A POLARIZATION-ELECTROTONIC HYPOTHESIS OF FORMATION OF SIMPLE FORMS OF TEMPORARY CONNECTION*

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The polarization-electrotonic hypothesis is examined with regard to simple forms of temporary nervous connection, i.e., of a summation reflex and dominant focus, which, although related to the conditioned reflex, differ from it in a number of essential features. Conditioned reflexes are formed, and the initial stages of their formation are the summation reflex and dominant focus. It is therefore quite logical to define these last two forms as temporary connections or as the initial phases of a single complex process of formation of new connections.

The dominant focus and its physiological mechanisms are more complex than a simple summation reflex. Such a reflex does not possess the great inertia of the dominant focus. During a summation reflex even if reciprocal inhibition is present, it does not arise in the same way as in a dominant focus. Reciprocal inhibition in a dominant focus differs from the ordinary reciprocal response of inhibition in that it does not spread along communication structures which have become consolidated anatomically in the course of evolution, but along connections arising during the formation of new interrelationships in the CNS.

Phases and conditions of conditioned reflex formation are well known as a result of the study of higher nervous activity. Physiological mechanisms of conditioned reflex formation are genetically linked with summation, but the conditioned reflex cannot be reduced either to a dominant focus or to a summation reflex, although both of the latter play a definite role, by virtue of their mechanism, in the formation of complex forms of temporary connection.

The general scheme of the principles of relationship between the physiological mechanisms of the summation reflex, dominant focus, and conditioned reflex may differ from relations between concrete forms of manifestations of the dominant focus and of conditioned reflexes, for each of them may differ in the degree of complexity of the structures implicated in the response, in the levels of these structures, and in their significance for the animal's behavior.

The basic theoretical postulates of my hypothesis were Pavlov's theory of the dynamic localization of functions and Ukhtomskii's concept of the dominant focus. In connection with the theory of the dynamic localization of functions, Pavlov put forward the concept of the "center" as a functional combination of nervous formations located at different levels of the CNS. The variable value of functions of cerebral cortical nerve cells, according to Pavlov, depends on their state which, other conditions being the same, determines the response to a stimulus. Ukhtomskii arrived at the same understanding of the "center" starting out from Vvedenskii's theory, on the basis of different concrete material. As a general conclusion from Vvedenskii's theory he accepted the view that the functional state of an excitable substrate, other conditions being the same, determines its response to a stimulus.

These general principles enunciated by the pioneer physiologist served as the original theoretical basis for my own experiments involving the action of a direct current on the cerebral cortex and deep brain formations. In fact, I argued, if Pavlov and Vvedenskii, together with Ukhtomskii, are right in suggesting that the functional state of the nervous substrate, other conditions being the same, determines the response to a stimulus, a direct current must be introduced into experiments, especially on the cerebral cortex. The general physiology of the nervous system knows of no better factor to use as an agent gradually

changing the state of the nervous substrate than a weak direct current. I considered that by gradually changing the strength of the direct current within physiologically normal limits, I could study all the gradual changes in functional state and discover the optimum at which the state which arose would be precisely that required for the formation of a simple, but new temporary connection in the cerebral cortex.

The view that the state of the nervous substrate is of decisive importance and, other conditions being the same, determines that the response to a stimulus is one which combines the theories of Pavlov and of Vvedenskii and Ukhtomskii, despite the fact that it has arisen as a conclusion from different experimental data.

The first principle of the polarization-electrotonic hypothesis is as follows: A weak direct current or, more accurately, the electric field created by it, by its action on the cerebral cortex, changes the state of the nerve cells and is an important factor determining the variable value of the function of these cells.

From experimental data obtained in my laboratory and from observations published in the literature I concluded [17] that the rhythmic pattern of cortical electrical activity is evidence primarily of the existence of a connection between neurons, and that this functional interneuronal connection can be manifested in three different forms or types. The first type of functional interneuronal connection is the gradual spread of excitation (I called this originally "local spreading excitation"). The second type is a traveling wave of excitation, reflected electrographically as the action potential (AP). The third type of connection is electrotonic, i.e., resembling the action of a direct current. All three types of interneuronal connection, forming the general system of connection, determine the functional unity of the nervous system.

Let us examine which of these types of functional interneuronal communication plays the most important role in the formation of simple forms of temporary connection.

Modern neurophysiology shows that discrete processes in the nervous system, in the form of action currents from spike transmission, take place mainly in the nerve fiber, at the input and output of the neuron; i.e., at the most decisive points of integration in the neuron, they act as gradual processes and, consequently, they can be represented as continuous functions. There are indications in the literature that changes in the state of a neuron, not necessarily accompanied by spike generation, may affect the activity of neighboring neurons, and this compels us to accept that the discharge of the neuron is stochastic in character. It has been shown that an electric field can influence the activity of neighboring neurons. In other words, processes in the nervous system are a complex tangle of both the analog and the discrete properties of a system which is deterministic and stochastic in character.

Much attention is currently being paid to the functional role of gradual electrotonic potentials and their possible role in the transmission of information to a neighboring neuron, especially via dendro-dendritic or axo-axonal junctions, or even as a gradual process spreading along the axon itself.

Because of difficulties of a technical nature, no precise direct electrophysiological answers can yet be given to these questions, but we have indirect evidence to show, in particular, that gradual electrical activity can spread along an axon in the form of a monophasic potential. The concept of the first type of functional interneuronal connection appeared as the result of experiments with repeated alteration of a segment of the frog sciatic nerve by KCl. Vvedenskii regarded such a segment of a nerve and the processes taking place in it in response to stimulation as an analog or model of a cell of the CNS. In my own laboratory it was shown that, under certain conditions, namely after repeated alteration of a segment of the frog sciatic nerve with KCl, gradual potentials can spread along a nerve in the form of monophasic waves, resembling local excitation, also called "local spreading excitation"; this should more accurately be described as gradual spreading excitation [8].

Consequently, the concept of gradual spreading excitation as one possible type of functional interneuronal connection rested on factual data. At the present time A. A. Frolov and I. I. Manyanin, working in the Laboratory of Neurocybernetics, Institute of Higher Nervous Activity and Neurophysiology, Academy of Sciences of the USSR, have demonstrated on a mathematical model the spread of a potential intermediate between an AP and an electrotonic potential in the dendrites of the CNS. Our first type of functional inter-