errors in the responses to psychological tests during stimulation of the neuronal populations of the nucleus caudatus. Disturbances in the body image during electrical stimulation of the deep structures described by Smirnov (1967) apparently can be regarded as another manifestation of a disruption of the error-detection apparatus (of the stable activation type).

It can be imagined that the error detector also may take on, as it were, independent, more "natural" conditions of pathology, changing from a detector–an optimizer of the activity–to a determinant of disturbance in the activity. A process of this type might, in particular, be thought to underlie those psychopathological syndromes in which there is a repetition of certain actions and other behavioral inadequacies are exhibited. Constant activity of the structure which is not determined by an error but is fundamental to some action connected with error detection, constantly signals a mismatch between the action being performed (or some other situational reality) and the intent, regardless of the correctness or incorrectness of the action.

Although the structural-functional basis and certain mechanisms employed by the system of cerebral control of mental functions are being studied rather widely at this time, the elucidation of specific physiological correlates of specific mental processes requires a methodological "leap" forward.

The prerequisites for this advance have been provided by the development of a special method for the analysis of impulse activity which permits very subtle changes to be demonstrated. This and other new methods for the investigation of the human brain have enabled us to define problems which are new in principle and to attempt their solution. These new methods can be roughly characterized by pointing out the relative ease of answering the question "Where?," since they can be used to determine the brain zones (neuronal aggregates) related to the maintenance of an activity and, hence, the possibility of answering the question "How?," "In what way?" The second question relates to the types of general and local changes in the brain that not only accompany the process of maintaining mental activity but also are at its base. Primarily, it involves the problems of how the perception, recognition, and reproduction of words and word use take place, and from this, of how the brain handles especially human information. These problems may be solved in part by studying the physiology of the coding and decoding of verbal signals in the brain, and the manner of formation of these important signals, without which the performance of thought processes is impossible.

It is important to emphasize that the physiology of mental processes is a key problem at the present stage of research. Only its elucidation will make it possible to bridge the gaps between what would appear to be widely separated biochemical and psychological data on the brain, which must be the basis for a coherent theory of human thought processes. A general theoretical prerequisite in the search for subtle physiological correlates of neurophysiological mechanisms of mental processes is the concept that the activity of specific structural-functional units may quite specifically correspond to mental processes—to their codes, particularly the code of verbal signals—and that the coding process of verbal signals is effected, if only in part, by means of bioelectrical processes, or is at least reflected in these processes.

Are there, however, sufficient grounds for searching for such codes in bioelectrical processes? Is it possible that a search for these codes in neurophysiological terms merely represents the pursuit of a chimera? A final answer to this question would be found, however paradoxical this may be, only in its answer. This is not the only case in science where the voices of the skeptics are very loud. Nevertheless, certain foundations for a search for these codes do perhaps exist.

First, the experiments of Lettvin, Maturana, McCulloch, and Pitts (cited by Vasilevsky and Soroko, 1969) showed that specific neurons of the frog's optic system selectively react to characteristic properties of a stimulus, and produced many analogous observations, including some on human subjects, of changes in neuronal activity related to specific properties of the stumuli (Jasper, 1966; Mountcastle and Granit, cited by Jasper, 1966; and others). Second, it has been found that the application of a strong stimulus, particularly a visual stimulus with a specific structure (Vasilevsky and Soroko, 1969), will lead to a reproduction of the same structure in the pattern of neuronal activity and to the retention of traces of the stimulation in the activity of certain neurons. Third, observations on patients with implanted electrodes (Bondarchuk, cited by Bechtereva, Bondarchuk, Smirnov, and Trokhachev, 1967) revealed that when trigger visual stimuli were presented, according to the program of an electrical stimulation closely related to the regulation of arterial pressure, a significant increase in bioelectrical activity lasting for more than 24 hours was observed with biopotential leads from the brain regions involved in vision. Fourth, there are some data on the very characteristic spectrum of the impulse activity in the phase of retention in memory during the performance of the psychological tests we used (involving reproduction of a series of arbitrary numbers), a spectrum that differs substantially both from the background and from what is observed during "non-retention" of the test in the memory, followed by its incorrect reproduction. None of these findings bear directly on the problem under discussion, yet the common basic character of the neurophysiological mechanisms of different forms of activity allows us to hope that in the neuronal activity of the elements of the system for maintaining mental activity, we may also be able to find correlates of specific mental phenomena, even though the signal-noise problem is extremely complicated. At what stage in the approach to solving this problem are we now?

It can be said without exaggeration that the first steps toward deciphering the impulse code of mental phenomena were very promising. Zones in which changes in impulse activity depended on the acoustic characteristics of a word were found in deep structures of the human brain. It can be imagined that this type of change could also, in principle, be detected in a response to any less specific acoustic signal, not only in humans but also in animals. A year after these changes were detected in humans, very similar phenomena in response to verbal signals were detected in animals (Walker and Halas, 1972). These data showed that an initial analysis of verbal signals takes place in the brain, which permits a further "address" to the long-term memory for the signals' semantic meaning, that is, for decoding. These concepts were supported by the detection of a second type of pattern, unrelated to the acoustic properties of the signal, in the human brain. This pattern, provisionally called "autonomous," is evidently related to the semantic properties of the signal (Bechtereva et al., 1973).

Some quite characteristic changes in the shape of biopotentials were noted when words with a high frequency index were presented. When words with a low frequency index were presented, the changes observed were less distinct. This is apparently related to a noise effect on the bioelectrical pattern that produces changes of a relatively nonspecific nature connected with processes involved in activating engrams of long-term memory, which are processes of an energetic nature. Nevertheless, a kind of microstructure of the patterns found from 6 to 12 seconds after words with a high frequency index were presented was also detected in this case. This second type of pattern must be regarded as one of the elements of the bioelectrical code of especially human verbal signals, a very important element in the further integration of strictly mental activity.

A third pattern was characterized by a dynamic reorganization of the interaction between neuronal aggregates, and thus was designated as a space-time code. It was observed both in those neuronal populations where an acoustically dependent change in the current frequency of neuronal discharges occurred and in those where a change of this type did not occur. This code, which was demonstrated by factor analysis, made it possible to detect space-time bioelectrical correlates of the individual phonemes, and thereby opened new possibilities for the control of the cerebral code of words. This space-time code of phonemes is an element in the complex reorganization of the activity of neuronal aggregates during acoustic coding.

With this space-time code, it was possible to detect the neurophysiological correlates of a word even before it was pronounced by the patient in those neuronal populations where the acoustic code was not detected either at the moment of perception or at the moment of pronunciation of the word. This made it possible to move from an investigation of the coding of words in the brain to a study of the mechanisms by which their common semantic character is revealed in the brain. Thus, for example, by interpretating the code of different words, it was possible, after presenting the words "chair," "table," and "wardrobe" to the patient, to detect the code of the word "furniture" in the brain even before the word was pronounced by the patient (Fig. 32).

This space-time code may thus be a very significant element in the semantic code. An indirect, although quite impressive piece of evidence for the hypothesis of the presence of a semantic code in the brain is the occurrence of similar bioelectric changes in response to words that are very dissimilar in their acoustic properties but similar in their semantic properties (Gogolitsyn, 1973). Many years of child psychology experiments on the interaction of signal systems in the learning process, and also the data of Livanov (1972) on spatial bioelectric dynamics in the brain during mental activity, provide an impressive basis for investigations of the space-time code, especially the processes of semantic coding. In this connection, it is important to investigate the spatial relationships not only in one neuronal population but also between distant populations.

In such investigations, some data on the mechanisms of verbal memory have been obtained. The stability of the bioelectric patterns related to acoustic characteristics and of the autonomous patterns during the presentation of infrequently used words, words of unknown semantic significance, and quasiwords is related to the mechanisms of short-term memory, one aspect of which is a relatively large expenditure of energy at the bioelectric level. Pattern stability during short-term memory is probably related not only to the activating mechanisms but also to the absence of an inhibiting effect of a clear-cut engram of long-term memory on the bioelectric reverberation process. From the available data, it can be postulated that stable reverberation processes, characterized by high synchronization of neuronal activity and thus by limited "degrees of

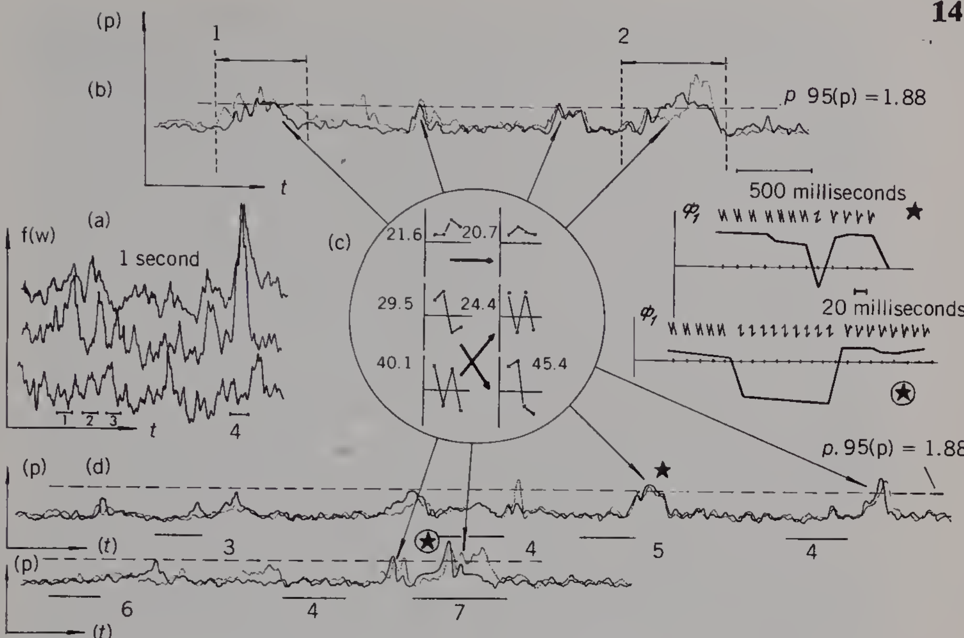

Figure 32. Change in function of current frequency of three neuronal populations during an induction test. (a) 1, 2, and 3, moments of presentation of words "chair," "table," and "wardrobe"; 4, response "furniture" by test subject. (b) Results of the selection of a space-time form of organization of the neuronal population specific for the treatment of a verbal signal of generalized meaning ("furniture"). (c) Profile of the interaction of neuronal aggregates isolated by the factorial analysis method and specific for the treatment of the verbal signal "furniture." (d) Selection of a specific form of aggregate organization from the results of a multicellular activity analysis in an induction test. Horizontal axis, time; vertical axis, degree of similarity of current aggregate organization of population to specific form. Asterisks, periods of maximum similarity. 1, assignment of "furniture"; 2, response "furniture"; 3, assignment of "table"; 4, response; 5, assignment of "chair"; 6, assignment of "wardrobe"; 7, "furniture."

freedom" of the neuronal systems, lead to changes in synaptic conductivity and to conformational changes in the subsynaptic membranes of nerve cells, i.e., that these processes provide the consolidation of new engrams of long-term memory (Bundzen, cited by Bechtereva, Bundzen, Keidel, and David, 1973). Of course, the early investigations of a bioelectric code did not explain all the bioelectric manifestations of memory.

The assumptions stated above are in complete agreement with Bundzen's concept (1972) of a hierarchical organization of memory and may be compared with some aspects of Belenkov's hypothesis (1973) of an interaction between long-term and short-term memory. The implication is that retarding effects of long-term memory engrams are particularly distinct in tests using words with a high frequency index. The stability of the neural code of verbal signals is apparently achieved by a feedback mechanism, which depends on the degree of functional activity of long-term memory engrams. The trace patterns are stabilized not only by a time limitation but also by a spatial limitation of this code, with the latter evidently being achieved by lateral inhibition processes (Matveev, 1971).

The concept of "codes" in physiology has become rather broad. One often speaks of central nervous system coding and decoding of signals from the outside world when it is a matter, essentially, of a transfer from neuron to neuron through biochemical mediation, by highly specific processes in the membrane and in the nerve cell itself, of more or less complex signals in an "undeciphered" form whose neurophysiological characteristics are unknown (Keidel, 1971). In the broad sense of the word codes, this is legitimate, the more so since in this context the question of the principles and specific characteristics of the bioelectric and biochemical coding of signals in the brain is not always raised.

With respect to especially human (mental) activity, the problem becomes immeasurably more complex. It is not only a matter of "coding" the physical properties of the signal, or of the need to use this "coded" signal to trigger a more or less complex behavioral reaction, but it is also a matter of coding these signals, each of which, upon decoding, regains its meaning (frequently taking on an "individual coloration" at the same time) and forms the basis of thought processes through numerous interactions and mutual exclusions. To begin a study of this problem, it is necessary not only to select adequate approaches but also to determine, even if only approximately, the real present-day limits of the potentials of each discipline in this field of investigation. The problem of elucidating the laws of the most complex intellectual activity is apparently the task of the psychologists for today and tomorrow, although it is not impossible that neurophysiologists may also find approaches to this problem the day after tomorrow.

Neurophysiologists can approach this problem by investigating the laws of coding and decoding verbal signals at different levels of the central nervous system—where "input" and "output" take place in the structures that code the signal according to its acoustic characteristics, in structures where a direct interaction with the long-term memory takes place, and finally, in structures where the semantic code is formed. Our success, to a considerable extent, will depend upon the method used to determine the bioelectric characteristics of the brain that are most closely related to these phenomena. Investigation of the problem can be considered to have been started in 1971 (Bechtereva, Bundzen, Matveev, and Kaplunovsky, 1971).

The search for the neural code should undoubtedly be carried out on the level of impulse activity of the cerebral cortex (Milner and Taylor, 1972), primarily the temporal lobe. It is possible that a large number of active zones will be detected there with memory engrams both separate and functionally joined.

In line with current concepts of long-term memory, we assume that memory is based on conformational changes in protein molecules. However, it may be possible to detect a bioelectric pattern in the storage region for the engrams of long-term memory, since the computation mechanism is evidently related to a bioelectrically determined activation of the membranes.

Most current concepts of biochemical mediation in the brain are difficult to reconcile with data on the detection of bioelectric patterns in areas remote from the periphery, particularly patterns of the primary (acoustic) type, which can be correlated with the characteristics of so complex an input signal as a word. If one imagines the movement of impulses through a multiplicity of synapses, with electrical impulses passing through an intermediate biochemical phase of epinephrine, norepinephrine, acetylcholine, or other medication, then the central focus for coding, since there would be an inevitable loss of specificity of the characteristics of the bioelectric flow, would, even during the very first phases of coding, have to shift from a bioelectric pattern to a specific neuronal or neurological structure. Thus, correlation of cerebral bioelectric phenomena with the characteristics of the input signal would appear to be impracticable, in principle. Nevertheless, investigations have demonstrated a link of this type.

Relationships between bioelectric and biochemical phenomenon in the brain are best explained on the basis of theories developed by Bogoch (1968) and similar ones advanced by Adey (1970) on the role of glycoproteins and mucopolysaccharides in the transfer of information in the central nervous system. Adey (1970) emphasizes the role of cell membrane mucopolysaccharides, which combine easily with ions, in the high sensitivity of the central nervous system to electrical impulses. Even more tempting, it would seem, is Bogoch's view (1968, 1972) that glycoproteins might provide a very rapid and highly selective transfer of electrical impulses between neurons of the central nervous system and an equally specific and rapid contact between neurons and glia. Concepts of this type could adequately explain the retention of specific connections of the input signal in brain activity. However, these and similar hypotheses have not yet received widespread dissemination because there has not yet been sufficient confirmation.

The direct (bioelectric code) and indirect (dynamics of coding in relation to a long-term memory base) data obtained from human subjects make it possible to construct an approximate scheme of the *coding* and *decoding* of verbal signals in the human brain (Fig. 33). According to this scheme, the initial coding of words is carried out according to the laws for the coding of complex acoustic signals and is independent of the semantic content of these words. The resulting acoustic code is then addressed to the long-term memory, accumulated through individual experience, and activates a corresponding word engram, or forms it if none exists. At the level of acoustic coding, depending on a number of additional factors (the emotional coloring of the situation, other motivation or other stimuli, etc.), a preliminary selection, a "filtering" of the information is possible. Activation of the long-term memory leads to the formation in the brain of a new operative unit, a semantic

Figure 33. Diagram of coding and decoding of verbal signals in the human brain. 1, integrative activity; 2, decoding of semantics; 3, secondary code; 4, control code; 5, primary code (acoustic).

code, which can serve as the basis for other, significantly more complex mental processes. If the mental process in the brain is realized verbally, a control code is formed. If there is no corresponding word engram in long-term memory, the functions of the control code may also be carried out by the primary acoustic code formed in the brain upon presentation of an unknown word.

The study of the cerebral coding of mental processes has a high priority in Soviet science. Data on the cerebral code of words are very important in studies of the most subtle cerebral mechanisms of the most complex mental processes. In this field, investigators undoubtedly still have a vast amount of work ahead of them. The investigation of ever more complex mental processes—and a consolidation of the advances made—should create an increasingly full archive of the codes of wide variety of words.

An understanding of the neural code of mental activity would obviously have exceptional importance in physiology, psychology, neurology, psychiatry, and philosophy, apart from its fascination for all who are interested in the workings of the mind. But how would it affect humanity? By making mental processes much more thoroughly controllable than is possible now by neuropharmacological or electrophysiological means, would not scientists again (and how many times this has happened already!) be letting a "genie out of the bottle," a genie they would not be able to put back again? Is it therefore necessary to try to interpret the neural code?

Yes, it is, as is continued work in all other areas of science, including those in which progress has unintentionally proved to be a threat to humanity. It is a truism that knowledge itself is never dangerous.

Deciphering the neural code would give humans true power over themselves, and would make diseases affecting the code—disturbances that still doom hundreds of thousands of people throughout the world to a long stay in the wards of psychiatric hospitals—treatable.

All this is still in the future. But if we return to the purely applied level, if we carefully analyze the present store of neuroscientific knowledge from the viewpoint of its clinical value, then it is evident how many problems related to brain disease now seem capable of being solved.

Thus, for example, specific avenues for the treatment of mental disturbances may be opened up by the use of data on disturbances in the error-detection apparatus. Studies of the activity of neurotropic agents with respect to this apparatus indicate that certain drugs may correct detector disturbances of both the *despecialization* type and the type in which the detector is converted to an error determinant. In very severe cases of stable activation of the error determinant, the destruction of this disease element of the error-detection apparatus apparently may be rational therapy. Further, it has been convincingly shown that emotional reactions are related to shifts, in specific brain structures, of the slow electrical processes, apparently primarily of the steady potential. The shift in the steady potential is observed in the brain during the development of emotions; when evoked artificially, it leads to the development of an emotional reaction.

When these shifts in the slow electrical processes (steady potential) are combined according to the conditioned reflex principle) with some environmental factor, extremely stable behavioral reactions may develop in the patient. Physicians whose practice does not include the treatment of emotional disturbances consider such a possibility dangerous and they attempt to avoid it. However, the correction of emotional disturbances may be regarded as an independent problem that can be solved by using implanted electrodes.

The introduction of implanted electrodes and neurotropic drugs into clinical practice has, in principle, equalized the methodological level of animal experiments and observations on human subjects. Furthermore, this equalization has essentially raised the potential of clinical practice above that of animal experiments, since, in clinical investigations, the verbal contact that is established with the patient makes it possible to determine the subjective component of the reaction as well as its objective expression.

This has greatly enriched the study of emotional and mental phenomena; the subjective verbal response makes it possible, literally within seconds, to answer many questions which formerly could be answered only approximately, even after long years of experimentation. For instance, it is well known how complex a task it was to explain the subjective nature of the phenomena observed in the experiments by Olds before data were obtained from human subjects.

In a relatively small group of patients, whose diagnosis and treatment were carried out by the implanted-electrode method, it was possible, by combining this method with the use of neurotropic drugs, to obtain a whole series of data that could be applied in physiological research as well as medical practice. Maps of the emotion-producing zones and maps of the structural-functional organization for the control of other functions were constructed, and it may be possible in the very near future to draw more precise maps of the central biochemical mediation (Kambarova, 1969). The superimposition of maps of biochemical mediation on to a map of the organization of the central control of any function may provide, in neurological, neurosurgical, psychiatric, and other types of clinical practice, guidelines for the reproduction of a desired reaction, no longer just by means of implanted electrodes but also with neurotropic agents. When drugs are used, a reaction will not always be reproduced as selectively as is possible with the use of implanted electrodes, though it may be assumed that by means of more specific neurotropic drugs more localized changes will be produced in the brain. Thus, through the development of specific emotional reactions, combined with a selected environmental factor, therapeutically advisable, behavioral changes will be effected. In the case of emotional reactions, by using maps of biochemical mediation, together with maps of central emotional control, according to the conditioned reflex principle, we will be able to produce changes in behavior of a type similar to those that were sometimes produced so skillfully in long-past years by experts on the neurotropic action of plant extracts. However, this is only a loose comparison. Such empirical folk medicine remedies, which frequently involved substantial danger not only to the life of the "patient" but also to the life of the "physician," could resolve only a very narrow range of problems. The advances in scientific medicine we have been discussing, with measures to ensure safety and to correct any complications that may arise, should make it possible to help patients with a very wide range of emotional disturbances.

It should be emphasized in passing that even in the treatment of emotional disturbances in this "case of the future," as well as in our current, in many ways purely empirical, administration of neurotropic drugs, one must take into consideration the possibility of a phasic development of changes in the SEP during emotional reactions which may themselves develop in a phasic manner. It was shown above that the same structures can participate in emotions of opposite significance when there is a change in the electrical sign (or tendency toward shifting) of the steady potential. The physiological study of this problem would not be complete if we did not also consider the possibility of another, more complex pattern of physiological phenomena in space and time. The involvement of a structure in a reaction may be indicated by a change in the slow electrical processes, probably in a negative direction. The phase dynamics of the SEP in any structure may therefore be merely an indirect reflection of the phase development of emotional states. A structure is closely related to the emotional reaction when there develops in it, let us say, a negative change in the slow electrical processes, whereas a subsequent positive change may indicate not the same emotion with an opposite sign, but a "deviation" of this emotion, and closely related in time to this deviation, the "connection" of structures that actively ensure the development of the new emotion. In this case, the "connection" of this second group of structures may be related to the development in them also of a negative change in the SEP. When data from animal experiments are taken into consideration, this second possibility seems more probable.

The development of a new emotion can apparently be correlated with the "connection" of new brain structures, accompanied by the "disconnection" of the formerly connected structures. It may be that the development of a negative emotion depends not only on the activity of the brain zones directly related to its maintenance, but also on the inactivation of other zones "operating" during positive emotions. It is not impossible that these processes reflect the characteristic complexity of the development of negative emotions, and thus have a protective role in maintaining an optimal level of positive emotions. If this is so, then, unfortunately, a negative emotional state produced by the same mechanisms will hamper the development of a positive emotion. This might cast a little light on the nature of emotional inertia and the treatment of related problems.

A strong negative deviation of the SEP, correlated with a positive emotional state, may lead to a distinctive "secondary action" in the form of a positive deviation of the SEP, which may favor the development of a negative emotional state. Apparently this is particularly significant in cases of emotional unbalance.

These findings should be considered in the treatment of behavioral disorders since the phasic nature of the reactions may lead not to the desired change in behavior but to an opposite one. The phasic nature of these processes evidently may also account for the phenomenon crystallized in folk experience by the popular expression "from love to hate is but a single step."

This same possibility of phase changes must be taken into consideration in prescribing and administering neurotropic drugs, since the prolonged administration of these drugs may entail not a "balancing" but rather a "shattering" of the whole complex dynamic system for the control of emotions, and thus facilitate the development of phasic emotional reactions. Also, it could be that the substantial increase in the number of mentally disturbed persons in different countries at the present time is related, to some extent, to the use of tranquilizers, particularly to "self-treatment" with them, which has taken on immense proportions. This statement, of course, must not be regarded as a call for the abolition of tranquilizers and other neurotropic drugs, but rather an expression of the desire to control their use and to consider the risk of drug abuse.

We have considered the fundamental principles and mechanisms of the reliable operation of the system for the maintenance of mental activity. The functioning of this reliable and dynamic system always simultaneously involves the "non-connection" into the system of many neuronal populations—elements with an evolutionary potential for participation. But any system, even the most dynamic one, has a certain stability which more or less limits the degree of freedom in its utilization of the brain's resources.

The functional systems underlying a stable state of health may (within certain limits) be reorganized, for example, during changes in the external environment or during the teaching process (including experimental teaching).

However, it is precisely the functional stability of the cerebral systems, though only relative, which leads to the result that with pathological changes in the brain, particularly in adult human subjects, all of the brain's reserves are by no means always used. In therapeutic planning and practice, it is very important to take into account the fact that if a substantial injury is not eliminated but is compatible with life, then the organism's existence in the environment will be maintained by the formation of a new stable state—a stable pathological state—that replaces the normal stable state (Bechtereva and Bondarchuk, 1968). The specific mechanisms for maintaining stable pathological states differ for different diseases; this also determines the need to shape methods of treatment to individual cases. Nevertheless, in the treatment of chronic diseases of the brain, it is necessary to consider the general factor—the *stable pathological state*—maintained by reactions of the homeostatic type that are directed at a steady state of disease rather than health. This factor explains the relative ineffectiveness of surgical or pharmacological treatment of many diseases, particularly the frequent transience of an initially positive effect.

Procedures to induce general changes in the brain and throughout the organism, such as electroshock, have long been used in psychiatry. More promising because it can be applied in a more quantitative manner is the recently suggested method of therapeutic electrical stimulation, which alters routine brain function by means of an effect on its modulating formations. Their stimulation produces a significant general effect, in addition to suppressing manifestations of the disease (Bechtereva et al., 1972). Thus, only with electrostimulation has it been possible to observe a long-lasting "break-up and a sharp decrease in intensity of the phantom-limb syndrome, a stable activation of mental functions in patients very seriously ill with epilepsy, and an improvement in hyperkinetic patients. Electrostimulation of the brain has eliminated acute and chronic phobic syndromes, has evoked and suppressed other emotional reactions, and has reorganized emotional states. Clearly, the use of therapeutic electrical stimulation, a procedure which is significantly milder than the destruction of brain tissue, should be expanded, particularly for those diseases in which a stable pathological state is dominant. It will probably be of value in a wide range of obsessive states and other mental and neurological diseases that cannot be treated by the usual methods.

Another method directed at modifying the conditions of function—biofeedback—is being increasingly used in therapeutic practice. This method has objectives that are relevant to the study of brain physiology and pathology: (1) a precise consideration of changing brain states, (2) "retraining" and the formation of new stable states by electrical stimulation of the brain (Walter and Shipton, 1949; Bechtereva and Usov, 1960; Simonov and Temnikov, 1965; Livanov et al., 1966; Vasilevsky, 1972; Bundzen, Tchubarov, and Shishkin, 1973).

The results of biofeedback experiments (which reflect the conditioned reflex principle), combined with new data on the organization of the brain, opens up still another possibility for the treatment of brain disease. The "break-up" of a stable pathological state, the establishment of new relationships in the brain, can be accomplished by electrical stimulation of zones whose activation in a given direction suppresses the disease symptomatology: this procedure includes automated incorporation of reinforcing stimulation. New stable states can be developed, in principle, by stimulation of emotionally active zones—those regions of the brain whose activation evokes positive or negative emotional reactions. The repeated reinforcement of a desired reaction (state) by a stimulus evoking positive emotions and, conversely, the reinforcement of a morbid reaction by a stimulus evoking a negative emotion, may prove to be an extremely powerful method for retraining the brain. The effect may be unusually rapid and stable; it may be achieved through a "forced" and directed use of the brain's reserves, leading to the formation of new functional systems.

With an improvement in the stereotaxic techniques, stimulation of the brain is becoming a clinical reality in a wide range of neurological diseases. Of course, this is only one of the possible methods of treating any given manifestation of disease. In the overwhelming majority of cases, it has been possible to conduct "training" sessions using informational and motivational techniques without electrical stimulation of the brain. With the use of informational and motivational stimuli, it has proved possible to change the electrical activity of the brain, the frequency of the manifestation of a tremor (Chernigovskaya et al., 1972a,b,c), the state of consciousness (Gaarder and Chase, 1971a,b), and muscle tone (Jacobs and Fenton, 1969; Budzynski et al., 1970; Whatmore and Kohli, 1968).

The new methods of treatment just described can be used separately, depending upon the case. In principle, however, they should be considered elements of a complex treatment, in which a specific action on the disease in question is combined with an effect on the general mechanisms characteristic of morbid processes and, above all, of chronic diseases of the brain. The concept of a stable pathological state, supplementing the old concept of a "vicious cycle" and the theory of homeostasis applied to disease, makes it possible to understand the general mechanisms of a whole class of diseases. Thus, at the present time, there are new possibilities at various levels for the treatment of brain diseases. It should be noted, however, that both the new data on the brain and the new therapeutic possibilities resulting from advances in brain physiology are not being exploited to any great extent in the treatment of brain disease. It may be that in psychiatry there still exists, in this respect, a guilty memory of the early and sometimes tragic failures of psychosurgery, with which the present status of the problem has little in common.

The Pavlovian principle of conditioned reflexes is clearly the basis for the most complex activities of the brain in both animals and human beings. Applications of the conditioned reflex method in clinical practice, however, have not been as far reaching as in animal research. Although these applications have underscored the universality of the conditioned reflex principle, they have not made it possible to understand the details of the mind nor to help create in clinical practice a basis on which the injured human mind could be reconstructed. When the conditioned reflex method was introduced into clinical practice, variations were necessary, although the basic principle was still maintained. The "return" of the conditioned reflex method to clinical practice is not only possible, but also necessary; however, it must be raised to a new level and modified on the basis of new data on the mechanisms of the human mind. Together with advances in modern human neurophysiology, the conditioned reflex principle certainly can, at this time, contribute much toward the alleviation of human disease and suffering. Some possible approaches in the application of the conditioned reflex principle in clinical practice have been examined in this section.

The growth of clinical neurophysiology will, in turn, promote a further accumulation of theoretically important information on the human brain. An analysis of data on the mechanisms of normal and pathological mental reactions obtained by expanded application of neurophysiological methods in combination with a more thorough study of the brain by implanted electrodes, and further improvement in the extraction of information from neurophysiological data, will undoubtedly help to construct a sufficiently general theory of the neurophysiological foundations of human mental activity.

The Study of Human Brain Physiology and Animal Experimentation

Advances in the study of the neurophysiological maintenance of different brain functions are closely related to technical advances and to the use of implanted electrodes in clinical practice. From electrical stimulation data, a start has been made in preparing maps of the cerebral maintenance of emotions; the completion of these maps seems to be only a question of the number of observations to be made and the variety of brain formations to be investigated. These maps are no longer being constructed only from electrical stimulation data but also from recordings of slow electrical and other brain processes.

One would think that by now observations on humans in this area should have acquired the rigor necessary for experimentation and that a variety of technical approaches would have provided many more opportunities for the demonstration of a subjective component of reactions than is possible in animal experiments. If this were the case, a complete physiology of the cerebral maintenance of human emotions might be expected in the very near future.

However, the situation is not as simple. In human investigations, with physiological methods that are essentially the same as those used in animal experiments and, naturally, with the great possibilities of the psychophysiological complex, the real barriers in brain research are medical and ethical. The selection of a region for electrode implantation is always made on the basis of the patient's best interests. The expansion of the range of diseases that can be treated, which is justified by the therapeutic tasks and technical possibilities, is also slowly expanding the range of brain structures serving as stereotaxic targets. In very complex forms of epilepsy, one of the regions into which it is dangerous to introduce foreign bodies, the hypothalamus, has already become a target of this type in a number of hospitals. It is true that very few investigators are as yet risking implantation in this zone of the human brain, since they know well that other types of dystrophic complications could develop. Caution with respect to brain stem structures is also justified. Electrodes are implanted into certain regions of the cortex in cases of epilepsy and are beginning to be used in optical and acoustic prosthetics. Nevertheless, taking into account the specifics of these diseases, there is no reason to assume that it will be possible in the near future (disregarding limitations of a medical-ethical nature) to implant electrodes into a large number of zones in all cortical regions. Compared to animal experiments, our investigations of the cerebral maintenance of human emotions are therefore at a substantial disadvantage with respect to the potential for a complete examination of the brain.

A more precise definition of the emotional effect observed during diagnostic stimulation requires its repeated reproduction, but repeated stimulation of emotion-producing zones for diagnostic purposes is not permissible. The therapeutic electrostimulation of zones provides a somewhat greater scope for the observation of the resulting dynamic pattern. But therapeutic stimulation must be carried out only when there is evidence of emotional disorder, that is, for an initial disturbance in the activity of the system for the maintenance of emotions; a repetition of the stimulation, in a favorable case, should lead to a change in the quality of the emotional reactions. In studies of cerebral maintenance of emotional reactions, the possibilities opened up by recording physiological indices during emotion-producing tests are also limited. An animal can be placed in a wide variety of very complex emotion-producing situations. *For a patient, emotion-producing tests must be selected with the utmost care, particularly those evoking a negative emotion.*

The possibilities of direct contact with the brain through the therapeutic use of implanted electrodes are difficult to overestimate, particularly as compared with other methods for studying the physiology of the human brain. Of course, many methods can be used to study both sick and healthy human subjects. Electrode implantation is carried out only in accordance with medical indications, and the results obtained in all cases should be evaluated with due regard for this circumstance. The fact that investigations with implanted electrodes always take place in a diseased brain seriously limits this method of studying the human brain.

It is difficult to suggest effective measures for overcoming this limitation in human brain research. One approach would be to investigate in each patient both the affected and less affected systems and to base concepts of brain physiology primarily on data from the less affected systems. The accumulation of data from different groups of patients might then help describe the physiology of emotions that more or less approximate the normal. Another method of overcoming the limitations related to the investigation of a diseased brain is to carry it out against the background of compensation or replacement drug therapy.

Thus, although modern technical possibilities, expanded by multidisciplinary progress in the diagnosis and treatment of brain disease, have made possible a decisive "leap" in the study of human neurophysiology, and particularly in its most complex area, the neurophysiological maintenance of mental functions, these technical possibilities have not removed, and must not remove, the medical-ethical limitations.

If we were to go into the particular limitations in the study of the physiology of human higher nervous activity enumerated above, we could probably fill up more printed pages than are contained in this book. For this there is no need. But it is important to re-emphasize that the potentialities of human brain physiology have substantially increased during the last two decades. Objective observations of humans are helping us penetrate the depths of those mechanisms for which conclusions made on the basis of animal experiments can only be indirect. Of course, in the study of many of the problems of human brain physiology, animal experiments will never be replaced by investigations of humans.

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