NEURON STRUCTURE OF THE BRAIN

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INTRODUCTION

The purpose of this monograph is to present some aspects of the origin, development, differentiation and specialization of reflex mechanisms in animals.

The structure of the brain as an organ interpreting the environment and directing the organism's reaction and behavior accordingly has played an increasingly important role in research and has been the subject of detailed experimentation. Further enlightenment in this field undoubtedly depends on the accumulation of relevant experimental data and on new information on the ultrastructure of the brain obtained with the light or electron microscope to reveal the interrelation between each of its constituent elements.

As more and more data have come to light, the need to interpret them has become increasingly important. Here an attempt has been made to correlate available data on the anatomy, physiology and evolution of the nervous system with results of more recent experimental methods reproducing physiological systems in vitro. At present, discussion must naturally be limited to hypotheses which help to clarify the general pattern of brain structure. Comparisons made between living and technical systems have usually been limited to the simplest models of the reflex arc or a single neuronal unit. When more complex CNS mechanisms were studied (such as models of a conditioned reflex), the actual analysis of these mechanisms was, in most cases, replaced by general schematic procedures, which by no means reflected the full real complexities of CNS structure. In spite of the undoubted value of these experiments on a simple cybernetic plane, the neuromorphologist is forced to acknowledge that they represent more of the cybernetic aspect than an exact knowledge of the brain.

In the first chapter a range of problems is examined; the queries raised vary in complexity and are set out in a certain order related to animal evolution, with reference to a basic plan of activating reflex mechanisms. At this stage it should be stressed that we did not base our concept of brain structure on the accepted anatomical division, but rather applied a new principle of functional localization; this is examined in detail in Chapter II.

In correlating the various stages of differentiation of animal reaction during the processes of evolution with alterations in neuronal structure, we integrated the relation of the three main functions which determine all possible adaptation mechanisms of the organism: regulatory function, control and direction, the last including autoregulation, etc. [autonomous nervous system functions]. *

* In our article "Problema regulyatsii, kontrolya i upravleniya v neirofiziologicheskom aspekte" (Problems of Regulation, Control and Direction in the Neurophysiological Aspect), published in the book "Problemy kibernetiki," No. 11, 1964, we used the terms self-regulation and regulation, self-control and control, self-direction and direction. In the present monograph we have substituted the prefix "auto" for "self" so that our definitions may be differentiated more precisely from the interpretations of these terms used mainly in the psychological literature. The meaning remains unchanged.

To confirm our theory as stated above, our aim is to demonstrate that the morphological structure together with the functional aspects studied provide a feasible neurophysiological mechanism responsible for active orientation of the organism in relation to the environment, both external and internal, including analysis of signalization systems and appropriate responses. These reactions will then explain the mechanism of reflex response at all stages of evolutionary development. Further on it will be explained how the individual (topographic) pattern of the accurately delineated reflex mechanism for each of the given functions is determined, and how it is related to the corresponding neuron complexes and their interrelationships.

To avoid misunderstandings, it seems necessary to make the following proviso.

We could not find exact definitions for the terms "regulation," "control" and "direction" in the relevant literature, but arrived at our understanding of these functions exclusively through logical analysis of the reflex mechanisms in the animal organism. We consider these to be neurophysiological functions, brought about by absolute rules of inherent self-organizing systems.

It must be stressed that in the interpretation which follows, we consider the function of direction, along with the most complicated forms of analytical-synthetic processing of all information received by the organism, to be the highest expression of reflex activity (higher nervous activity, according to Pavlov's definition). We relate this function to the most highly organized parts of the central nervous system and ascribe the functions of regulation and control (according to our understanding of these definitions) to the lower levels of analyzers, considering them as being auxiliary to the main functional control which is recognized as the true organizer of all planning and direction of behavior. Our definitions of regulation and control thus differ from those generally accepted. We consider the manifestations of higher nervous activity in man, which on the psychological plane are often designated as regulation and control, as different forms of expression of the function of direction. In this respect we are more in agreement with those representatives of the cybernetic trend, who in determining the tasks of this trend, prefer to speak expressly of control function.

Chapters III and IV deal with the development of the system of neurons and the general pattern of neuronal structure and transmission in the CNS. We claimthat a single common principle of general significance is responsible for the structure of all animal nervous systems from the simplest to the most complicated. According to this principle, any neuron, acting as the basic unit of the transmission process, is responsible for the collection and distribution of impulses passing through it, i. e., it fuctions as a physiological unit which fulfills the tasks of certain forms of analysis, synthesis and selection (filtration) of crossing impulses on the nerve cell level. This rule, which applies to all stages of evolution, at all levels of the nervous system, has enabled us to project a general pattern of successive differentiation of organization of neuronal transmissions, from the primitive neurons of the lower multicellular organisms to the most highly differentiated brain of the higher vertebrates and man.

With reference to the general nature of CNS structure, we will discuss here in greater detail the problem of rational classification of the cerebral cortex into different zones (anatomical areas and zones), depending on their function. The classification of cortical areas as delineated in this work has been confirmed by extensive long-term experience of clinical observations of cortical injuries.

The theories set out in this book are actually only working hypotheses, and are naturally subject to discussion. A thorough acquaintance with these theories may be of interest to a variety of specialists — not only neurologists, neuroanatomists, neurophysiologists and clinicians but also psychologists, pedagogues, biologists, physicists, as well as all scientists studying experimental models of biological systems.

It is our belief that the material presented may also assist in clarifying the philosophical concepts of the structure of the brain as an organ registering all aspects of environmental stimuli and processing them in the human and animal consciousness.

In Chapter IV we review more fully the mechanism's reflex activity in involving signalling systems, and the interstimulation of neurons, as an anatomical-physiological basis for registering and interpreting information in the cerebral cortex; in fact we stress that this is the underlying anatomical entity which functions as the interpreter of changes in the environment and regulates the organism's reaction to it. We also consider it of value to integrate into our concept of brain structure and function the known facts of evolutional transitions in structure which have enabled the brain gradually to perceive and interpret not only usual sensory stimuli but also complex abstract ideas.

We regard the data presented in this work as a blueprint for a future concept of the neuronal construction of the brain.

Chapter I

REFLEX MECHANISMS OF THE BRAIN

1. ORGANS OF SIGNALLING ACTIVITY

In the evolution of the animal world the nervous system has developed as an interacting complex of organs which provide a highly effective structure for the adaptation of an animal to alterations in its environment, with the aid of the signalling system and its activity. Unlike plants, which react with changes in their activity only to direct external influences, animals are able to react to more highly complex signalling systems. The various stimuli are perceived by the animal not only as physical or chemical effects on the organism, but also as signals which are interpreted as indicators of certain vital changes. Animals thus differ from plants in their capacity to perceive and convert particular information received as impulses into certain relevant responses.

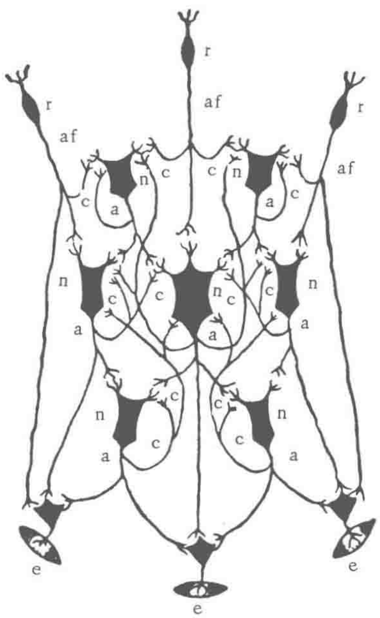

FIGURE 1. Diagram of the differentiated network of neurons:

r – receptors; af – peripheral sensory (afferent) fibers, carrying impulses from receptors to neurons; n – neurons; a – nervous fibers (axons) of nerve cells with dendrites (collateral branches – c), contracting with bodies of other nerve cells and their dendrites; e – effectors.

The following three basic elements, linked with each other in a definite order in the reflex arc pathway (Figure 1), are regarded as the physical basis of signalling (impulse) activity:

Receptor cells of the sensory organs, registering stimuli and transforming them into nervous impulses;

nerve cells with their dendrites, participating in various transmissions of nervous impulses in the course of their transfer from the primary to the terminal link of the reflex arc;

effector cells, such as muscles or glands, i. e., elements which effect reflex responses of the organism to stimuli.

The basic elements of the nervous system – the neurons – emerge and develop in the evolution of the animal world as a special apparatus connecting receptors and effectors. These neurons are responsible for determining the impulse significance of stimuli and for producing biologically expedient adaptive reactions.

The elements of the reflex arc are interconnected by special formations — the synapses. These structures will be described in greater detail in Chapter III. The subsequent transmission of impulses proceeds through the synapses, which receive and transmit from receptors to neurons, from one group of neurons to another, and finally from neurons to effectors.

In the course of development of the animal world, and in connection with the differentiation in interrelations with the external world, the mechanisms of the reflex impulse activity become very complicated. In their elementary form they are represented by a network of neurons (Figure 1), consisting of relatively simple combinations of receptors, neurons and effectors, which appear for the first time in lower multicellular organisms (Coelenterata).

This organization of the nervous system, on which its progressive differentiation is based, is already able to accomplish coordinated, i. e., regulated and biologically expedient, reflex responses to a stimulus.

Further differentiation of the system responsible for receiving impulses and activating effector reactions consists of the following elements.

The nervous mechanism of coordinated nervous activity, which emerges in the early stages of animal evolution, is capable of effecting regulated responses to a limited range of combinations of impulses with vital importance for the self-preservation and persistence of the species. However, this mechanism proves inadequate in cases where the organism is compelled to adjust to more complicated combinations of signalling systems. In themselves, these stimuli may not endanger the balance of the organism and may not originate directly from the sources of food; they simply inform the animal on the various changes in the environmental situation.

In subsequent stages of the evolutional scale, the organism is able not only to carry out rapidly coordinated reflex responses to certain complex stimuli, but also to interpret in its more complicated reactions a space and time relationship between objects and events. This allows for a more differentiated orientation of external objects and their effect on the organism.

The development of more complicated mechanisms of perception and response have provided a means of constructing more complicated brain models for purposes of study. This evolutionary process has brought about a more highly developed signalling activity, or, according to another definition by Pavlov, to a higher stage of development of higher nervous activity.

Animals with a more primitively evolved signalling activity, capable of reacting in an orderly way only to a relatively narrow range of stimuli, may be compared in some way to living reflex self-adjusting "automatons." Organisms reacting to a wider range of stimuli, and presenting higher forms of reality perception, must interpret a considerably larger amount of incoming information from the environment. Compared with lower evolutionary orders, able to interpret a minimum of information, such organisms can be said to possess "surplus information" and are capable of "selecting" optimal solutions to various problems, including "deliberation" and "solution" of logical tasks. It is the evolvement of this quality that has led to the development of thinking beings.

With differentiations of receptions, the nature of responding actions has also become more differentiated. In the complicated fusion of conditioned and unconditioned reflexes which make up animal behavior, there is a continuing tendency to predominance of various forms of motivated co-ordinations perfected during life.

These changes in the manner of functional interrelations between the organism and the environment inevitably affect the structural organization of the sensory organs and nervous system and find their expression in the development of the analyzers.

Complicated neuronal linkages, of which the analyzers are composed, serve as the physical basis for a multitude of functional connections between separate signals and their combinations; in this manner the nature of relations between stimuli and the pattern of action response structured on this basis is determined.

In animal evolution the analyzers have developed as the most highly organized part of the neuronal structure of the brain, with the basic biological designation of fractional isolation of the separate signals, and the reaction to certain complexes of stimuli and their relations. As Pavlov pointed out, the analyzers are highly effective instruments for fine analysis and multifaceted synthesis of stimuli.

In the highest representatives of the vertebrates complicated networks of neuronal transmissions, of which the systems of analyzers are composed, are distributed in the various levels of the CNS (see Figure 7) and are adapted to the regulation of various components of reflex reactions, thus patterning the total behavior of the animal. The systems of analyzers which are distributed throughout the central nervous system are the most important part of brain structure; they play the role in the physiological unity of conditioned and unconditioned activity and thus ensure a balanced adaptation of the organism to the environment.

It should be pointed out that the differentiation in evolution of the physical components of the impulse activity mentioned above corresponds to some extent to the theories of McKey. * It is possible to find an analogy between the coordinating mechanism and the analyzers (see below) on the one hand and between the lowest and highest automatons on the other. The lower automatons (of the first order) work on an automaton-environment schedule. They are able to accomplish only the elementary function of direct "coding over" of external signals. The higher automatons (of the second order) possess an internal mechanism of confronting the external signalling system with their own programs of behavior; this mechanism is able to reproduce copies, models of certain features of objects and phenomena acting on the automaton, thus fulfilling the function of an analogue of the environment. As will be shown in the next section of this chapter, one of the significant differences between the analyzers and the coordinating mechanism is that the former provide the organism with a more complete and comprehensive orientation in the environment.

* See D.M.McKey. Development of the Concept of Action of Automatons. In "Automatons," edited by K.E.Shannon and J.McCarthy.

2. FUNDAMENTAL SUBDIVISION OF THE NERVOUS SYSTEM

Below is set out the general plan of the brain reflex mechanism in its different stages of differentiation, and the next chapter will deal with the relations of these mechanisms to the basic nervous functions of regulation, control and direction.

As already mentioned, in the evolution of the animal organisms possessing a nervous system there is an initial formation of a mechanism capable of carrying out coordinated reflex responses to stimuli. In other words, the elementary network of neurons (see Figure 1) has the basic function of a coordinating mechanism.

This organization is already clearly discernible in the earliest phases of animal evolution. Thus, the simplest unicellular organisms possessing only rudimentary sense organs and nervous system are in a position to accomplish well-regulated reactions, e. g., to use from their limited range certain definite, biologically expedient reflexes in a given situation, and inhibit reflexes hindering continuous activity.

In the course of progressive evolution the given mechanism of coordinated responses to stimuli becomes highly differentiated and specialized. Nevertheless, special groups of neurons responsible for this aspect of reflex activity can be formed in all representatives of invertebrates and vertebrates, both primitive and on a higher evolutional scale.

In animals with bilaterally symmetrical bodies (including worms and higher animals), the coordinating mechanism forms a central axis of their central nervous system (Figure 2). In invertebrates it is connected with the thoracic ganglion (Figure 2A), by nerve cords in lower worms and by a chain of interconnected ganglia in annelids, crustaceans, arachnids and insects. It seems that at these stages of evolution the chain of ganglia distributed along the trunk carries out reflex functions that are analogous with the more complex coordinating activity mechanism in vertebrates.

In vertebrates this mechanism extends along the entire axial part of the central nervous system (the spinal cord and brainstem) (Figure 2B), occupying its central parts. Here it is important to mention the relatively direct character of interrelationships between receptors, neurons and effectors constituting the coordinating mechanism; one may assume that there are as many of these elements (but no more) as are essential for carrying out a particular coordinated reflext act.

The formation of analyzers is another development of this system which is of significance in the development of orientation of the organism in the environment and the far-reaching transformations of the entire sphere of its perception and relevant reaction. The physiological reason for the formation of these divisions of the entire reflex organization in the animal world is that the divisions enable the organism to perceive a multitude of "subsidiary" stimuli in a differentiated way, in addition to stimuli which are directly reprocessed by the coordinating mechanism, and ensure vitally important adaptations to environmental conditions. Thanks to the development of the analyzers, the organism receives a multitude of "inputs" and "outputs" to and from the periphery of the body in touch with the outside world. Thus, the organism is able to react in a selective way to the various signals, in a manner which functions beyond the scope of direct safety for the living system.

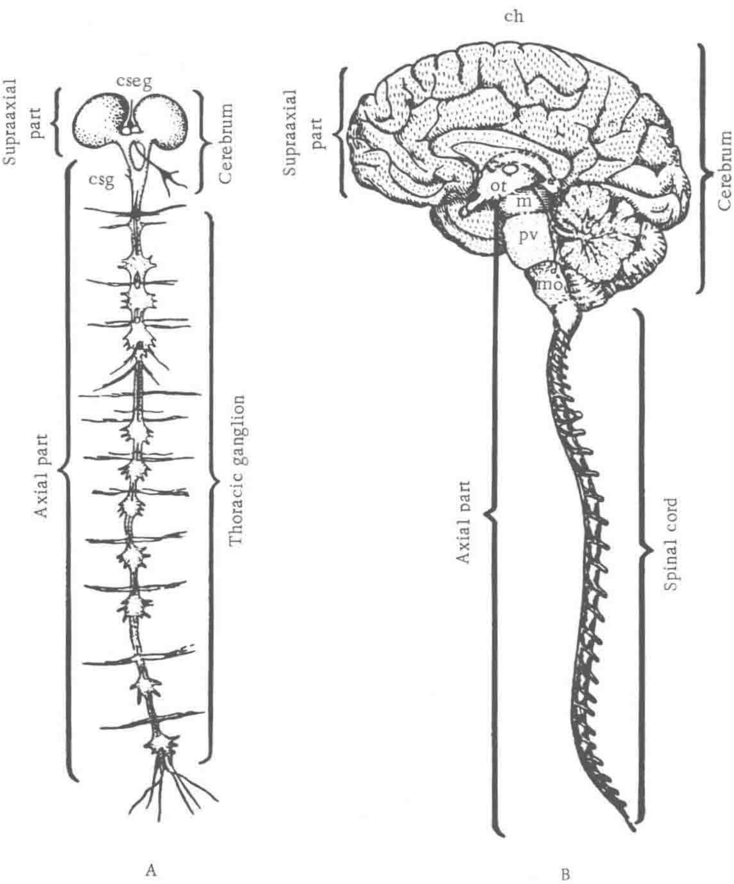

FIGURE 2. A – centralized ganglionic nervous system of a higher invertebrate (insect): cseg – cephalic supraesophageal ganglia; csg – cephalic subesophageal ganglia; B – central nervous system of the vertebrate (human brain): ch – cerebral hemispheres; ot – optic thalamus (diencephalon); m – mesencephalon (lamina quadrigemina and brainstem); pv – pons varolii; mo – medulla oblongata.

Pavlov defined analyzers as the complex links involved in transmission of nervous impulses, beginning with various sensory organs and ending with the brain. To clarify this function, he differentiated in each analyzer its peripheral and central (cerebral) end. In more highly organized representatives of the animal world the highest cerebral terminus of the system of analyzers is coordinated with the corresponding area in the cerebral cortex (see Figure 7).

The significant differences of the cerebral parts of the analyzer from the peripheral are as follows. Receptor elements of the sensory organs, and the peripheral sensory neurons directly connected with them (Figure 3, spn), are adapted exclusively to the purely "mechanical" discrimination of stimuli in accordance with their physical qualities (frequency, intensity, duration, etc.). The cerebral parts of the analyzers are specialized in central processes of analysis and synthesis of stimuli, not simply according to their physical and chemical parameters, but mainly according to their signal function as part of the life of the organism. Only on the basis of such mediatory processing of nerve signals are programs or formulas of responding actions and reactions of the organism developed.

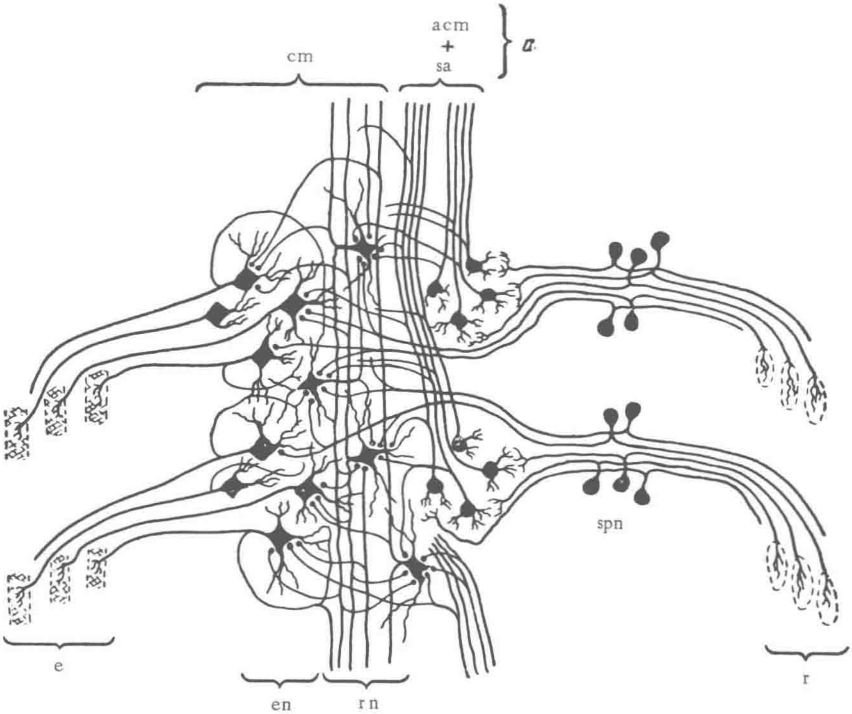

FIGURE 3. Diagram of transmitting arrangements of the CNS which form the coordinating mechanism (cm) and analyzers (a); the latter are composed of the analyzing-coordinating mechanism (acm) and systems of analyzers (sa); r – receptors; spn – sensory peripheral neurons present in ganglia of the cerebrospinal and cerebral nerves; rn – special transmitting neurons of the coordinating mechanism (reticular formation); en – effective (motor) neurons which innervate the effectors; e – effectors (skeletal muscles).

We include in the cerebral part of the analyzers only those groups of centrally transmitting neurons, with their interrelations, which could be considered as complementary superstructures to the transmitting neurons of the coordinating mechanism itself (Figure 3, see also Figure 18). In the centralized nervous system analyzers are represented as collections of neurons which are formed primarily in the "input" system of neuron networks, i.e., at points of transfer of impulses from peripheral sensory neurons into the coordinating mechanism. Analyzers represent an additional transmitting device, which is wedged in between the receptor sphere of the organism, and devices which directly organize its coordinated responses to stimuli.

From this topographic-anatomic correlation it follows that the basic physiological and biological designation of the analyzers is the organization of the sphere of reception of the organism itself. The cerebral parts of the analyzers participate in carrying out the interaction of various centripetal impulses incoming from the sensory organs. This type of interaction takes place even before the signalling impulses, transformed in a certain manner, are transmitted to the coordinated mechanism and are converted there into a specific corresponding effector activity.

The coordinating mechanism is concerned mainly with the reprocessing of relatively simple combinations of biologically adequate stimuli, which have not yet converged into more complicated physiological syntheses. The activity of the cerebral parts of the analyzers ensures the most highly organized central coordinations inside the receptor sphere itself, i. e., an analysis and synthesis of complexes of stimuli regulated in space and time and united in definite interrelated systems. Thanks to this complex mechanism the organism is able to orient and function as a complex differentiated entity in the external environment.

A useful illustration of this type of coordination, formed in the sphere of receptions of the organism, may be given by the results of the well-known experiments of Stratton,* using eyeglasses provided with lenses that give an inverted picture. After only a few days, complete reorientation in the environment is accomplished in the subject tested, and a normal perception of objects is established.

In organisms possessing developed analyzers, all reflex responses appear to undergo a special adaptation process through the prism of all processes of analysis and synthesis occurring in each case.

In the sphere of interrelations between the organism and the environment, the functional possibilities inherent in the coordinating mechanism itself are extremely limited. This reflex device is only suitable for the realization of separate, more or less elementary adaptations to relatively narrow distribution areas of life. The analyzers considerably extend the limits of adaptative possibilities of the organism.

Reactions achieved with the help of the coordinating mechanism are to a certain degree of a "transient" nature, each moment correlating the physical parameters of stimuli (their intensity, duration, frequency, etc.) with the physiological parameters of relatively simple reflex arcs.

The functional potentialities of the cerebral parts of the analyzers are much greater than those of the coordinating mechanism; thanks to their more complicated neuronal organization, they develop indispensable conditions not only for the synthesis of various reactions occurring at a given moment, but also for the functional connections of reactions in time. In other words, in the cerebral parts of the analyzers there is not only a direct correlation of the type of action of stimulus, and the nature of corresponding effector response at any moment, but there is also a complicated mediation of activity which occurs at a given moment, correlating with results of reflex actions performed earlier.

Analyzers apparently represent a more highly specialized instrument of reflex image of the environment as a complex and interrelated entity. Because of these analyzers, the organism is in a position to adapt itself to an increasingly greater number of variable combinations of stimuli.

* G. M. Stratton. Vision without Inversion of Retinal Image. – Psychol. Rev. No. 4. 1897.

The development of analyzers in the animal world has thus brought about a differentiated physical basis on which the continuity of individual experience is patterned. The potential of the organism to "foresee" probable consequences of its actions is increased accordingly. As will be shown below, particular formations of the cortical type especially adapted to performing the most complicated reflex functions have developed in the cerebral parts of the analyzers.

The formation of analyzers is conditioned by a qualitative differentiation of reactions coordinating the organism with the outside world. The effect of the outer, as contrasted with the inner, environment of particular importance in the progressive development of the analyzers.

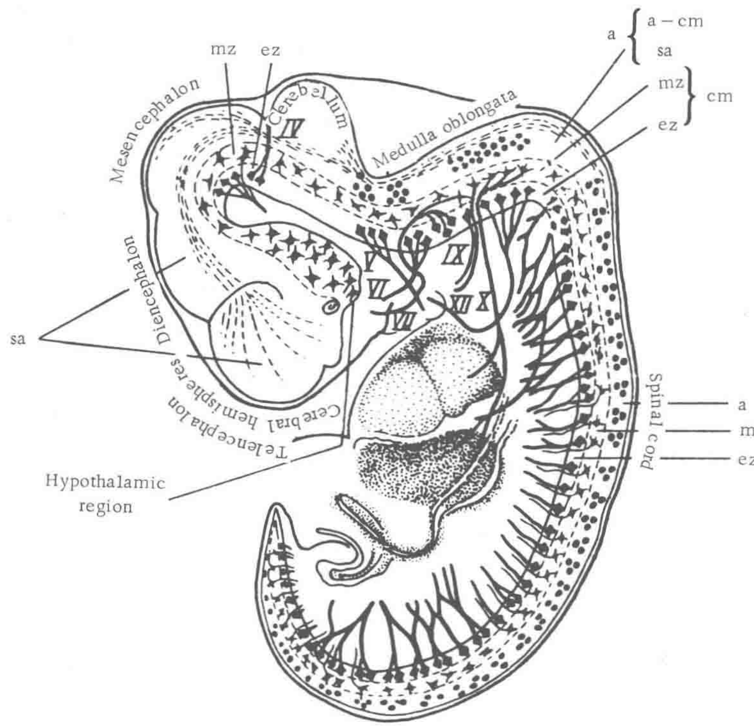

FIGURE 4. Diagram of the division of the CNS in a vertebrate. A human embryo at an early stage of development. Roman numerals denote the motor areas of the cerebral nerves; ez – zone of effector (motor) neurons with their exit points to the periphery; mz – zone of special transmitting neurons of the axial part of the CNS (reticular formation); mz + ez are included in the coordinating mechanism (cm); a – zone of analyzers, which later differentiate into the analyzer-coordinating mechanism (a–cm) and system of analyzers (sa); it may be seen that the reticular formation also extends into the supraaxial part of the CNS (see hypothalamic region of the diencephalon). The higher parts of the CNS – the cerebral hemispheres of the telencephalon – developed in their entirety from the zone of analyzers. (With partial use of the scheme of V. Gis and with reference to the latest research by G. P. Zhukova and T. A. Leontovich.)

The analyzers have appeared in the more highly developed invertebrates in a more rudimentary form; their central nervous representation here is in the more primitive brain (supraesophageal nerve ganglia in worms, insects, and crustaceans — see Figure 2A). However, only in vertebrates do the analyzers enter the decisive phase of their development, occupying more and more sections of the central and peripheral nervous system (Figure 4).

The chains of neuronal transmissions that constitute the analyzers are built on collections of neurons which make up a coordinating mechanism (see Figure 7). Guided more and more by the coordinating mechanism, the analyzers make use of its possibilities for more effective and adjustable adaptation of the organism to the variety of changing situations. With progressive development of the analyzers, the coordinating mechanism becomes more and more dependent on them, being transformed into a pliant instrument which carries out orders issued by the analyzers. In the course of evolution the coordinating mechanism, occupying a control position, becomes more and more superseded ("overgrown") by analyzer formations (Figure 5). At the same time, the analyzers become gradually independent from the coordinating mechanism from which they originally emerged.

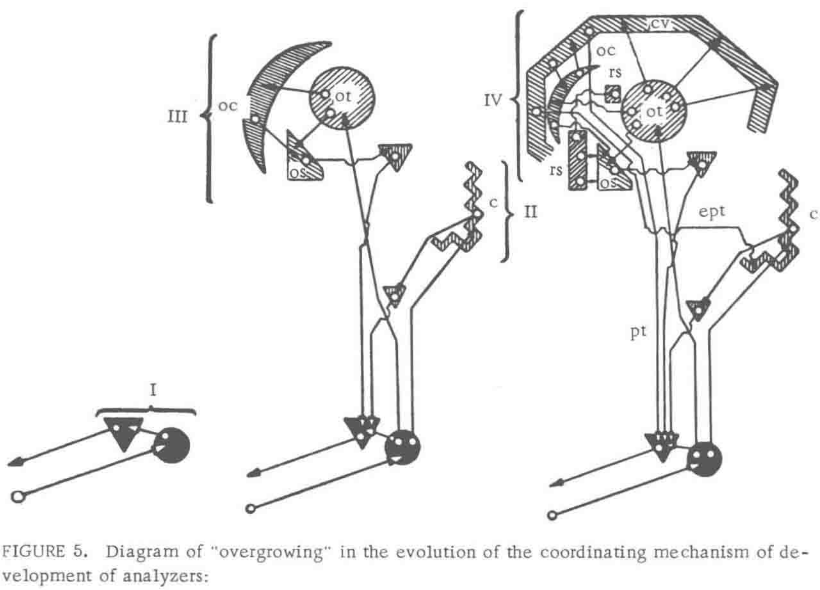

FIGURE 5. Diagram of "overgrowing" in the evolution of the coordinating mechanism of development of analyzers:

c — cortex of the cerebellum; ot — optic thalamus; oc — complex of phylogenetically older formations of the cortex; os — phylogenetically older part of the subcortical nodes of the cerebral hemispheres; rs — recent part; cv — the latest to appear in the evolution of vertebral formations of fully developed new cortex of the cerebral hemispheres; pt — pyramidal tract for the transmission of impulses of voluntary movements formed in the cortex to the reflex centers of the coordinating mechanism; ept — extrapyramidal path for the transmission of effect of the cerebral cortex on the cerebellar cortex. The lower reflex centers of the spinal cord and brainstem are represented by black circles and triangles. I corresponds to the coordinating mechanism, II to the analyzing-coordinating mechanism, III and IV to the two subsequent stages of progressive differentiation of higher (supraaxial) brain ends of the analyzer systems. (Somewhat modified sketch of N. A. Bernshtein.)

Thus, beginning with certain stages of evolution of animal organisms, the centralized nervous system* may be defined as the coordinating mechanism plus the aggregation of cerebral parts of the analyzers, closely interlinked. In this, the progressive increase in absolute and relative numbers of centrally transmitting neurons in the analyzers, relative to the neurons of the coordinating mechanism, can be used as a standard for measuring the level of neuron organization. On the relative-evolutional plane two main divergent directions in the differentiation of the analyzer structure can be distinguished — representing two consecutive stages of their development — which complement each other and are included in a uniform functional architecture.

At the lowest stage of development, formed relatively early during phylogenesis, one can detect those formations of analyzers which are arranged at different levels of the axial part of the CNS and which are closely interconnected with elements of the coordinating mechanism. Those collections or groups that ensure further differentiation and expansion of the coordinating resources of the organism are designated here the analyzer-coordinating mechanism (see Figure 5 II). The latter is thus formed as a result of superimposition of the coordinating mechanism by elements of the analyzers.

The cephalic subesophageal nodes (see Figure 2A) are considered as an embryonic homologue of the analyzing-coordinating mechanism of the vertebrates, in which this mechanism is already distinctly formed. However, in the lower vertebrates (Cyclostomata) the basic mass of the central transmitting neurons can still be attached to the coordinating mechanism, whereas in fishes there is a rudimentary development of an analyzing-coordinating mechanism in the zones of all analyzers (Figure 6).

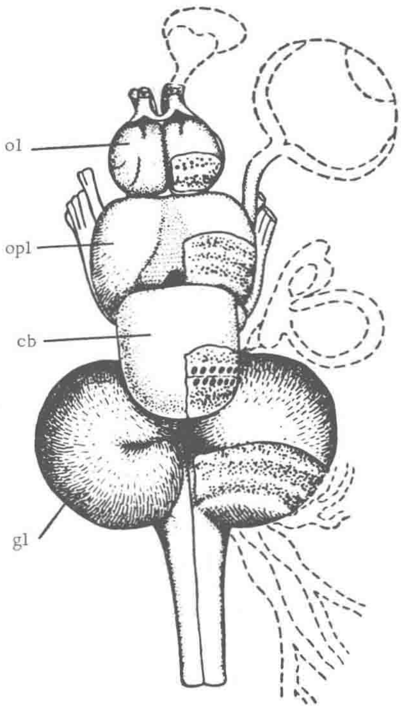

FIGURE 6. Diagram of the brain of a fish (carp) showing the relationships in the development of the cerebral parts of the various analyzers:

ol – olfactory lobe (prosencephalon); opl – optic lobe (mesencephalon); cb – cerebellum; gl – gustatory lobe of the medulla oblongata. On the right are sketched the transverse sections through the various parts of the brain to illustrate their structure according to the cortical type. (With partial use of Gerrik's figure.)

The highest degree of development of analyzers, which can be described as the greatest constructive achievement of living nature, is represented by systems of analyzers in the strict sense. The latter, as already mentioned,

* By centralized nervous system we understand the nerve ganglia in invertebrates and the central nervous system in vertebrates.