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CERTAIN ONTO-PHYLOGENETIC CORRELATIONS IN THE DEVELOPMENT OF THE STRUCTURAL BASIS OF REFLEX FUNCTIONS OF THE ORGANISMS

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Chair of Physiology of Higher Nervous Activity of Moscow State University

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The results of studies carried out in the cytoarchitectonics and conducting pathways, in the cytology and histochemistry of neural elements, and in the minute characteristics of the structure of neurons and interneural bonds of various sections of the central and peripheral neurous system at various stages of intrauterine life and after birth in certain animals and humans, may serve as a basis for certain conclusions and generalizations relating to the general problem of the development of structure and function in phylo- and ontogenesis. The data available to us and compared with the data in the literature enable us also to make a comparative analysis of the periods of emergent rates of development and maturation, and the peculiarities of structural differentiation of various neural formations which participate in the arrangement of the reflex activities of the organism.

Among the basic problems related to various aspects of the entire area, one can single out the following: 1) the sequence of differentiation, development, and maturation of the neural complexes which form various links of simple and complex reflex arcs in the systems of analyzers; 2) the onto-phylogenetic correlations in the development of homologous central and peripheral neural formations in various animals and humans; 3) the connection between the structure and function at various stages of development of reflex mechanisms.

As pointed out by I. P. Pavlov, the complex interconnection of the systems of analyzers forms a perfect organ of equilibrium between various states of the organism and environment. The emergence and growing complexity of neural structures in ontogenesis is, undoubtedly, conditioned by the entire previous history of a given species and, especially, by the character of adaptive reactions of its nearest and remote ancestors to the external stimuli. However, as has been demonstrated by B. S. Matveyev (1946, 1953, 1957), the transformations of structure and function of various organs during the process of the individual development of the organism are conditioned not only by their definitive organization in an adult organism and by the course of their formation in phylogenesis, but also by the character of adaptation of a developing embryo to the special conditions of its embryonal life. During ontogenesis these conditions undergo multiple changes, which leads to a change in the functions of the embryo's organs and a corresponding alteration of their structure. The complex interaction of various moments which determine the embryonal development was noted by S. V. Yemel'yanov (1941) who had singled out four basic factors under the effect of which the formation of organs and their parts takes place: 1) historic, 2) functional, 3) correlative, and 4) the factor of general differentiation rate.

The rules formulated by A. N. Severtsov in his teaching on phylembryogenesis, as related to the analyzer of animals and humans, are still being very insufficiently studied. An attempt is made below to carry out certain morpho-physiological comparisons in this plan, on the basis of the reflex principle of development and organization of the brain.

The most important turning point in the process of individual development of an organism is the moment of its birth, when the character of stimuli affecting it undergoes a powerful and sudden change. Obviously, this is the precise moment to which is timed the definite degree of maturation of all sections of analyzers and executing apparatus which ensure to a given organism the transition from intrauterine life to extrauterine existence.

The idea of the presence of a definite system in the character of functional localization was developed by P. K. Anokhin (1948, 1958) in his concept of systemogenesis. On the basis of the data of his own studies and those of his associates on the embryogenesis of the central nervous system (K. V. Shuleykina, 1953, A. M. Ivanitskiy, 1955; Ya. A. Milyagin, 1957; Ye. L. Golubeva, 1958), P. K. Anokhin formulated the thesis that definite complexes of neurons jointly participate in the formation of a definite reflex-act, which is phylogenetically conditioned and is of adaptive importance to the organism, and develop as a functional system with extensive ramifications in various sections of the cerebrum and spinal cord.

This idea proved very fruitful in the theoretical interpretation and rational explanation of multiform heterochroniae which are actually observed during the ontogenetic establishment and development process of various reflex reactions and their morphological basis.

In this connection, attention is attracted to the considerable variations in the course of structural and functional differentiation of various groups in interrelated neurons by means of which specialized reactions of a developing organism to stimuli are effected. In the cerebral areas of the analyzers, pronounced accelerations and retardations take place when, during ontogenesis, aggregates of neural cells and bundles of neural fibers form which differ in function. These variations of growth and differentiation extend also to the corresponding areas of peripheral innervation.

Of particularly great interest are the changes in the periods of initial anlage and rates of differentiation of neurons which selectively involve in the process of accelerated development the elements of definite reflex systems which, thus, undergo an earlier maturity in the ontogenesis. We have in mind the systems developed in the course of prior evolution and possessing substantial importance in the adaptation of the organism to its environmental conditions of existence during the early stages of extrauterine life.

As indicated by P. K. Anokhin, the functional development of structures at each stage of ontogenesis is adapted precisely to the ecology of the animal. The stimuli in a developing embryo are precisely those influences which had been active factors in the prior evolution of a given species. Such adaptation of embryogenesis to ecological conditions is made possible through heterochroniae which ensure a prompt setting into motion of services formed during the entire preceding history of the development of the species.

The importance of ecological factors to the characteristic development of definite organs and tissues in ontogenesis was demonstrated by B. S. Matveyev (1946) in a number of convincing examples. Thus, during embryogenesis vibrissae develop considerably earlier than hair on the body, a phenomenon connected with the adaptive significance of these formations to the nutrition of infants during the lactation period. As noted by B. S. Matveyev, in instances where an an earlier functioning of an organ is useful to the organism as an adaptation to environmental conditions the entire process of morphogenesis shifts in the direction of earlier stages of intrauterine life, a change consolidated by natural selection. As a result, the corresponding organ reaches its definitive state sooner than other organs.

It is interesting to compare the correlations of periods and rates of development of neural pathways and centers of the upper and lower extremities in humans with the results of these investigations.

Thus, the works of old authors (P. Flexig, V. M. Bekhterev, etc.) have already established the fact that the bundle of Burdach in the posterior columns of the human spinal cord, which transmits sensation from the upper extremities, begins to get enveloped in myelin earlier (in five to six lunar months) than Goll's fasciculus which transmits sensation from the lower extremities (in six to seven lunar months). Obviously, these differences in periods of myelinization of the corresponding fiber bundles are caused by their different functional significance. In the phylogenesis of vertebrates the anterior extremities became specialized for a considerably wider circle of adaptation reactions (obtaining of food, snatching, attack and defence, play) than the rear extremities which are narrowly specialized, mainly for the implementation of locomotor and static reflexes of the body.

Interesting data on the correlations of periods of development of the anterior and posterior extremities in various representatives of mammalia are cited by B. S. Matveyev (1943) who connects these correlations with the ecologic peculiarities of the development of progeny in the corresponding species.

In the evolution of primates, the hand represents an organ which achieves an incomparably more complex and finer structural differentiation than the leg. Correspondingly, during embryogenesis, the fingers of the hand in humans, especially the index finger, begin their differentiation earlier than the entire wrist. It has been established also that, during the early stages of prenatal ontogenesis, the skin on the finger cushions is particularly rich in sensory nerve endings (N. I. Zazybin, 1935). Here also the peripheral nerves grow in first.

The consecutive stages of the development of the complex functional system of nutrition-reaction in rabbits during the postnatal period were studied by A. M. Ivanitskiy (1955).

In this study, too, there was elicited the characteristic conditioning of the change in various morphological components of this complex reaction via the sequence of their formation in the phylogenesis of lower mammalia. Phylogenetically, the more ancient cortical formations, which form the cerebral end of the olfactory analyzer (the ancient and old cortex according to I. N. Filimonov's classification), mature as early as during the first two days following birth, whereas the majority of cells of areas which appear much later in the phylogenesis of mammalia complete their differentiation and become capable of a circuit-closing function only toward the 13th to 16th day following birth.

Similar periods are indicated also by I. I. Gutner (1946) who notes that toward the 15th day of life, the development of dendrites of cortical cells and their lateral appendages is completed in rabbits. During the same period of postnatal ontogenesis changes in the bioelectric activity also occur. Thus the distinguishing characteristics inherent in the cortical fields of an adult animal brain (A. S. Pentsik, 1940) are acquired.

One can not help seeing in this sequence of complications of various cortical formations in rabbits during ontogenesis a reflexion of the definite sequence of participation of various analyzers in the implementation of corresponding reactions during the phylogenesis. The same rules are followed by the temporary correlations in the course of the morphological development and maturation of analyzers during the entire length of the individual life of the organism.

In this scheme of correlations of ontogenesis and phylogenesis, of interest are the data relating to the differences at the moment of birth of analyzers in full-term immaturely born animals, as well as full-term and miscarried organisms of the same species.

Interesting results were obtained regarding the degree of maturity of the cerebral cortex neurons in both instances. Thus, even in the old works of M. Stefanovskaya it was demonstrated that cortical neurons in a mature-born guinea pig possess even at birth a sufficient mature form; the dendrites of the pyramidal cells are well ramified and are covered with numerous lateral appendages, approximately the same in number as in an adult animal. In contrast, in an immaturely born mouse the cerebral cortex at birth still has a patently immature character; the dendrites of the majority of pyramidal cells are little ramified and almost completely devoid of lateral appendages, and their number markedly increases only toward the 10th day, and approaches that of an adult animal only toward the 15th day after birth. Also in a newborn kitten the cerebral cortex has few lateral appendages on the dendrites; the number of the latter increases considerably toward the end of the first month of life (M. L. Borovskiy, 1936-37).

The obtained morphological data coincide with the physiological ones: in mature-born animals (guinea pig), as contrasted to the immature-born (rabbit), the conditioned reflexes develop, starting with the first day of life, and are distinguished by their constancy.

The study of the developmental characteristics of reflexes and their structural mechanisms in miscarried animals and humans represents a very promising field in the elicitation of the substance of changes created by a sudden transition from the environment of a maternal organism into the external world. Unfortunately, so far, very few studies of this type have been carried out. However, the data relating to this problem, though scarce, are nevertheless sufficiently definite.

The studies of N. K. Kasatkin (1948) have established a possibility that conditioned reflexes form in prematurely born infants during the period between the moment of actual birth and the date of normal termination of the intrauterine period. On the other hand, observations of the Moscow Brain Institute (L. A. Kukuyev, 1955) prove that the cerebral cortex development in prematurely born proceeds with notably more intensity than in a normally developing fetus. One can see, in comparing the cyto-architectonic preparations of the brain of a full-term infant and a premature one who had lived for two or three weeks, that in the latter the cerebral cortex progressed further in its development. This is manifested macroscopically in the greater growth of convolutions and grooves, and microscopically, mainly in a clearer differentiation of the cortical mass into layers and in a somewhat greater general thinness of cells connected with the more extensive ramification of their appendages.

The myelinization of fibers (of the optical nerves, for instance) also proceeds in the prematurely born in an accelerated manner, as compared to normal newborn infants.

Thus, it becomes clear that the turning point in the life of an organism connected with its initial subjection to a stream of external stimuli represents a powerful factor which stimulates and accelerates the development of the structure of analyzers.

Certain instances of heterchroniae were mentioned above which have a narrow specific significance in the adaptation of the organism to individual conditions of its existence at various stages of development. However, these instances do not exhaust the complexity of correlations in the differentiation of neurons in the ontogenesis and phylogenesis of vertebrates. The heterochroniae is embryogenesis extend to a large group of neurons located in various sections of the central and peripheral nervous systems.

In eliciting these complex rules of phylembryogenesis, certain interesting differences are observed in various representative mammalia. These differences concern the periods of anlages and differentiation rates during the intrauterine period of homologous anatomical formations which are consecutively formed at various evolutional stages of the entire comparative-anatomical order.

On such a comparative analysis of the data, one succeeds in detecting a definite relationship expressed in the fact that the greater the height and complexity of the structural and functional organization achieved in phylogenesis by one part of the brain, the longer is the time required for its ontogenetic development, and correspondingly earlier is the phase of intrauterine life to which the moment of initial differentiation of its anlage is shifted.

Similar phylembryogenic changes were observed in regard to other organs by Menert who thought that the rate of the process of ontogenic development of an organ is proportional to its achieved level of development. Menert as well as A. N. Severtsov connected heterochroniae of this type observed in ontogenesis and manifested in an earlier embryonal anlage of an organ, with the progressive evolution of the organ. A. N. Severtsov wrote: "At the present time the problem of the change of rate of ontogenetic development, i. e., the problem of heterochronia, regarded as an independent method of phylogenetic mutation of adult organisms, has come to the fore." (1939, page 527).

According to B. S. Matveyev (1946), the relegating of the process of morphogenesis to earlier stages is utilized by natural selection for progressive differentiation of the organ which is not forced to remain at the stage of its forebears but to further progress in its development.

Even, upon cursory acquaintanceship with the history of cerebral development of vertebrate animals, the researcher comes in contact wiyh an amazing abundance of facts which are difficult to evaluate otherwise than as various forms of heterochroniae of this order. Obviously, this circumstance is explained in the extraordinary complexity of organization of this organ which effects the highest functions of regulation and control of activities.

We must, first of all, note the considerable extension and acceleration of the entire cycle of embryonal development of the nervous system and, connected with this, its considerably earlier differentiation, as compared to all other organs and parts of the body. This can be seen from the very fact that the anlage of the central nervous system in the form of a nervous groove appears in a vertebrate embryo much before the beginning of differentiation of all other organs.

As an example of the lead of the nervous system, compared to the formation of other derivatives of the body, one can also cite the following circumstance. In a seven-weeks-old human embryo, the spinal and cerebral brain show a clear cytoarchitectonic differentiation of certain areas within the gray matter, and the early-maturing bundles of neural fibers within the white matter begin to be differentiated. The peripheral innervation of extremities, from the anatomical point of view, is also clearly defined at this stage while the extremities themselves do not as yet manifest differentiation into their component parts. The studies, mostly recent, have also demonstrated that the motor neural fibers grow into the anlages of skeletal muscles prior to the emergency of a transverse striation in them (N. I. Zazybin, 1935). It is further necessary to point out that more highly developed animals show a more or less considerable shift in the development of the central nervous system toward earlier stages of embryonal life, as compared to animals of lower organizational levels. A. N. Severtsov called attention to this heterochronia which he based on the fact that birds and mammals show an earlier anlage of the brain and a more rapid development than do reptiles.

We set ourselves the task of comparing in mammals, which differ in complexity of cerebral organization, the periods and formation rates of various sections of the brain, including their bonds with the periphery.

In the accompanying diagram (Fig. 1) we attempted to compare the results of a number of studies on the ontogenetic development of various central and peripheral neural formations in man, rabbit, and rate and selected the objects most completely investigated in this regard. The diagram has a roughly orientational, fragmentary character; it includes only a certain part of the data available in the literature. A considerable part of it could be used by us in view of the contradictions between the factual data of various authors and the disparity of criteria on the basis of which the authors determined and evaluated morphological signs which characterized the emergence of the anlage, the rate of differentiation and maturation of various structures, etc. For the same reason we were forced to omit the indication of periods of termination of structural development; in this respect the disparities were particularly marked.

Despite all these defects of the summary table, the basic differences in the correlations of development of definite homologous formations in these mammalian representatives arrest attention at once.

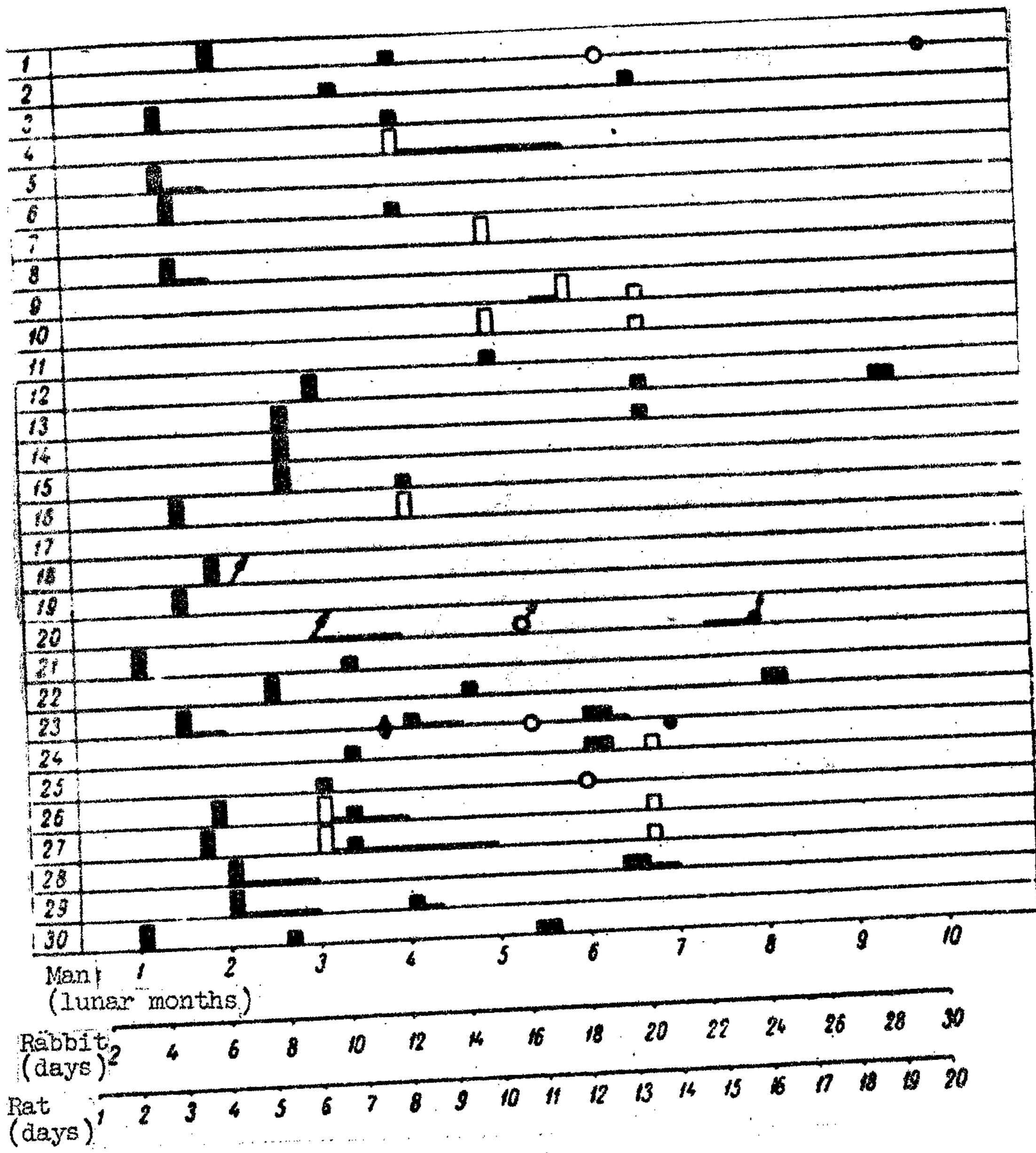


Fig. 1. Periods of differentiation of certain cellular and fibrous formations of the central and peripheral nervous system in man, rabbit, and rat (according to the data of various authors).

Numbers on the vertical line: 1 -- new cortex; 2 -- large hemispheres; 3 -- inner sac; 4 -- bundles of the corpus striatum and pallidum; 5 -- striopallidum; 6 -- thalamus opticus; 7 -- bundles of stem nuclei; 8 -- nuclei of the stem and diencephalon; 9 -- inner loop;

/Continued on next page/

[Continued from Page 9]

10 -- posterior columns of the spinal cord; 11 -- nuclei of posterior columns; 12 -- posterior horns of the spinal cord; 13 -- nuclei of Clark's column; 14 -- reticular formation of the spinal cord; 15 -- lateral horns of the spinal cord; 16 -- proper bundles of the spinal cord and stem; 17 -- nuclei of the vestibular nerve; 18 -- motor nucleus of the trigeminal nerve; 19 -- nucleus of the facial nerve; 20 -- first reflex responses; 21 -- white commissure of the spinal cord; 22 -- fibers of posterior radicles to the anterior horns; 23 -- anterior horns of the spinal cord; 24 -- anterior radicles; 25 -- spinal and cranio-cerebral nodes; 26 -- posterior radicles; 27 -- peripheral nerves; 28 -- neuro-musculer endings; 29 -- cutaneous innervation; 30 -- neural tubula.

Designations: the moment of the initial differentiation of anlages of groups of neural cells and bundles of neural fibers -- [symbol] (for man), [symbol] (for rabbit), [symbol] (for rat); the moment of appearance of myelinization of neural fibers (correspondingly) -- [symbol] ; the tigroid (correspondingly) -- [symbol] appearance of the [symbol] ; the moment of appearance of the first reflex responses -- [symbol] (for man); [symbol] (for rabbit), [symbol] (for rat). Horizontal lines from the conditional mark -- the length of the initial differentiation of corresponding anlages. Along the axis of the abscissae -- subsequent stages of intrauterine development.

If we divide the entire length of the intrauterine life of man, rabbit, and rat into three periods -- the early, middle, and late periods -- it will be found that in man the separation and the initial phase of structural differentiation of cellular and fibrous formations of the central and peripheral nervous systems (receptors in the skin and muscles, neuromuscular endings, peripheral nerves, cerebrospinal and cerebrocranial nodes and radicles, nuclei and bundles of the spinal cord and the cerebral stem, subcortical nodes and the cortex of the large hemispheres) is relegated to the early period of prenatal ontogenesis (approximately during the period of five to 13 weeks). With the transition to the middle period, however, the processes of differentiation of the inner structure of neural cells and the myelinization of neural fibers develop intensively.

In the rabbit, in contrast to man, the initial separation of groups of neural cells and bundles of neural fibers in the central and peripheral nervous systems manifests itself only during the transition from the early period of prenatal ontogenesis to the middle one, whereas the cytological differentiation and myelinization occur mainly in the later period. Even later than in the rabbit, the anlages of cellular and fibrous formations begin to form in the rat not until approximately the second half of the middle period.

These morphogenetic correlations have their equivalent in the physiological manifestations of a developing embryo.

In connection with the fact that all basic structural elements of the cerebrospinal reflex arc (receptors, peripheral nerves, posterior and anterior ramuli radicles, cells of the anterior horns with the adjacent collaterals of the sensory afferent fibers, and the motor neural endings in the muscles) are established in man earlier than in rabbit, and in a rabbit earlier than in a rat; the initial reflex responses to stimul are correspondingly earlier in a human embryo (as early as during the first third of pregnancy, within the first two to three lunar months), somewhat later in a rabbit (during the second third of pregnancy, starting on the 16th day), and still later in a rat (in the final third of pregnancy -- from the 16th day.

Similarly, the differences in the differentiation periods of the cerebral cortex in man and rabbit are very clearly observed (we have here in mind the new cortex, according to classification of I. N. Filimonov).

According to our data, during the intrauterine life of humans this cortical formation, which occupies in an adult about 95 percent of the entire surface of the large hemispheres, passes through three periods of consecutive sytoarchitectonic differentiation which coincide approximately with the three periods of prenatal ontogenesis indicated by us.

During the early period (second to fourth lunar months) a separation and initial formation of the anlage of the cortex takes place; during the middle period (fourth to seventh lunar months), a preliminary separation of the cross-section of the cortex into layers takes place which, with the transition into the later period (seventh to tenth lunar months), leads to the final differentiation of all cytoarchitectonic layers characteristic of the new cortex.

According to the studies by S. A. Troitskaya (1953, 1957), an analogous stage-by-stage sequence of the cytoarchitectonic development is observed also in the new cerebral cortex of a rabbit. In this animal the enlage of the

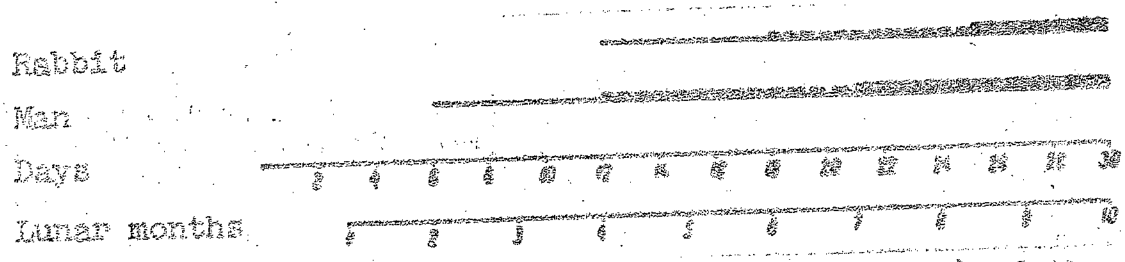


Fig. 2. Scheme of correlation (in man and rabbit) of the periods of the appearance and duration of the three periods of new cortex differentiation during the prenatal ontogenesis.

Along the axis of abscissae -- consecutive stages of intrauterine development. Continuous line -- early period; broken line -- middle period; vertical strokes -- late period of ontogenesis.

The turning points in the development of the cortex in embryogenesis analogous to those described were also noted in guinea pigs (Peters and Flexner, 1950; La-Vells, 1956). The first turning point occurs approximately in the middle of pregnancy and is connected with the increasing cytologic differentiation of the cortical cells. The second is timed to the beginning of the last third of pregnancy (from 41 to 45 days of intrauterine life) and is characterized, as in the rabbit during corresponding periods, by a pronounced separation of the cytoarchitectonic layers and the emergence, shortly afterward, of initial biopotentials in the cortex (in 48 days).

There is reason to assume that in more highly developed mammals, the entire cycle of development of nervous structures not only begins earlier but also ends later than in the lower mammals, and extends to a more prolonged segment of the prenatal as well as postnatal ontogenesis. Thus, according to the studies at the Moscow Brain Institute (I. A. Stankevich), the cytoarchitectonic development of the cerebral cortex in man reached its completion later than in the monkey.

Concerning the data cited in our figures (see Figs. 1 and 2), the following reservation is important. In these figures the different degree of maturity of the organism at the moment of birth in various mammals was not taken into consideration. Therefore, from the comparison of the indicated periods of ontogenetic separations of various neural formations in man, rabbit, and rat, no conclusions seem possible regarding the acceleration or retardation of the development of corresponding formations in the mammalian representatives which we used for comparison. Thus, on the basis of the division of the entire embryonal period into embryonal, prefetal, and fetal phases of development (G. A. Shmidt, 1953-1955), it will appear that in a rabbit the separation of certain anlages starts at earlier stages than in man.

We analyzed certain phylembryogenetic relations conditioned by the progressive complexity of the structure of analyzer systems in the comparative series. As a result of the shifts analyzed above, certain neural formations, as we have seen, separate earlier during the ontogenesis of the progeny and develop at an accelerated tempo, while their entire cycle of development extends for a longer segment of time than in the ontogenesis of the ancestors. These shifts of the temporary correlations in the individual development of the organism of the progeny, as compared to the organism of the ancestors, involve during the earliest stages the entire anlage of the central neural system together with its bonds with the peripheral organs. They are thus reflected in the extensive spheres of the reflex activities of the organism and, as one may assume, are of the utmost importance in the widening, complication, and perfection of the environmental adaptation possibilities in the higher members of the systematic group as compared to its lower representatives.

We shall turn now to the analysis of other aspects of the temporary correlations of development and growth, during ontogenesis, of complexes of neurons, diverse as to their functional significance, in the system of analyzers. Here we encounter a complex alloy of onto-phylogenetic correspondences and heterochroniae. Let us cite several instances of both.

In 1935, we noted a certain peculiarity of differentiation of cortical formations differing in their organization level in the individual development of man, which did not conform to the sequence of their origin in the phylogenesis of vertebrates. We found that, during ontogenesis, the formation of the anlage of the new cortex (neo-cortex), which is the latest to become separated evolutionally, somewhat precedes the demarcation of the anlage of the old cortex (archi-cortex according to I. N. Filimonov's classification) which appears earlier (Fig. 3). At the same time, as stated by Filimonov (1949), the old cortex, while becoming separated later than the new cortex, nevertheless completes its cytoarchitectonic differentiation noticeably earlier than the new cortex.

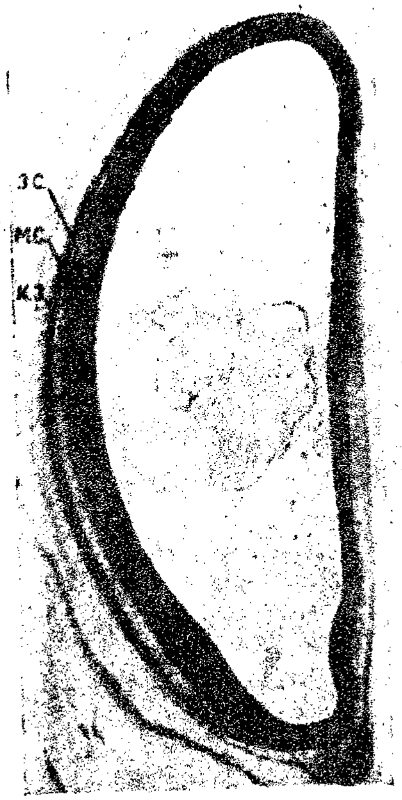


Fig. 3. Frontal section through the cerebral hemisphere of a human embryo, nine weeks old.

k.z. -- anlage of the new cortex; z.s. -- embryonal layer of the embryonal wall; m.s. -- intermediary layer of the embryonal wall. At this stage of ontogenesis the anlage of the old cortex has not been differentiated as yet.

Due to the shifting of the beginning of new cortex separation to an earlier period and a later completion of its architectonic differentiation, the entire cycle of the new cortex development extends to a more prolonged segment of ontogenesis than that of the old cortex. We have here a sui-generis heterochronia caused, obviously, by the extreme degree of complication and evolution of the most perfected form of cortical organization -- the new cortex.

We also ascertained the morphological factors important in the origin of this heterochronia.

The most substantial difference in the character and formation rate of the new and old cortex is in the size of the reserve of embryonal cellular material used in the construction of either of the two cortices. (Fig. 4). The entire cellular reserve of the old cortex is supplied by the first basic wave of migration of neuroblasts coming from the embryonal layer of the hemisphere wall (matrix) to the anlage site of the old cortex. This same initial phase of transfer of neuroblasts from the depth of the wall to the hemisphere surface is responsible for the formation of the new cortex anlage with its subsequent consolidation. (See Fig. 4, I, M.S.).

In the part of the embryonal layer of the wall which feeds neuroblasts to the old cortex, the available reserve of the embryonal material needed for the formation of the old cortex becomes exhausted as the result of this first wave of migration.

The embryogenetic conditions which determine the formation of the new cortex take shape in a substantially different manner. The first migration wave of neuroblasts, which is already spent at the early stages of prenatal onotogenesis, seems to lay only the foundation of the new cortex anlage. After a certain interval, the second wave follows, a stronger wave and of considerably longer duration of neuroblast migration (Fig. 4, II, M.S.), which extends almost through the entire remaining segment of prenatal ontogenesis. At the expense of precisely this supplementary influx of neuroblasts the subsequent supply and the immense quantitative accretion of neurons of the new cortex is effected, representing the basis for the development of complicated processes of its preliminary and final stratification. Hence, the prolongation of the entire cycle of new cortex development is naturally conditioned by the increase in the embryonal material which has been accumulating during eons of evolution of mammals and which is used in the formation of the most complex section of the entire central nervous system.

In the macroscopic development of the part of hemisphere engaged in the formation of new cortex in man, one can also observe definitely outlined shifts in the ontogenesis of phylogenetic correlations. Thus, the older island area, which constitutes the boundary zone of the new cortex, shows definite retardation in development, as compared to the new

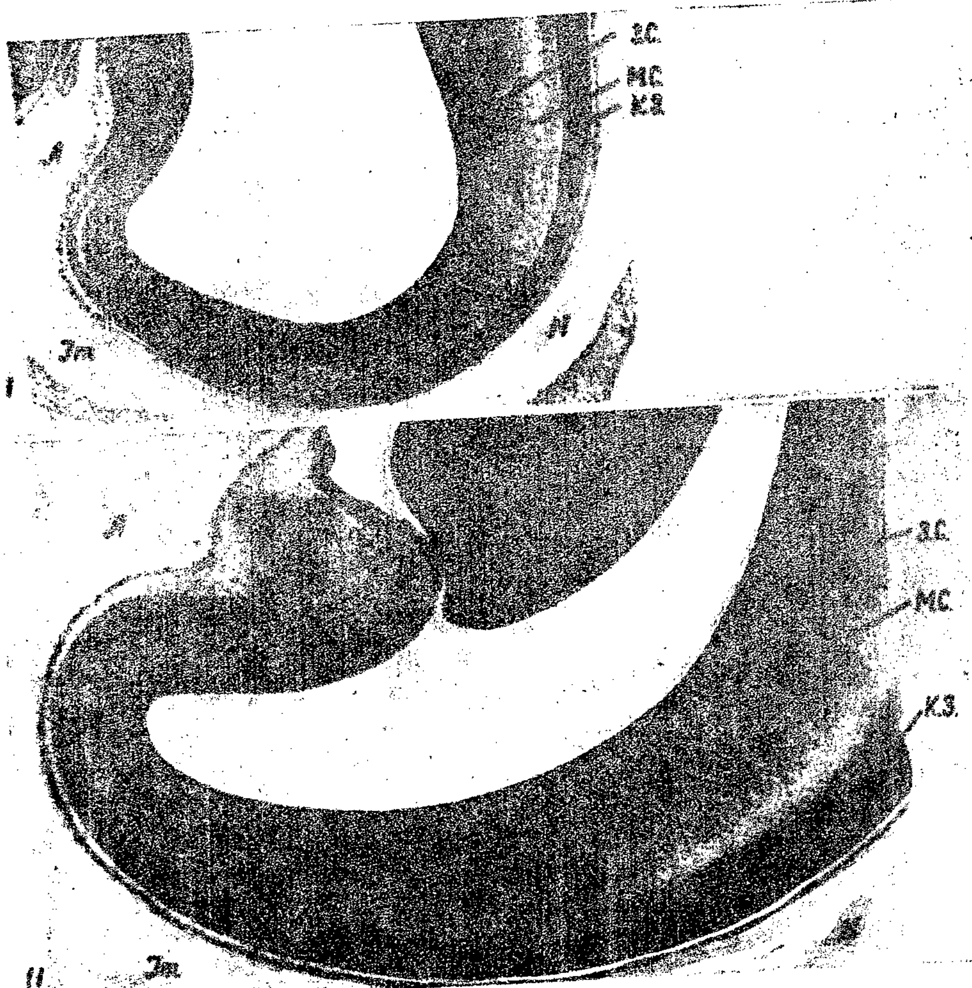


Fig. 4. Differences in the cytoarchitectonic differentiation and the migration rates of neuroblasts in the areas of the old, intermediary, and new cortex at the early stages of prenatal ontogenesis.

Part I of Fig. 4 -- frontal section through the lower part of the cerebral hemisphere of a human embryo, 11 weeks old.
Part II -- the same, at 13 weeks.

A -- old cortex, lm -- intermediary cortex, N -- new cortex; K. Z. -- cortical anlage; Z.S. -- embryonal layer of the hemisphere wall (matrix); M.S. -- intermediary layer of the hemisphere wall filled with neuroblasts migrating to the cortex.

areas evolutionally more recent, situated on the convex surface of the hemisphere, whose growth and complex development proceeds during the ontogenesis at a more intensive rate. The first grooves in the island area are anlaged only toward the 32nd week of the intrauterine life, and on the convex part of the hemisphere surface -- as early as at 25 weeks (I. A. Stankevich, 1957). At the same time, the cytoarchitectonic differentiation is being completed in the boundary regions of the cortex (the island and limbic areas) somewhat earlier than in the new cortex areas which achieve the highest degree of development.

As a manifestation of the same regularity one can regard also the correlations in the periods of ontogenetic development of the cortical and subcortical cerebral formations in humans and animals.

In man, as well as in a rabbit, the anlage of the new cortex emerges, as mentioned above, relatively early, almost simultaneously with the initial separation of the phylogenetically ancient reflex pathways and centers of the spinal cord and the brain stem (see Fig. 1). At about the same time the anlages of the adjacent subcortical formations -- the caudate body, putamen, globus pallidus, thalamus opticus, and certain other nuclei of the dien- and mesen-cephalon -- undergo initial separation. These reflex centers situated below the cortex and formed in the process of evolution prior to the separation of, the new cortex with its most perfect locking function, complete during ontogenesis, according to the data of various researchers (S. A. Troitskaya; L. A. Kukuyev, 1953; A. M. Ivanitskiy, 1955), their topographic, cytoarchitectonic, and histochemical development much earlier than the new cortex.

Thus, these examples confirm the idea that the new cortical formation, phylogenetically the most recent, catches up, according to the periods of its emergence in embryogenesis, with phylogenetically older subcortical formations, completes its structural differentiation, and achieves maturity at a later date.

Together with the heterochroniae cited, a definite succession in the course of formation of various links of neurons may be elicited during the process of ontogenesis which corresponds to the one observed in phylogenesis. As a basis for a rational interpretation of these correlations, a general concept must be posed of the complexity during the phylo- and ontogenesis, of the construction of a reflex arc and analyzer systems along the entire length of the numerous pathways of the transfer of neural impulses from the receptors to effectors.

In the evolution of reflex mechanisms in animal organisms the initial link is the one which is directly connected with the effectors and which controls their work. This working or executing link of the reflex arc is represented in the central nervous system by the motor neurons in the proper sense of the word (the motor neurons of the spinal cord and brain stem).

The proper analyzers, which form the most important and most complexly constructed part of the entire apparatus, include all other links of the simple and complex reflex arcs situated at various levels of the central nervous system up to their contacts with the motor neurons. In the evolution of the animal world, this part of the reflex mechanism (aggregates of sensory neurons in the broadest sense of the word together with their interconnections), is the site of the analysis and synthesis of stimuli; here also the character of response reactions of the organism to stimuli is determined; this part experiences far-reaching transformations and through its complex development and territorial growth is immeasurably more intensive than the executing organs of the reflex arcs.

The development correlations in the phylo- and ontogenesis of various groups of neurons of the central nervous system form in accordance with the succession of construction complexity of the reflex arc, as discussed.

This is particularly clearly observed in the correlations in the development of the anterior and posterior radicles, intervertebral nodes, and the anterior and posterior horns of the spinal cord. In the lower vertebrates (fish, amphibiae) the basic links of the reflex arc which closes in the spinal cord -- links, represented by the neurons of the intervertebral nodes and anterior horns of the spinal cord together with the posterior and anterior radicles -- are already well differentiated. In contrast, the posterior horns of the spinal cord are still weakly developed, poorly separated, and deficient in neurons.

Starting with reptiles, the aggregates of commutator neurons of the posterior horns, which complexly distribute somatic afferent impulses to various segments of the spinal cord and to various sections of the central nervous system, achieve a certain level and acquire a corresponding configuration. At the same time, during phylogenesis, the quantity of small cells of gelatinous substance and the areas of the posterior horn adjacent to it increase considerably. These neurons concentrate where the afferent fibers of posterior radicles enter into the spinal cord, and play a presumably important role in the interrelations of afferent impulses and in the reflex closed circuits which occur at the level of the spinal cord. The axons of these neurons, according to the latest studies (G. P. Zhukov), are distinguished by numerous ramified collaterals, distributed among the adjacent cells and serving to establish interconnections between the neurons.

Analogous correlations are also observed in the course of ontogenesis in animals and humans. One can consider it a firmly established fact that the neurons of intervertebral nodes and the cerebro-cranial neural nodes, as well as of the motor nuclei of the spinal cord and brain stem, have a considerable lead as compared to the neurons of posterior horns and sensory nuclei of the cerebrocranial nerves (see Fig. 1) concerning periods of initial separation, development, and structural differentiation. According to the opinion of certain authors, the motor neurons of the anterior horns of the spinal cord commence their development womewhat earlier than the nodal cells. On the other hand, in the latest study by S. A. Troitskaya, the formation of the afferent link of the cerebrospinal reflex arc asserts a precedence over its efferent link.

The neurons of the vegetative nuclei and reticular substance of the spinal cord occupy in their development periods an intermediary position between the motors and sensory somatic elements (A. S. Iontov, 1949; M. P. Sukhetskaya, 1957), a fact which is in keeping with the topographic characteristics of these neurons, forming as they do an intermediary zone of cerebrospinal gray matter between the anterior and posterior horns.

Another example of correspondence of chronological correlations in onto- and phylogenesis is the succession in the development of both compound parts of the red nucleus which represents an important commutator instance on the path of impulse transfer from the cerebellum to the subcortical formations and reflex centers of the medulla oblongata and the spinal cord. The phylogenetically older large-cell part of this nucleus, better developed in lower mammals, also appears earlier in the prenatal human ontogenesis than the phylogenetically more recent part of the nucleus which reaches a high degree of development in higher animals and humans.

The correlations in the development of definite systems of conducting pathways, which connect various formations in the cerebral parts of analyzers distinct in their phylogenetic origin, are also arranged in analogous chronological sequence during onto- and phylogenesis. As mentioned above, the evolutionally most ancient systems of bonds of the brain stem and spinal cord, distinctly formed already in cyclostomata and fish, develop at an accelerated rate and mature very early in the ontogenesis of higher mammals.

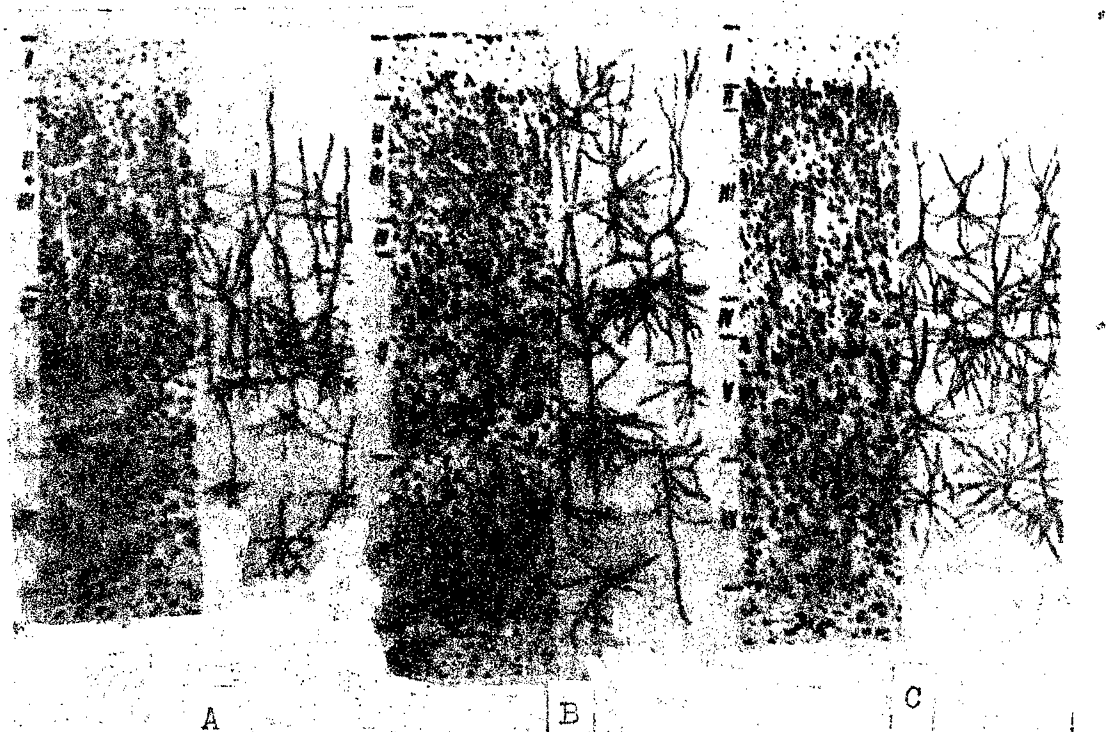
Of all conducting pathways of the central nervous system, one of the last to separate and mature in ontogenesis is the pyramidal path which, also in the phylogenesis of mammals, emerges later than other bundles of neural fibers in the central nervous system. This complex system of impulse switching from definite areas of the new cortex to the motor nuclei of the brain and spinal cord, still poorly developed in most mammals (below primates), begins to undergo myelinization in humans only after birth, and completes this process at later periods than other projection and association bonds of the cortex.

The onto-phylogenetic correspondences of this character are also clearly manifested in the development periods of commissural bonds between the cerebral hemispheres of the brain in various mammals. According to the data of the work of E. E. Rosina (1951), the phylogenetically more recent interhemisphere commissure -- the corpus callosum -- formed only in placental mamals, is anlaged in humans in the third lunar month, i. e., appears almost simultaneously with the anlage of the new cortex. The anterior commissure of the large hemispheres, more ancient in origin, and already present in nonplacental mammals, also starts its separation in humans much earlier than the corpus callosum.

Of considerable interest are the correlations in the development of the layers and areas of the new cortex in phylo- and ontogenesis.

Certain studies (G. I. Polyakov, 1937; E. G. Shkol'nik-Yarros, 1954; G. P. Zhukova, 1953; I. A. Zambrzhitskiy, 1956; S. A. Troitskaya, 1957, etc.), have established that in phylogenesis, as well as in ontogenesis, a definite sequence exists in the development and differentiation of various architectonic layers of the cortex which differ between themselves in the character of arrangement of interneural associations in the cortex proper, as well as between the cortex and the subcortical formations.

In the mammalian comparative order, the basic accent in the complex development of the cerebral cortex organization falls mainly on the progressive differentiation of neurons of the evolutionally more recent cortical surface strata (layers IV, III, and II) (Fig. 5); the neurons of the layers of the deep cortical strata, formed earlier, (layers VII, VI, and V) are more stable and undergo during the evolutional process less significant changes than those of the surface stratum. Thus, the complexes of neurons which form the surface layers and gather the basic afferent and associative bonds of the cortex represent the most progressively developing and most complexly differentiating formations of the new cortex in the mammalian order. These



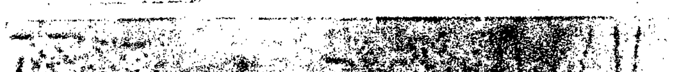


Fig. 5. Progressive differentiation of the cytoarchitectonic and neuron structure of the layers of the new cortex in the evolutional sequence of mammals. Successive complication of differentiation of the cortical area near the pole of the frontal cerebral lobe.
A -- hedgehog, B -- rabbit, C -- dog, G -- rhesus monkey, E -- Man. On the left of microphotos of the cytoarchitectonics of the cortex are marked the layers and sublayers of the cortex (according to I. A. Zambrzhitskiy, the microphoto of the cortical architectonics of a dog is taken from the Atlas of the Brain of a Dog, O. S. Andrianova and T. A. Merring).

layers are differentiated at later periods than the deep layers of the cortex.

The differentiation of cytoarchitectonic layers in the ontogenesis of animals and humans develops in correspondence with the course of the phylogenetic development outlined here. (Fig. 6 and 7). The deep stratum layers, set up earlier also in the comparative series, begin their anlage very early in the embryogenesis of man and rabbit. These layers develop during the course of the entire prenatal ontogenesis at a considerably accelerated rate as compared to the layers of the surface stratum, and acquire earlier than the latter the structural specialization features characteristic of the adult brain.

The layers of the surface stratum of the cortex commence their intensive morphological (cytoarchitectonic and cytological) differentiation only during the latter months of intrauterine life and during the first few months following birth. During postnatal ontogenesis, these layers complete the cycle of their development and maturation at later periods, as compared to the layers of the deep cortical stratum.

Analogous regularity can be traced also concerning formations which differ in the remoteness of their phylogenetic separation -- the cytoarchitectonic areas and fields of the new cortex, the number of which progressively increases among the lower mamals and primates.

In the analyzer systems and, particularly, in their higher divisions represented by the cortex of the large hemispheres, certain sections, areas, and subareas are separated in the course of evolution. These regions are characterized by substantial differences in the particularities of specialization of neuron and interneuron bonds, as well as in the correlations of development and growth in the course of phylogenesis.

The extensive data obtained to the present on studies conducted in various directions (comparative morphology and physiology, clinic) confirms the idea that, in the evolution of mammals, a process of ever increasing complication of topographic correlations of the cortical ends of various analyzers is occurring in connection with the reorganization of their functional relations, under conditions of life of the organism in an ever more complicated environment.

Parallel with the increasingly more precise separation in the cerebral cortex, during the transition from lower to higher forms, of nuclear analyzer zones with their characteristic maximum concentration of special functional elements (vision, hearing, cutaneous and kinesthetic sensitivity), a territorial expansion of the cortical ends of

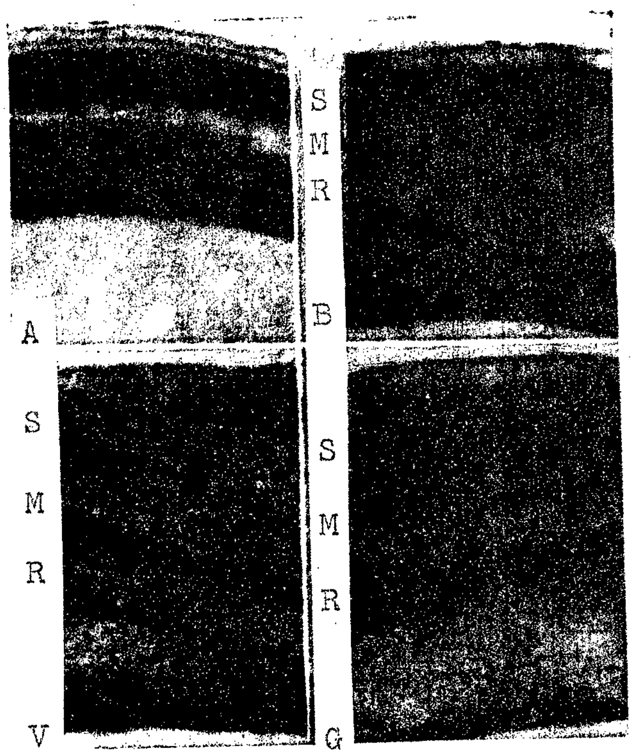


Fig. 6. Progressive differentiation (cytoarchitectonic) of the layers of the new cortex in rabbit during prenatal ontogenesis.

A -- 19 days of intrauterine life, B -- 22 days, V -- 28 days, G -- newborn infant rabbit, S -- upper stratum of the cortex (layers II, III, IV); M and R -- lower stratum of cortex (layers V, VI, VII).

various analyzers occurs with their ever-increasing mutual overlapping. In the primates the nuclear zones, as well as the zones of overlapping analyzers, are already represented by anatomical divisive formations -- corresponding to the cytoarchitectonic areas and fields -- which reach the highest degree of differentiation and specialization of structure in humans. In the evolution of mammals lower than monkeys in their development of the central nervous system -- from Insectivora to rodents and Carnivora -- essentially a progressive separation of nuclear zones occur while the zones of overlapping cortical analyzer-ends, ac-

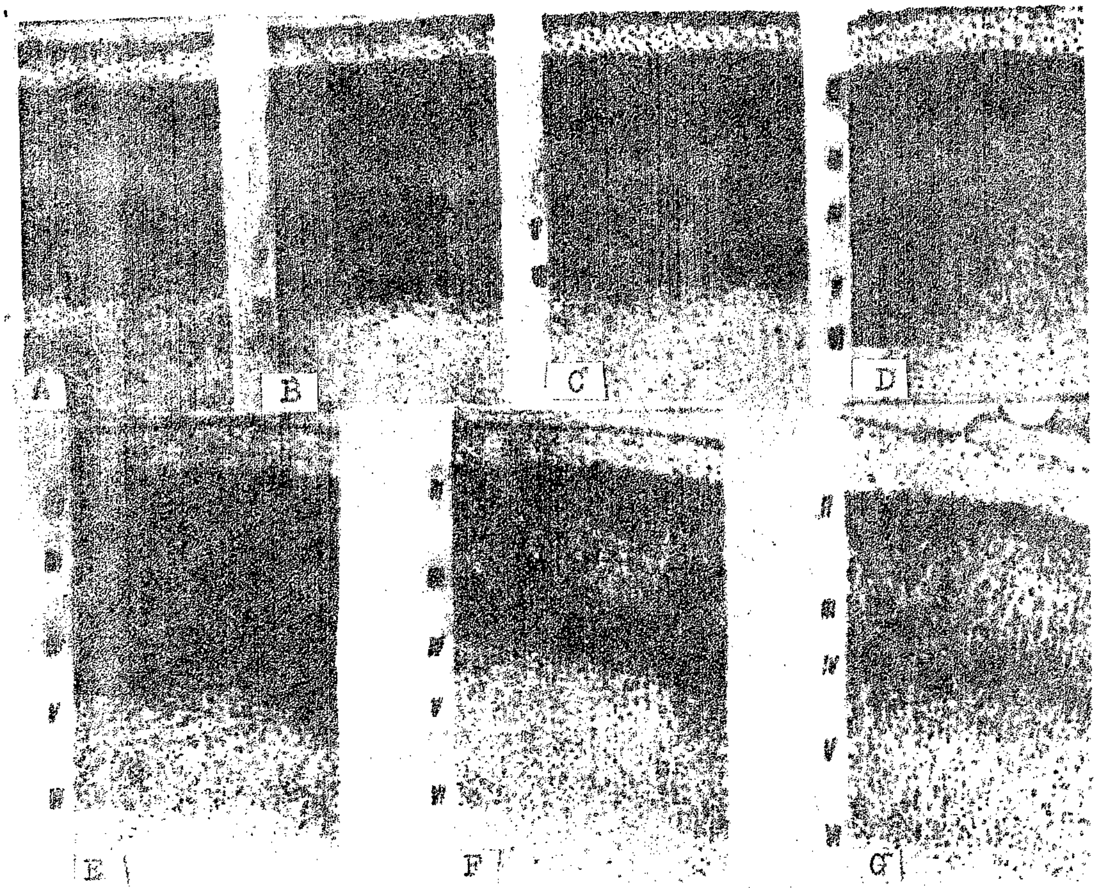


Fig. 7. Progressive differentiation (cytoarchitectonic) of the new cortex layers during prenatal ontogenesis in man.

A, B, C, D -- during ontogenesis from fourth to sixth lunar months; E -- in the seventh lunar month; F -- in the ninth lunar month; J -- in the 10th lunar month. To the left of each microphoto are marked the cortical layers.

cording to all morphological indicators, achieve a considerably lower development level than in the primates (Figs. 8 and 9).

The same order of progressive differentiation of corresponding fields and areas is preserved in its basic features also in the ontogenesis of humans, as shown in our studies of the development of cytoarchitectonics and neuron structure of the cerebral cortex at various stages of the intrauterine life and after birth (Fig. 10).

The earliest to be formed are the anlages of the central fields of nuclear zones, as sites of the most highly specialized corresponding analyzers. According to our data, the anlages of some of these fields clearly manifest the characteristic peculiarities of neuron structure as early as in a five-lunar-months-old human enbryo. During the entire period prior to birth, precisely these formations of the new cortex develop at an accelerated rate and manifest the greatest degree of maturity at the time of birth.

The peripheral fields of nuclear zones, particularly the fields which we relate to the zones of overlapping analyzers (the fields of the lower parietal, parietal-temporal-occipital and frontal areas), enter much later the phase of intensive development and growth -- not until the first weeks and months following birth.

These data are in accord with the sequence of the myelogenic maturation of corresponding cortical areas, shown long ago in the old Flexig studies; they are also supported by the cytoarchitectonic studies of the Moscow Institute of the Brain during the past few decades, which have demonstrated the extensive correspondence in the development of the basic areas of the new cerebral cortex in onto- and phylogenesis.

This correspondence is particularly clearly manifested by the changes in the comparative size of the area occupied in the cortex by the giant-pyramidal field (field 4 on Brodman's chart) at various stages of the evolution of primates and the ontogenesis of humans.

As has been established by the studies of L. A. Kukuyev (1953), the territory of this field in the order of primates decreases progressively, in regard to the entire cortex, from the tamarin monkey to man: in the tamarin monkey it constitutes 8.88 percent of the entire cortex, in the rhesus monkey -- 4.57 percent, in the marmoset -- 4.46 percent, in the gibbon -- 3.82 percent, in the orang-outang -- 3.64 percent, in the chimpanzee -- 3.44 percent, and in man -- 1.74 percent. In the ontogenesis of man the comparative size of this field also changes in analogous manner, according to L. A. Kukuyev (1955): in a human embryo of six lunar months it constitutes 5.41 percent of the entire surface of the hemisphere, at eight lunar months it is 3.25 percent, at birth -- 2.85 percent, in a child one year old -- 1.89 percent, and, finally, in an adult -- 1.74 percent.

A similar trend in growth-changes is observed also in another new cortex formation which separates comparatively early in phylogenesis, namely, the central ophthalmic field (field 17, according to Broadman).

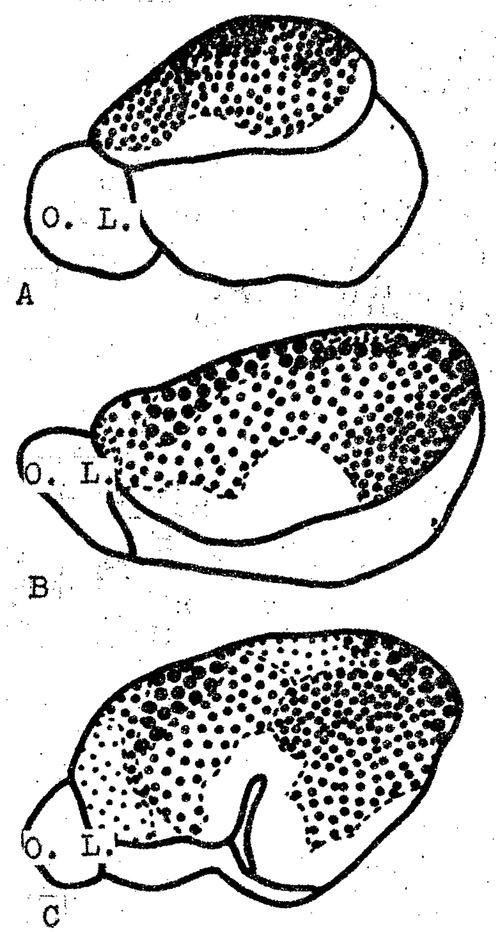


Fig. 8. Schematic charts showing the correlations in the development of nuclear zones and zones of overlapping analyzers in the new cortex in mammals differing in the level of cerebral organization.

External surface of the hemisphere. Territory of the ancient, old, and intermediary cortex, as well as the island area, are left white; o.l. -- olfactory bulb. A -- hedgehog, B -- rat, C -- dog. The central fields of the nuclear zones are marked with large dots, the peripheral fields of the nuclear zones -- with medium size dots, the zones of overlapping analyzer -- with small dots. Concentration of medium dots (A) represent the initial stage of differentiation of the

/Fig. 8 continued on page 27/

central fields in Insectivora. Concentrations of medium dots (B and C) represent the insufficient degree of separation of the central field within the nuclear zone of the aureal analyzer in rodents and Carnivora. As the basis of Scheme B, the cytoarchitectonic chart of the cerebral cortex of a rat developed by V. M. Setukhina is used (Chair of Physiology of Higher Nervous Activity of Moscow State University); as the basis of scheme C -- the cytoarchitectonic chart of the cerebral cortex of a dog, according to O. S. Andrianov and T. A. Mering (Institute of the Brain, Acad. Med. Sci. USSR).

In primates the space occupied by this field is reduced by 10 percent in a marmoset, and to three percent in man (I. N. Filimonov, 1933).

During postnatal ontogenesis in man this space also decreases by four percent in a newborn infant and three percent in an adult (N. S. Preobrazhenskaya, 1948).

In contrast, during the phylogenetically later differentiating new cortex formations, a considerable and progressive growth of relative sizes of the areas, is observed among primates, in comparative order, as well as at various stages of individual development of man. Thus, for example, the area of the frontal lobe increases from 10 percent of the entire new cortex in lower apes to 13.5 percent in higher apes and reaches in humans almost a quarter of the entire surface of the new cortex. In human ontogenesis the territory of this area increases from 21 percent in a newborn infant to 24-25 percent in an adult (Ye. P. Kononova, 1940). The lower parietal area constitutes in lower apes only 0.4 percent of the entire cortical area, in higher apes -- 3.3 percent, and in humans -- 7.7 percent (Yu. G. Shevchenko, 1940). During the postnatal ontogenesis the comparative sizes of this area increase from 6.5 to 7.7 percent in a newborn infant and 8 to 8.5 percent in an adult (I. A. Stankevich, 1957).

From these comparisons of the quantitative correlations of development and growth in phylo- and ontogenesis of new cortex formations, different in their origin and functional importance, the dynamics of progressive changes inherent in the primate type of cerebral organization is clearly manifested.

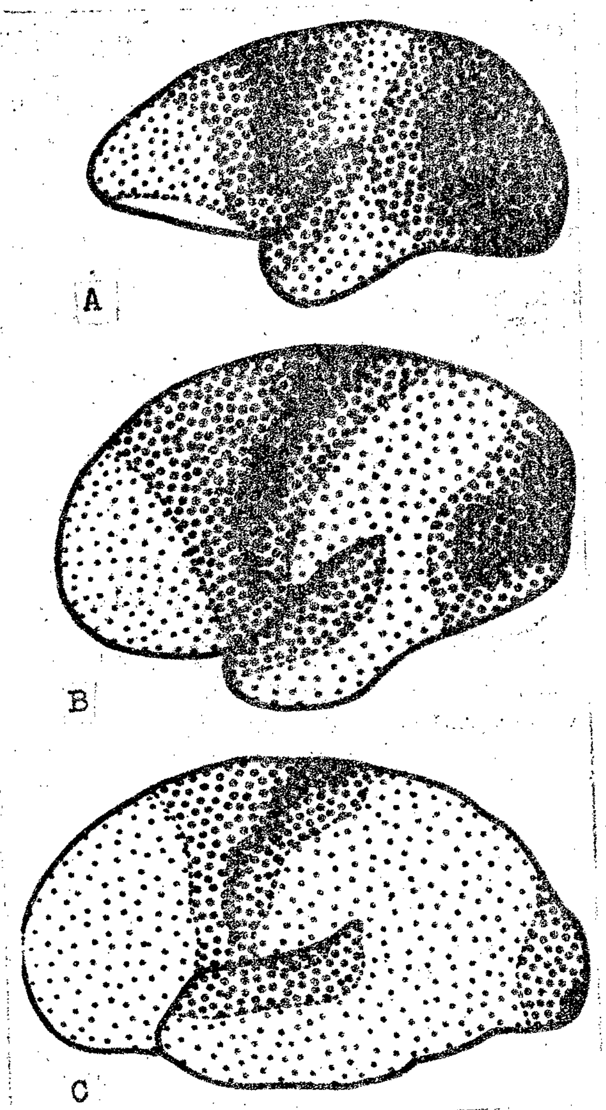


Fig. 9. Schematic charts showing the same correlations as on Fig. 8 in primates differing in the level of their cerebral organization. External surface of the hemisphere.

A -- lower primate, B -- anthropoid ape, C -- man. The dot-marks are the same as on Fig. 8. As the basis of scheme A, the architectonic chart of the cerebral cortex of a marmoset, as per K. Brodman, is used; as the battle of scheme B -- the myeloarchitectonic chart of the cerebral cortex of an orang-outang, as per Maus, is used; as the basis of scheme C -- the cytoarchitectonic chart of the cerebral cortex of man developed at the Institute of the Brain Acad. Med. Sci. USSR is used.

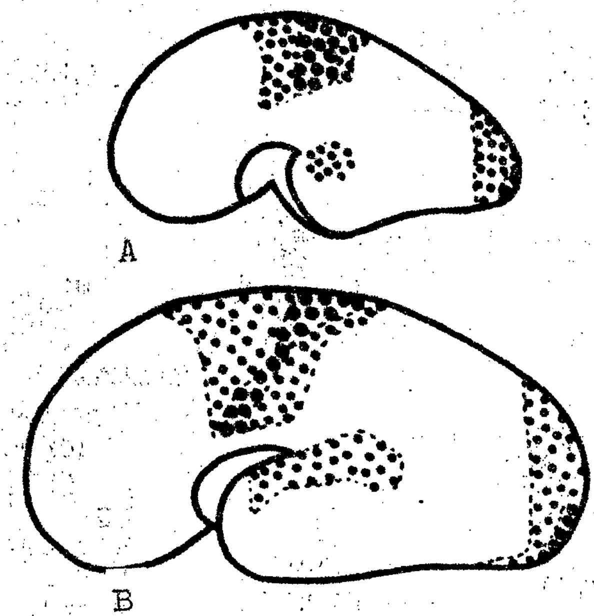


Fig. 10. Schematic charts showing the correlations in the development of the central and peripheral fields of the nuclear analyzer zones in the new cortex of a human embryo during the earlier stages of intrauterine life. The external surface of the hemisphere is shown.

Dotted marking as on Figs. 8 and 9. A -- embryo on the fifth lunar month. B -- embryo of five-and-a-half lunar months. As the basis of these schemes we used our cytoarchitectonic charts of cerebral cortex of man at the corresponding stages of prenatal ontogenesis.

Conclusion

Various instances of correlations in the development of various central and peripheral neural formations in phylo- and ontogenesis, cited in the present work, can be summarized as follows.

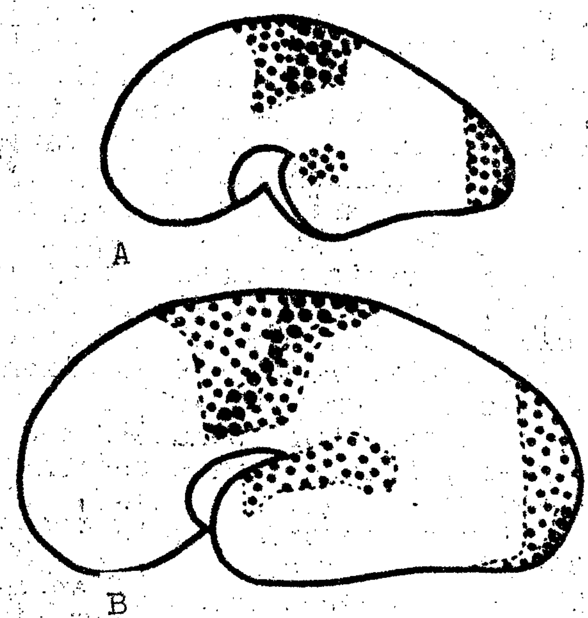
In connection with the growing complexity of reflex activities of the organism during the evolutional process, a progressive complication of the analyzer system occurs. At the basis of this complex development, in all representatives of the comparative-anatomical series, from lower to higher, a stable basic type of organization of interconnected neuron chains is preserved. These chains, jointly with their commutator centers, form reflex arcs with completed circuits at various levels of the central nervous system. The history of development of this type of neural organization, developed and reinforced as the result of phylogenetic transformations which led to the emergence of a given systematic group (apomorphoses, according to A. N. Severtsov), is recreated (recapitulated) in the ontogenic development of its separate representatives. The sequence of formation, during mammalian ontogenesis, of definite complexes of neurons of diverse functional significance, determined by the position of the neurons in the system of analyzers, is thus found to correspond with the sequence of their formation during the entire course of the preceding evolution of a given species.

Against the background of this recapitulation of ancestral traits in the progeny, multiform chronological shifts develop in the correlations of anlage periods and development rates of corresponding formations in phylo- and ontogenesis, i. e. heterochroniae. These phylembryogenetic shifts of the heterochroniae-type ensure a prompt setting into motion and utilization of the reflex mechanisms which had been formed in the process of ancestral evolution and which effect the adaptation of various representatives of the evolutional series to the special conditions of their existence at various stages of individual adult development (idioadaptation, according to A. N. Severtsov).

The basic correspondence of the ontogenetic development of analyzer systems to the general sequence of their complex development in phylogenesis is expressed in various sections of the central nervous system.

In the lower sections this correspondence is expressed in the correlations of the periods of appearance of anlages and the rates of the structural (topographic, architectonic, cytological, and chodological) differentiation in ontogenesis of the central and peripheral links of the simple and more complex reflex-arcs which complete their circle at these levels of the central nervous system (sensory and motor neural endings, nerves, and radicles, and motor, sensory, and commutator nuclei of the spinal cord and brain stem, together with their associations, etc.).

In the higher sections represented by the cortical formations of the large hemispheres, these parallels are expressed in the sequence of separation and formation, in ontogenesis, of various layers, areas, and fields of the new cortex and systems of their interconnection and their contact with the subcortical cerebral formations, in corres-



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In the higher sections represented by the cortical formations of the large hemispheres, these parallels are expressed in the sequence of separation and formation, in ontogenesis, of various layers, areas, and fields of the new cortex and systems of their interconnection and their contact with the subcortical cerebral formations, in correspondence with the complex construction of higher cerebral analyzer terminals among mammals, primates in particular.

Various phylembryogenetic changes of the heterochronia type are expressed:

1) in the shift to earlier stages of ontogenesis of the periods of anlage separations, and in the considerable extension of the entire cycle of development, growth, and differentiation of homologous formations in the higher representatives of the evolution as compared to the lower ones;

2) in earlier separation and accelerated formation, in ontogenesis, of the morphological basis for definite reflex mechanisms which possess biological value in the adjustment of the organism to special conditions of existence at various stages of individual development;

3) in shifts to earlier stages of ontogenesis of the initial anlage of those systems of analyzers which in the course of phylogenesis achieve the highest level and the most complex differentiation and specialization of structure and function.

Bibliography

Anokhin, P. K. "Systemogenesis as the General Rule of the Evolutional Process." Byulleten' Eksperimental'noy Biologii i Meditsiny (Bulletin of Experimental Biology and Medicine), 1948, Vol. 26; "On the Morphogenetic Rules of the Development of Function in the Embryogenesis of Animals and Man." Thesis of the Report at the Sixth All-Union Conference of Anatomists, Embryologists, and Histologists in Kiev, 1958.

Blinkov, S. M. "Characteristics of the Structure of the Cerebrum of Man," 1955.

Borovskiy, M. L. "Embryonal and Postembryonal Development of the Cortex of the Anterior Central Convolution in Man, and the Postembryonal Development of the Motor Zone of the Cerebral Cortex in Cat." Reports I, II, III, IV. Arkhiv Biologicheskikh Nauk (Archives of Biological Sciences, 1936, Vol. 43; 1937, Vol. 44, 47.

Volokhov, A. A. "Rules of Ontogenesis of Nervous Activity in the Light of Evolutional Teaching," 1951.

Vul, I. M. "Nervous Activity in Ontogenesis." Dissertation for a Doctorate Degree, 1946.

Glezer, I. I. "Correlation of Field Areas of the Pre-Central Section in the Comparative Anatomical Order of Primates." Arkhiv Anatomii, Gistologii i Embryologii (Archives of Anatomy, Histology, and Embryology), 1958, Vol. 35, 2.

Golubeva, Ye. L. "Morphology of Central Correlations in the Development of the Sucking Reflex in Humans." Thesis of the Report at the Sixth All-Union Conference of Anatomists, Histologists and Embryologists in Kiev, 1958; "Morphological Characteristics of the Sucking Act in Human Embryogenesis." Session on the Problems of Pathology and Physiology of the Nervous System of Animals and Man during the Early Age-Related Developmental Stages." Referative Report, 1958.

Gutner, I. I. "On the Problem of Ontogenesis and Structure of the Large Cerebral Hemispheres." Report II. Bull Eksp Biol i Meditsiny, 1946, Vol. 21.

Emelianov, S. W. Heterochronie in der Anlage der Segmentalorgane, ihre Ursachen und Folgen. Comptes Rendus (Doklady) de l'Acad. des Sciences de l'USSR, Vol. 30, No. 8, 1941.

Zhukova, G. P. "The Problem of Development of the Cortical End of the Motor Analyzer." Arkhiv. Anat., Gistol. i Embriol, 1953, Vol. 30.

Zazybin, N. I. "Embryogenesis of the Peripheral Nervous System." Doctoral Dissertation, 1935.

Zambrzhitskiy, I. A. "Cytoarchitectonics and Neuron Structure of the Limbic Area in Certain Mammals." Arkhiv Anat. Gistol. i Embrio., 1956, Vol. 33.

Ivanitskiy, A. M."Correlations between the Development of Function and Structure of the Cerebral Cortex." Author's Report, Dissertation, 1955.

Iontov, A. S. "Certain Stages of the Embryonal Development of the Thoracic Section of the Spinal Cord in Man." In the symposium "Ontogenesis of the Brain." 1949.

Kasatkin, N. I. "Early Conditioned Reflexes in the Ontogenesis of Man." 1948.

Kononova, Ye. P."Development of the Frontal Area in the Postnatal Period." Trudy Instituta Mozga (Works of the Brain Institute), Vol. 5, 1940; "Development of the Frontal Area Fields and the Variability of its Cortical Structure in Man." Nevropatologiya i Psikhiatriya (Neuropathology and Psychiatry), Vol. 9, 1940.

Kukuyev, L. A. "On the Problem of the Evolution of the Nucleus of the Motor Analyzer and Subcortical Nodes." Zhurnal Vysshey Nervnoy Deyatel' nosti (Journal of Higher Nervous Activity) imeni Pavlova, 1953, Vol. 3; "On the Development of the Nucleus of the Motor Analyzer in the Ontogenesis of Man." Trudy Vtoroy Nauchnoy Conferentsii po Voprosam Vozractnoy Morfologii i Fiziologii (Works of the Second Scientific Conference on Problems of Age-Related Morphology and Physiology), 1955.

Matveyev, B. S. "The Law of Darwin on Hereditary Transmission in the Related Age and its Role in Evolution." Byulleten' Moskovskogo Obshchestva Ispytateley Prirody (Bulletin of the Moscow Society of Naturalists), Section of Biology, Vol. 51, Issue 6, 1946; "On Functional Changes in the Individual Development of Animals." Zoologicheskiy Zhurnal (Zoological Journal), 1957, Vol. 36.

Milyagin, Ya. A., "The Determining Effect of Ecological Factors on the Embryogenesis of Unconditioned Reactions." Doctoral Dissertation, 1957.

Pentsik, A. S. "Ontogenetic Development of Bioelectric Activity and Cellular Structure of the Cerebral Cortex." Trudy Instituta Mozga, Vol. 5, 1940.

Polyakov, G. I. "Development of the Isocortex in Man during the Early Stages of Ontogenesis." Trudy Instituta Mozga, Vol. 1 1935; "Early and Intermediary Ontogenesis of the Cerebral Cortex in Man", 1937; "On the Correlations of the Basic Types of Neurons in the Cerebral Cortex of Man." Journal of Higher Nervous Activity imeni Pavlov, 1956, Vol. 6; "On Certain Rules of the Development during Ontogenesis of the Structural Basis of Reflex Functions of the Organism." Conference on Problems of Physiology and Pathology of the Nervous System of Animals and Humans of the Early Age-Related Stages of Development. Referative Report, 1958.

Preobrazhenskaya, N. S. "Postnatal Development of the Occipital Area of the Human Brain." Trudy Instituta Mozga, Vol. 6, 1948; "Certain Cytoarchitectonic Data on the Development of the Cortical End and Subcortical Part of the Optical Analyzer." Trudy Vtoroy Nauchnow Konferentsii po Vozrastnoy Morf. olagii i Fiziologii, 1955.

Rozina, E. E. "Commissures of the Terminal Brain in the Individual Development of Man and in the Comparative-Anatomical Order of Mammals." Auto-report diss., 1951.

Severtsov, A. N. "Morphological Rules of Evolution." 1939.

Stankevich, I. A. "Development of the Lower Parietal Region in Man." Doctoral Dissertation, 1947; "Certain Cytoarchitectonic Data on the Development of the Cerebral Cortex of Man during the Uterine Period and After Birth." Data of the Third Scientific Conference on the Problems of Age-Related Morphology, Physiology, and Biology. Thesis of the Report, 1957.

Sukhetskaya, M. P. "Development of the Reticular Substance of the Spinal Cord in Man." Arkhiv Anat., Gistol, i Embriol, Vol. 34, 1957.

Troitskaya, S. A. "Prenatal Ontogenesis of the Cortical End of the Motor Analyzer in Rabbit." Arkh Anat., Gistol., i Embriol., 1953, Vol. 30; "Post-natal Ontogenesis of the Cortical Nucleus of the Motor Analyzer in Rabbit." Data of the Third Scientific Conference on Age-Related Morphol, Physio. and Biochemistry. Thesis of report, 1957.

Filimonov, I. N. "Comparative Anatomy of the Cerebral Cortex in Mammals." 1949; "On the Variability of the Structure of the Cerebral Cortex. Regio Occipitalis in Higher and Lower Apes." J. f Psychol. und Neurol., 1933, Vol. 45.

Shevchenko, Yu. G. "The Lower Parietal Region of the Cerebrum in Man and Apes." Doctoral Dissertation 1940.

Shkol'nik-Yarros, Ye. G. "On the Morphology of the Optical Analyzers" Journal of Higher Nervous Activity imeni Pavlov, 1954, Vol. 4.

Shuleykina, K. V. "Morphophysiological Characteristics of the Embryonal Development of the Grasping Reflex in Man." Author's report diss., 1953.

La-Velle, A. "Nucleolar and Nissl substance development in nerve cells." J. Comp. Neurology, 1956, Vol. 104, No. 2.

Peters, U. B. and Flexner, L. B. "Biochemical and physiological differentiation during morphogenesis." Am. J. of Anat., 1950, Vol. 86, No. 1.

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