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Neurophysiological Codes of Words in Subcortical Structures of the Human Brain

N. P. BECHTEREVA, P. V. BUNDZEN, YU. L. GOGOLITSIN, V. N. MALYSHEV, AND P. D. PEREPELKIN

Institute for Experimental Medicine Academy Medical Science, USSR

Investigations into the cerebral mechanisms of mental activity, using modern mathematical–technical capabilities, allows the transition from study of structural–functional organization to a new stage: the study of neural coding of these cerebral processes.

Here we present the results of studying the elementary components of the neurophysiological pattern-code of words and the neurophysiological correlates of the simplest mental processes, generalization, and mental conclusion. The elementary components of the pattern-code are the group sequences of neuronal firing with comparatively stable intervals in between. The processes of mental conclusion and decision making occur when full, compressed, and complex patterns-codes appear in the brain.

In discussing the data obtained, the problems of relationship between a part and the whole in activity of cerebral systems is considered, and the hypothesis of a dynamic pace-maker mechanism for cerebral organization of mental activity, is proposed.

INTRODUCTION

Increasing clinical opportunities for the study of human brain physiology has provided a growing volume of data on the role of different cerebral areas in mental activity (Ojemann, 1975; Luria, 1975; and others). In the course of diagnostic and therapeutic electrical stimulation of subcortical structures, changes of the wakefulness level, various emotional–mental responses, and changes of speech and of body image have been observed (Sem-Jacobsen, 1968; Ojemann & Ward, 1971; Smirnov, 1976; and others).

Complementary analysis of the results of electrical stimulation and of the recorded physiological parameters of the brain provides data on the role of deep brain structures in mental processes and reveals the general principles of structural–functional maintenance of these phenomena. This analysis indicates that the intellectual-mnestic processes in humans are maintained by a cortico–subcortical structural–functional system with

Reprint requests should be sent to Dr. N. P. Bechtereva, Institute of Experimental Medicine, Kirovsky 69/71, Leningrad 197022, USSR.

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links of different rigidity. The rigid links participate in the maintenance of activity largely independent of the organism's environment or the brain's inner milieu. The flexible links may or may not be involved in its maintenance depending on the conditions under which the mental activity occurs (Bechtereva, 1966, 1971, 1974).

Development of modern mathematical–technical capabilities for analysis of the action potential spike activity of the brain neuronal populations makes it possible, under conditions of the diagnostic–therapeutic usage of implanted electrodes, to study the neuronal spike patterns, to differentiate and investigate the activity of a small population of neurons, and to study the interaction of neurons both within a single neuronal population and in distant populations. In these studies, characteristic changes in the spike activity of single neurons can be identified, including specific patterns evoked by specific presented stimuli. It is then possible to carry out an automated dynamic extraction of analogous patterns from ongoing neural activity using the former patterns as standards, and, thus identify the elementary components of informationally-significant patterns.

In the study of cerebral mechanisms of mental activity these techniques enabled us to switch from investigation of the structural–functional organization to a new stage: the penetration into the subtle neurophysiological mechanisms developing in the links of the system for maintenance of mental activity and closely associated with the character of this activity. This stage can be designated as the study of coding of the mental processes in the human brain. From the physiological standpoint, the importance of this stage is emphasized by the fact that at the level of the cerebral maintenance of mental activity, the role of specific neurophysiological dynamics in the cerebral structure increases immensely, while the significance of the functional state of the structure itself remains preserved.

The investigation into this problem was started in 1971 (Bechtereva, Bundzen, Matveer, & Kaplunovsky, 1971). The action potential spikes (units) of neuronal populations within subcortical structures of the human brain were recorded during perception, retention in memory and reproduction of words. These events were associated with specific patterns of interspike intervals, and specific interrelationships between neurons in adjacent and distant populations. Varying psychological tests revealed that this pattern reflects characteristics of the words as complex sound signals, as well as their semantic characteristics. The semantic-dependent components were revealed primarily in regional and distant changes in interrelationships between nerve elements and groups of the elements, while correlation with the sound features of words was revealed mainly (although not exclusively) in changes in the firing frequency (Bechtereva & Bundzen, 1975). The adequate form of representation of the pattern-code reflecting most of the changes in spike activity and suitable for automated computer search for its analogs in ongoing spike activity, was the "distributive" form of patterns which included sequences of interspike intervals in an active group of neurons (Bechtereva, 1975; Bundzen, 1976).

These data suggest a number of research lines for further study: the deciphering of elementary components of the pattern-code of words and the investigation into the code of mental processes.

METHODS

The studies were based on recording and analyzing the action potential (spike, unit) activity of neuronal populations of different subcortical structures, mainly the thalamus, striopallidar system, upper portions of the brain stem, and also some cortical areas in patients whose diagnosis and therapy used implanted electrodes. The electrodes were 98% gold and 50–100 μm in diameter, and were covered up to the 1-mm tip with a neutral plastic phtoroplast-2 and gathered into bundles in such a way that each successive electrode terminated 3–5 mm above the preceding one. The electrodes' active surface varied from 0.008 to 0.15 mm^2.

The processing of multiunit activity data was performed with the aid of a Didac-4000 analyzer (Intertechnique, France) and Linc-8 (DEC, U.S.A.), M-6000, and Minsk-32 (USSR) computers (Bechtereva, Bundzen, & Gogolitsin, 1977).

Depending on the processing programs, different parameters were estimated during introduction of the multiunit activity data from tape recorders into computers:

(a) The digitizing of the multiunit activity, regarded as a continuous analog signal with a digitizing frequency of 50 kHz, was estimated.

(b) Time intervals between the maximums and minimums of the analog signal were estimated, as well as the amplitudes of the maximums and minimums.

(c) High-amplitude spikes of several neurons were singled out with the aid of the amplitude threshold, and estimation of successive intervals between them or simultaneous estimations of successive intervals and durations of action potentials were performed.

We estimated the statistical parameters of the multiunit activity by means of histograms of the interspike intervals, the action potential amplitudes and durations; two-dimensional histograms of "duration of action potential (axis X)–duration of the following interspike interval (axis Y)"; and two-dimensional histograms of adjacent intervals. Calculation of distributions of the centers of gravity over rows and columns of the two-dimensional histograms (David, Finkenzeller, Kallert, & Keidel, 1968; Bundzen, Gogolitsin, David, Kaplunsky, & Perepelkin, 1973) enabled us to determine the serial interrelationship between the spike duration and the following interspike interval or among the values of adjacent interspike intervals.

To determine if a process was stationary, we divided the multiunit activity records into fragments which either were of equal durations or contained equal numbers of interspike intervals. Histograms for each fragment were then constructed separately. In order to identify the components of multiunit activity associated with processes of perception, retention in memory, and reproduction of single words or classes of words, we used a group of methods for pattern selection specially evolved by us (Bundzen, Malyshev, & Perepelkin, 1975; Gogolitsin, 1976; Perepelkin, 1977). With these methods, one is able to select a certain standard pattern and search for it in the multiunit records, proceeding from the results of estimation of the statistical parameters of multiunit activity. The nature of the selected standard and the meaning of the results depend on the parameter of multiunit activity under study. Thus, if one performs the digitizing of multiunit activity regarding it as a continuous analog signal, one can select the standard pattern as a sequence of counts describing the form of an action potential. In this case the program of pattern selection identifies the moments of appearance of action potentials having the same form as the standard (with a desired accuracy), i.e., discriminates the multiunit activity by the form of action potentials.

If during introduction of multiunit activity into the computer we measured the interimpulse intervals between high-amplitude spikes of several neurons, the selected standard pattern was usually in the form of a sequence of two to five interimpulse intervals: the interval pattern. Using the program for pattern selection, we identified those moments when a sequence of interspike intervals similar to the given interval pattern appeared in the multiunit activity. Two intervals were considered similar if they differed from each other not more than by 10% of their value.

In a number of studies, the selection of interval patterns was performed on an M-6000 computer by a program working in real time which enabled us to process unlimited recordings of multiunit activity.

Results of data processing. The moments of appearance of the standard patterns among the current values of the multiunit activity parameter under study were compared with the results of analysis of the phonogram. This enabled us to judge whether there was a temporal connection between the appearance of certain patterns and the moments of commencement and cessation of sounding of presented or reproduced words.

We also applied an analysis of multiunit activity that differs in principle from the methods described above: the identification of synchronous neuronal discharges in different neuronal populations. For this purpose we used a coherence detector (Siemens, BRD) and an electronic multichannel detector of synchronous discharges (Bundzen, David, & Perepelkin, 1977). Action potentials of each neuronal population were transformed into standard impulses of 1-msec duration. The criterion of synchronizing involved the temporal overlapping of standard impulses by not more than 50% of their duration. At the moment of occurrence of synchronous discharges the detector emitted a signal. Sequences of such signals were processed by the same methods as ordinary multiunit activity.

For the identification and functional significance of the neurophysiological patterns described, the following items were used: (1) consideration of only those patterns which were identified during performance of specific tests, and were absent from the spontaneous activity; (2) meticulous comparative study of the elementary structure of unit activity of neuronal populations recorded at rest and during psychological test performance; (3) identification of the pattern-codes in the unit activity with the aid of standards, in particular when using the elementary components of the pattern-codes as the standards.

RESULTS OF THE STUDIES

1. Elementary Components of the Neurophysiological Pattern-Code of Words

The pattern-code identified in the unit activity of neuronal populations was a complex structure containing both the relevant signal (signals) and the noise. The latter in this case is understood as activity of a given brain area unrelated to a certain verbal signal but associated with its general functional condition and, probably, with responses of nonspecific activating and inactivating types. Hence, one of the most important tasks in the study of the neurophysiological code of verbal signals involved the dissection of the pattern into its elementary components.

The studies, based on the standard search and discrimination of the multiunit activity of action potentials, showed in the pattern-code of a functionally active neuronal population elementary components, which are reproduced in a repeating pattern. The code's elementary components

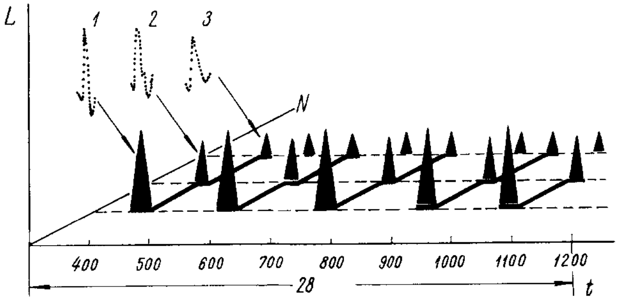

FIG. 1. The pattern of the spatiotemporal interaction of neuronal elements within the period of identification of batch-type activity singled out by means of selection of neuronal elements using standards of action potential shape. The digitizing of action potentials (see *1–3*) was carried out at 20-msec intervals. On the abscissa axis (time, in msec), the digits correspond to the sequential numbers of memory channels; on the ordinate axis (spike amplitude, in conditional units); on the applicata axis (position of the neuronal elements singled out, (N).

reflected the successive firings of two, three, four or more neurons of a population. These kinds of elementary components of the pattern-code are groups of spikes separated by interspike intervals (Fig. 1). The neurophysiological pattern related to the name "apple-tree" showed a sequence of firing with intervals of 13.0–4.0–4.0 msec between three neurons recorded from the centrum medianum thalamic nucleus of a patient and discriminated by the form of the action potentials. For the name of another fruit tree—"plum tree"—the intervals recorded from the same sites in the same patient were 4.0–4.0–10.0 msec (Fig. 2). As Figure 2

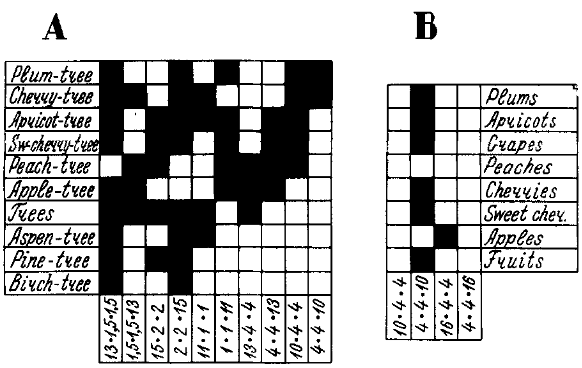

FIG. 2. The matrix representation of a set of verbally specific group sequences of the pattern-code's interspike intervals singled out from the unit activity of a neuronal population within the centrum medianum thalamic nucleus, during utterance of words connected with each other by their sense, in patient Sh. Along the horizontal line at the bottom are the averaged values of the group sequences of interspike intervals. Along the vertical line is a series of verbal signals, opposed by the corresponding sets of group sequences of interimpulse intervals. Black squares—certain code elements are present in the centrum medianum during a given verbal signal; white squares—the elements are absent.

shows, the patterns successively appearing in the same neuronal population related to names of different trees were characterized mainly by different group sequences of firing. Among the different group sequences, some highly similar sequences of firing occurred. In the pattern-codes of words belonging to a common semantic field (names of fruit trees), the general group sequence of firing in patient Sh.'s center median was characterized by the intervals 10.0–4.0–4.0 (Fig. 2).

Studies of the elementary components were performed not only in patterns successively developing in a single brain area, but also in patterns simultaneously appearing in several cerebral areas. In patient A, during perception of the word "table," sequences with successive intervals of 4.1–10.9–6.5–2.2 msec were observed in an area of the globus pallidus, while intervals of 0.8–8.6–6.8 msec were recorded in an area of the central pathway of tegmentum, and intervals of 2.2–4.2–7.4 msec in an area of the caudate nucleus. Thus in different brain areas simultaneously appearing patterns related to the same word show different group sequences of firing.

However, in studying the coding of mental operations of the probabilistic mental conclusion type, during the period of formation of complex code blocks, we found a duplication of code elements in different links of the system for maintenance of mental activity (Fig. 3). These code elements showing synchronous impulse discharges are important in the behavioral change involved in making a decision. In the particular case in Fig. 3, these code elements were the differential code signs of the word "summer." Unit activity showed a change as the result of the solution of the task presented, as indicated by the subject's verbal response.

The significance of group sequences of firing as the elementary components of the neurophysiological pattern was studied by means of a standard computer search in real time. When using the group sequences of firing as standards, we were able to determine the moment of appearance of the patterns related to certain words in the unit activity (Fig. 4). These studies are direct corroboration of the significance of group firing sequences as the elements of the pattern-code and of the code significance of the patterns themselves.

The simultaneous appearance of usually different elementary components of the pattern in different brain areas corroborates our previous assumption (Bechtereva, 1971) concerning the mutually complementary functions of different brain areas and, therefore, of distribution of the full pattern-code of words, distributed coding. It appears that separate highly similar group sequences of firing in these patterns are the concrete neurophysiological expression of a factor aiding in organizing a multitude of links into a system.

The neurophysiological correlates (mechanisms?) of the formation of this system include highly similar elementary components in the pattern-

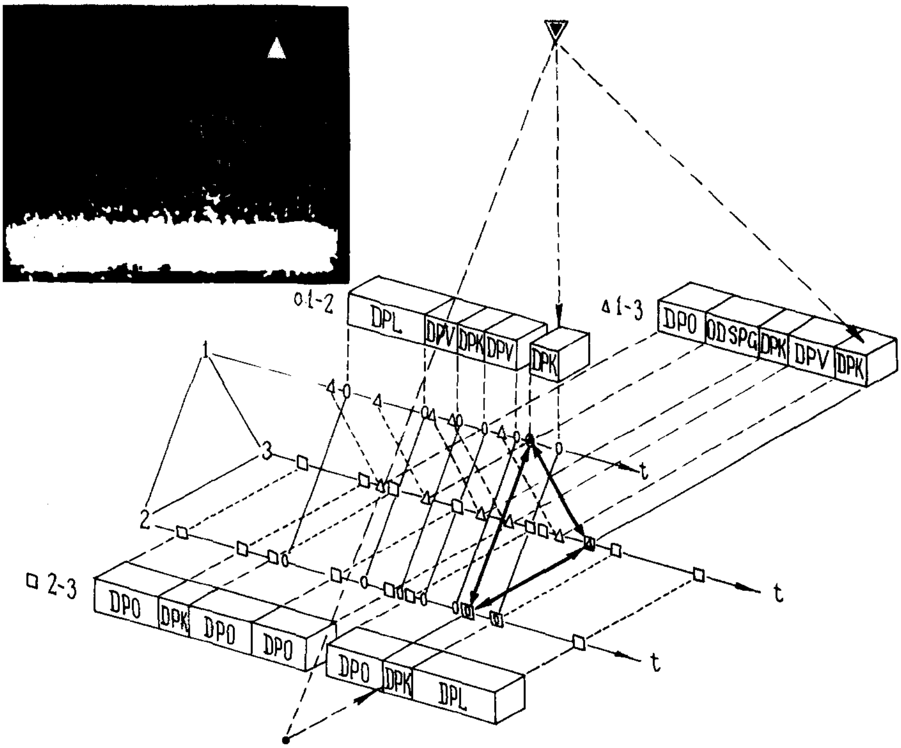

FIG. 3. The spatiotemporal structure of coherent discharges of three neuronal populations identified within the period of code block generation in the population *N* 1 (corpus subthalamicum). Upper left, original recording of coherent discharges averaged over the three neuronal populations: *1–2*, corpus subthalamicus; *1–3*, nucleus ventrooralis anterior; *2–3*, nucleus dorsooralis. The triangle denotes the moment of coincidence for all three pairs of populations. Total digitizing time, 80 msec (*t*).

Lower: *1–2*, *1–3*, *2–3*, the code components of sequential coherent discharges for the above pairs of populations. DPL, DPV, DPK, DPO, ODSPG—conditional identifiers of code elements. Triangles, squares, and ovals on the abscissa axis—the positions of coherent discharges for the pairs of neuronal populations. Coherent discharges for corresponding pairs of neuronal populations are connected with solid and hatched lines. Thick solid lines with arrows point to the moments of coincidence of impulse discharges of all three populations. Arrows radiating from the triangle select the common code element (DPK) and correspond to the position Δ on the original recording.

codes of words belonging to a common semantic field appearing in the same neuronal population on successive presentations of these words. In the second case, the common group sequences of firing can be regarded as the neurophysiological expression of commonness formed during the ontogenesis of the subject. These data can be compared with results of psychological investigations in which the semantic commonness was established with the aid of some peripheral parameters (Luria & Vinogradova, 1971).

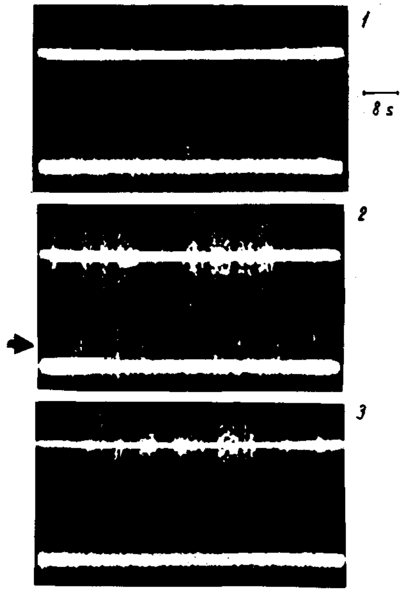

FIG. 4. The results of search in the impulse activity for the sequences of interspike intervals on a real time scale by a corresponding standard (2–2–15 ± 10% msec). *1*, Analysis of spontaneous activity (80 sec); *2*, analysis of activity during reproduction of the semantic field "trees"; *3*, the same for the verbal signals related to the semantic field "flowers" and "rivers." *Top*, Phonogram; *bottom*, moments of occurrence of the selected code elements.

The individual pattern-code in each neuronal population and the vast number of links in the system seem to create an individual cerebral code in every subject. The same word does not necessarily repeat the same code in different subjects. This is in agreement with psychological data on individual differences between subjects. As has been shown, however, the "kaleidoscope" of group sequences of firings in a neuronal population consists of the elementary code sequences. Similar firing sequences are present in the patterns of the same word in different neuronal populations and on successive presentations of words with elements of semantic identity in a single neuronal population, in a given subject. These data give rise to the hypothesis that the investigation into elementary code-forming sequences of firing will aid in revealing species commonness in the cerebral codes of words and intellectual-mnestic processes and aid in discovering species characteristics of the verbal signals that are reflected in the human brain. Much further work remains in the accumulation, analysis, and systematization of elementary code patterns to check this.

2. Neurophysiological Correlates of Coding the Simplest Mental Processes

We have started the study of the subtle cerebral correlates of intellectual-mnestic processes using the minimally sufficient representation of the neurophysiological pattern related to a word. The first evidence for the subtle neurophysiological correlates of the generalization process for words belonging to a common semantic field was obtained on the basis of a description of the pattern-code with the aid of factor analysis. This revealed some characteristics of the changes in interaction between activities of neuronal groups in the pattern. For example, analysis of unit activity in neuronal populations in the globus pallidus of patient L on presentation of the words "table," "chair," and "cupboard" revealed signs of the pattern related to the generalizing idea "furniture" prior to utterance of the word "furniture." Studies performed in this way make it possible to ascertain the moment of appearance of the signs indicating formation of a generalizing idea. They showed that the process of generalization can occur after presentation of two or three semantically related words.

A further investigation into the neurophysiological correlates (code) of mental processes used a form of word pattern-code representation which described more completely the changes in unit activity of neuronal populations: the "distributive representation" of the dynamics of interspike intervals in the active group of neurons (Fig. 5).

Though loosing some information on the neurophysiological changes in the brain related to words, the distributive representation still keeps the basic data on the spatial–temporal structure of unit activity. The distributive representation of the pattern was suitable for use as a standard for an automated search for the appearance of its analogs in the unit activity. Due to the individual character of the neurophysiological pattern-code for a given subject and for a certain brain area, the study of neurophysiological correlates of intellectual-mnestic processes each time requires a preliminary accumulation of a store of pattern standards.

One of the types of mental activity whose neurophysiological correlates were studied with the aid of the automated standard search, was decision making based on double determination. Presentation of a picture (slide) was followed by a question which the patient could answer considering a number of the picture's features, while the question itself was formulated in such a way as to limit many of the possible associations likely to arise on presentation of this picture.

Thus, for instance, a slide showing a basket full of fresh mushrooms was presented followed by the question "When (at what season of the year) was the photo made?" The unit activity of a neuronal population in the centrum medium of patient A contained a number of patterns related to the verbal reflection of the presented picture ("mushrooms"), of the answers ("June," "summer"), and of a number of other words associated semantically with the task under consideration. The pattern-codes of the words related to the task and answer were observed both in full form and in a form compressed in time. The majority of pattern-codes related to other words were in compressed form. Apart from compressed and full

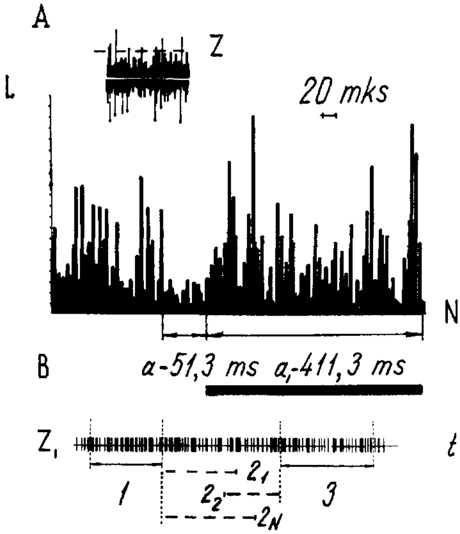

FIG. 5. Selection of the substandards of distributive patterns for optimal computer search. *Top,* An epoch of the impulse activity with amplitude section Z. (A) The analogous representation of duration digitizing for successive interimpulse intervals at the amplitude section (0.7 of the maximal amplitude) of the unit activity (Didac-4000). Abscissa, successive interspike intervals (N); ordinate, duration of the intervals (L) (each mark is 20 msec). Horizontal bar beneath the abscissa (the moment of utterance of the word "summer" by the subject): epoch a_1. Epoch a, the aggregate of intervals prior to utterance of the word "summer", epoch b, choice of the substandards for the following selection from the unit activity. Z_1 represents a formed flow of neuronal discharges singled out at the amplitude section of the unit activity, The vertical hatched lines delineate the time of perception of verbal signal (pattern 1), the interval between the perception and the utterance of the verbal signal (pattern 2_1–2_N), and the time of utterance of the verbal signal (pattern 3).

forms, various forms of complex patterns were observed as combinations in time and space of the compressed or incomplete patterns related to different words (Fig. 6).

These findings show, primarily, that this type of simple decision making

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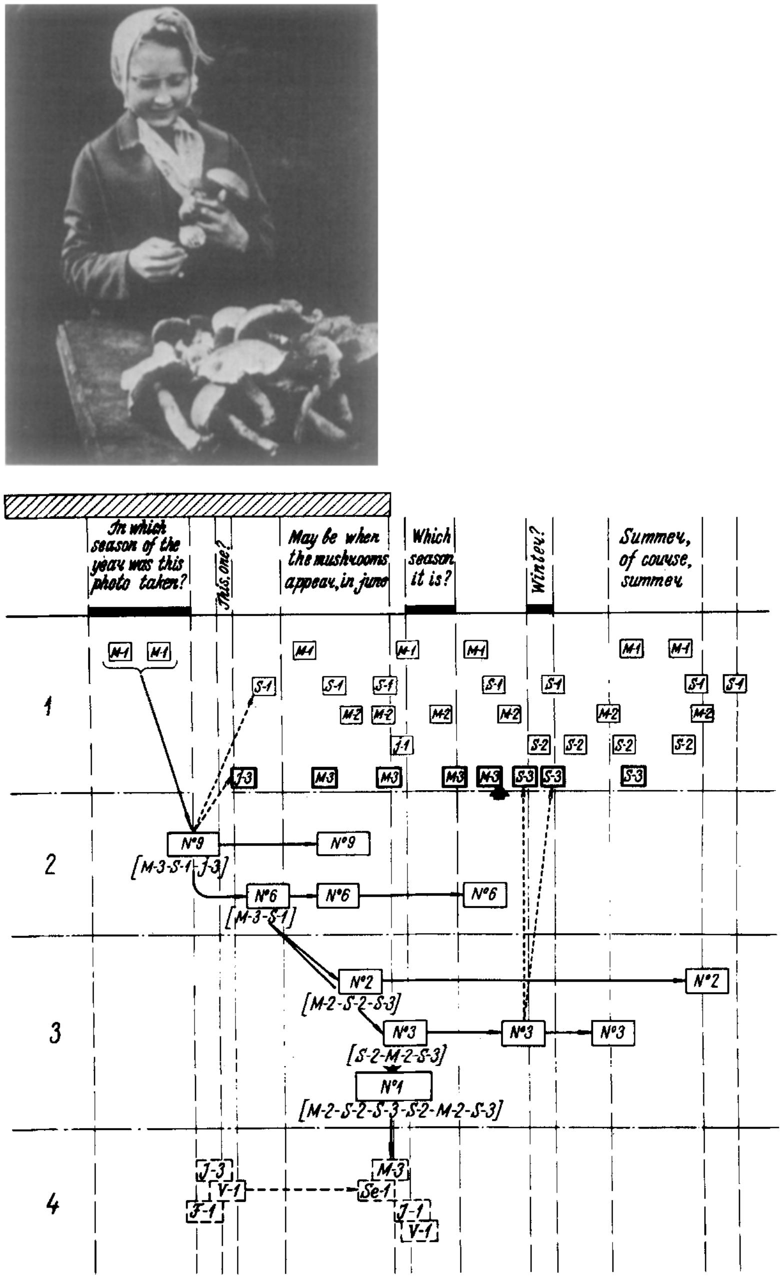
FIG. 6. *Top,* The presented picture; *bottom,* the results of the search for standard distributive patterns of verbal signals and their transformation in the course of a mental conclusion, the answer to the question: "In which season of the year was this photo taken?" The unit activity recorded from the area of centrum medianum in patient A. Hatched square, time of presentation of the picture. *1,* The results of direct selection from the unit activity's standard patterns of three substandards singled out during processing of the words "mushroom" (M-1,2,3), "summer" (S-1,2,3), "June" (J-1,2,3); *2,* The results of selection of the "hybrid" patterns formed as the result of temporal occlusion of the code forms. Code block No. 6 includes the substandards "M-3" and "S-1." Code block No. 9 includes the substandards "M-3," "S-1," "J-1," "J-3." *3,* The results of selection of the "overlapping" patterns. Code block No. 3 includes the substandards "S-2," "M-2," "S-3"; code block No. 1 includes "M-2," "S-2," "S-3." Code block No. 1 is the overlapping of code blocks Nos. 2 and 3. *4,* The results of selection of the unit activity's standard patterns by the



substandards singled out from the unit activity during presentation of the test, retention in memory, and verbal response which are the objective signs of the result of mental conclusion: "June," "vegetables," "fruit," "sea," "rest." The arrows show the temporal sequence in the formation of code blocks. The other designations are identical to the fragments *1–3* of this figure.

can be performed neurophysiologically by compressed and complex code forms. Hence, compressed forms of the pattern result not only from transformation of the full code forms under the effect of long-term memory; along with complex patterns, compressed patterns can act as operative units in intellectual-mnestic activity, because they are probably neurophysiological correlates of the "inner speech" process (Vygotsky, 1934). The full pattern-codes must, apparently, play the leading role in the processes of perception (recognition) of signals, the formation of long-term memory trace, and control of verbal response.

The appearance of various forms of patterns in the course of performing a task is reason to expect much from the application of this type of neurophysiologic study to one of the rather urgent problems of linguistic psychology: the relations and the role of imaginative and verbal processes in human mentality. Progress in these studies will aid in revealing how and what kind of experience is transformed from a latent form to an active form, from long-term memory to an operative one when one or another decision is being made. However, the studies based on revealing the moment of appearance of words' pattern-code in the unit activity of neuronal populations cannot answer the question *in what way* the process of mental conclusion, decision making, etc., occurs. The answer to this question is still very complicated. One of the approaches to its solution lies, apparently, in the analysis of cerebral neurophysiological processes performed with the aid of the above data on the elementary components of the pattern-code. Obtaining the data on the nature of elementary components of pattern-code characterized the transition from description of the code to its deciphering.

The elementary components of pattern-codes in the unit activity recorded from the globus pallidus of patient A were determined during tests for generalizing of the words by their meaning. In association with the first presentation of the word, the unit activity develops a great number of group sequences of firing which are a neurophysiological expression of activation of the associative search. After perception of the second word of the same semantic field, the obviousness of this phenomenon is sharply limited. On perception of the third word a complex block of elementary components of the patterns appears in the unit activity, which includes the group sequences of firing characteristic of the words already presented and the new elements. This complex block later appears as the element of the pattern-code for the generalizing idea (Fig. 7). Thus the appearance of signs of formation of the generalizing idea prior to utterance of the corresponding word, initially revealed with the aid of incomplete pattern representation (by means of the factor analysis), has been confirmed at a technically more perfect level (Gogolitsin, 1976). Further analysis of this question will certainly aid in assessment of the functional significance of this complex block and establish its role in the formation of

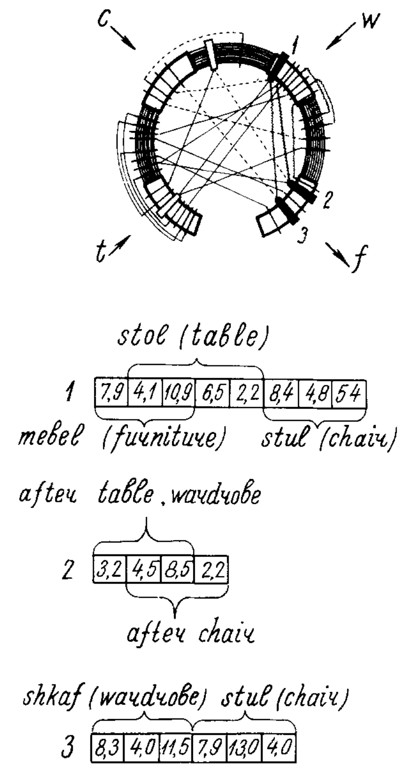


FIG. 7. The distribution of reappearing group sequences of firing in unit activity of a neuronal population within the globus pallidus in patient A. *Top,* The order of presenting the words and the subject's response (the time axis is in the form of an arc). Presentation of words marked with white sections of the arc are outlined with a solid line. *t,* table; *c,* chair; *w,* wardrobe; *f,* furniture. Intervals between words are emphasized with hatched arcs of different radii. The radially directed squares crossing the arc correspond to sequences repeatedly reproduced and to complex blocks of elementary components of the patterns. The radially directed lines crossing the arc designate the singled-out group sequences of firing. Solid lines connect the group sequences occurring during and after presentation of the word "table" with the loci of their reproduction; the hatched and undulate lines—the same for words "chair" and "wardrobe," respectively. *Bottom* (*1–3*), Structures of the complex blocks presented as solid squares above. Each interspike interval has a corresponding square containing the interval duration (in msec). Each group sequence which constitutes a block is indicated by a brace, and the place where, in addition to the given block, this sequence was reproduced is shown.

generalization within a given semantic field. This line of research may also reveal the neurophysiological signs of "making the decision about the possibility of generalization," the separate or general cerebral signals of the generalization process.

In the example illustrated in Fig. 7, the word "furniture" was absent from the test. It appears as a result of associative search and activation of the corresponding long-term memory matrix. This activation of long-term memory appears to comprise the elements of bioelectrical pattern-codes of words constituting the given semantic field. The pattern-code of a generalizing word reproduces separate elements of pattern-codes of these words in combination with its own additional specific(?) elements, which means neurophysiologically that the generalization is not a simple sampling of significant elements of already developed patterns and their summation but is also the appearance of a new quality.

These results on the neurophysiologic mechanisms behind cerebral operations are still preliminary. They indicate, however, that neurophysiological analysis of dynamics and relations of the pattern-codes' elementary components in a single population and simultaneously in a number of neuronal populations during mental operations will enable us to obtain data not only for comprehending *the conditions* in which generalization, mental conclusion, decision making, etc., are possible, but also for comprehending *the manner* in which these operations are performed.

DISCUSSION

The findings indicate the presence of informationally specific links of cerebral systems for maintenance of mental processes in subcortical structures of the brain. The data on neurophysiological coding of words and mental processes can be regarded as a development of the theory of the human brain mechanisms and can be a basis for the progress of neuropsychology. These findings also provide further technical possibilities in the study of similar physiological phenomena of a "lower" order, the processes of coding simple signals in the central nervous system, and the coding of complex signals at different levels of analytical systems.

At the same time, these neurophysiological studies of mental processes in neuronal populations present the problem of the relation between a part and the whole in the activity of cerebral systems and of the necessity of combining the data obtained as a result of analytical and integrative approaches to the study of the nervous system. The combining of the data of analytical and integrative approaches is impossible without an intense study of a number of crucial fundamental problems of brain physiology.

The most important and closely related problems of this kind are as follows: relations between the features of a neuron and a pool of neurons (groups, ensembles, populations); significance of different forms of connection in the nervous system for the activity of cerebral systems for maintenance of different kinds of activity; memory, its mechanisms and its effect on diverse neurodynamic processes and, in particular, on the features of the pools of neurons and realization of interaction of the cerebral systems' links.

The connection between mental operations and memory processes is unbreakable. Indeed, the simplest mental conclusions are unthinkable without activation and usage of a corresponding long-term memory basis of verbal and unverbal orders. In the course of the same processes, there occur replenishment of memory and the transformation of associations and of their hierarchy.

The behavior of the neuronal populations, the interaction of the cerebral systems' links, and many other cerebral mechanisms are determined by genetic memory, which unfolds rather than develops during ontogenesis and into which the individually acquired memory brings out adaptive corrections; by instantaneous memory of imprinting type, which is formed for events of the utmost importance for the individual as the species representative and only when separate components of the situation are individually unpredictable; by individually acquired memory, which forms rather rapidly but, as a rule, not instantly and determines the possibility of all other kinds of activity and even an individual's life itself in a changing environment—in particular, the life of a human being in its social milieu. The speed of memory formation, though associated with genetic features of the organism, is much more the function of the objective or subjective significance of an event and, therefore, of the corresponding motivation, and hence—in a general way—of the brain's functional background. The biological advantage of the noninstantaneous memorizing of the majority of events in the course of learning involves, apparently, not only the possibility of selection—of filtration of the incoming information—but also the possibility of its ordering and juxtaposition with different semantic fields with all the subsequent consequences of hierarchy for the following associative search.

The question of the determinant role of memory in neurophysiological coding of mental phenomena is extremely important and, therefore, has been considered in a more detailed way in a special study (Bechtereva, 1977).

The neurophysiological study of mental processes emphasizes the importance of yet other crucial problems of interaction between analytical and integrative approaches to the study of the nervous system's function. Revealing the pattern-codes related to words and occurring as a result of readjustments of pools of neurons, not of single neurons, led to consideration of features of functionally united groups of neurons in a population in the course of presentation of data on cerebral coding of mental processes. Special consideration of different aspects of the problem of the relation between features of a neuron and a pool of neurons is undoubtedly important and demands further intense study. However, in connection with the tasks of the present work, this problem is simply presented here rather than solved.

Extremely important is the problem of the role of different types of connection in the nervous system and the comparative significance of different forms of signal transmission. As has been mentioned earlier, in the course of investigating the neurophysiological correlates of mental processes, not only was the simultaneous development of patterns in distant links of the systems revealed, but also the practically simultaneous appearance of the patterns' elementary components in different brain areas was observed. How and on the basis of which connection mechanisms does the rapid and often instantaneous involvement of a multitude of links of different cerebral systems and particularly of the system for maintenance of mental activity occur? Is there a pace-maker mechanism?

Neurophysiological study of mental activity emphasizes both the features common to and the features different from other kinds of activity and its complexity, dynamic character, and cerebral organization. If mental activity proceeds with the participation of a functional pace-maker, the latter must differ in principle from rigidly structure-bound formations; rather, it must be a dynamic constellation of structures which springs up under the influence of inner or environmental factors. The concrete significance of a pace-maker mechanism depends on the character of the activity. Thus, for instance, its primary role in tasks for generalization of words by their sense creates conditions for a wide associative search in the brain which is resolved, apparently, with the aid of unspecific activating (synchronizing) influences. (Livanov, 1975; Livanov & Raeva, 1976). The recognition that two or three words (phenomena) belong to a common semantic (associative) field determines the direction of the following associative search and its limits.

If the activity is repeated, a facilitation of the formation of the pace-maker mechanism occurs due to creation and constant activation of a corresponding matrix in long-term memory. If the activity changes, structural components of the dynamic pace-maker change as well. In general, the role of this pace-maker primarily involves the control, organization, and reorganization of the system for maintenance of mental activity, with proper activation of the long-term memory associative fields and limitation of this activation, according to the situation, in different phases of developing mental activity. This hypothetical dynamic pace-maker does not exclude the presence of the comparison apparatus (Anokhin's acceptor of action results–1976). The acceptor is probably one of the phases of the development of the pace-maker. Considering the neuropsychological data of Luria (1976), which indicate that deep areas of the frontal lobes maintain the selectivity of memory, noise-proofing it and, along with deep areas of the temporal lobes (Brazier, 1962), maintaining ordinary activity in accordance with expectation, one can assume that as a rule these brain areas take part in the constellation of structures constituting the dynamic pace-maker. The pace-maker mechanism includes both specific and unspecific elements, with the role of the unspecific modulating elements in this apparatus probably rather great; in particular, they provide an important mechanism for interconnection between neural elements. The specific brain areas taking part in the pace-maker organization are primarily those to which a stimulus launching the developing activity is addressed.

This concept of the organization of mental activity assumes a pace-maker system generated by events occurring in the inner milieu and in the environment (including the social environment), formed of an ad hoc dynamic constellation of structures, rather than a rigid relationship to some structure (although the latter may occur in situations of stereotyped activity).

The dynamic character of the pace-maker's organization is extremely advantageous for adequate maintenance of the great variety of mental processes. The dynamic character of such a pace-maker may, unexpectedly, be economically advantageous, because the number of purely structural pace-makers needed for the large variety of mental processes would be astronomical. In addition, the individual formation and development of mental activity seem reasonable only on the basis of the hypothesis and are compatible only with the reality of a dynamic pace-maker. A structural pace-maker is the logically admissible element of genetically programmed activity.

Development of mental activity is possible if it is based on the principle of dynamic controlling mechanisms whose number and form are determined by the character of activity and are not limited by a structure. The phasic development and reorganization of pace-makers, in accordance with the dynamics of activity, either determine the course of mental processes or are the neurophysiological mechanism of their development, thus preventing the indeterminate chaos of associations and disorder in mental activity.

Excitation proceeds from pace-maker to other links of the system for maintenance of mental activity. Probably the most significant neuronal populations are first involved: the rigid elements of the system. The most important part in this transmission is the synaptic apparatus which takes part in formation of the elementary code sequences where the synaptic delays can play the role of a quantifying factor. However, even the assumption of the presence of pace-maker mechanism and the vast amount of intracerebral connections cannot, apparently, resolve the question of whether this apparatus is able to secure, when necessary, practically simultaneous involvement of *all* the important links needed for complex mental activity. This possibility is supported by the studies and theoretical views of Livanov (1975) concerning the synchronizing role of unspecific influences in the brain providing the optimization of conditions for impulse transmission.

Another assumption, however, should also be studied, which is reasonable in view of the theoretical arguments and data obtained by Kvassov (1957), Russinov (1969), Golikov (1970), Adey (1977), Bogoch (1973), and others. Considering the specific features of the activity and its cerebral maintenance, the spatial–temporal relations in the course of mental activity may be a consequence of interactions between different forms of information transmission.

The problems considered in this discussion are controversial. However, the focusing of attention on them is inevitable in attempts to comprehend the activity of the whole brain, and necessary to bridge the gap between two main modern lines in studies of the nervous system: the investigations of properties of a single nerve cell and of the complex behavior of the organism.

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