DEVELOPMENT OF NONSPECIFIC THALAMIC NUCLEI DERIVED FROM THE VENTRAL THALAMUS IN RABBITS

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UDC 599.325.1-148.112:591.3

The reticular nucleus of the rabbit thalamus is architectonically differentiated in the 20-day fetus. Cytological maturation of the greater part of its cells begins later than that of the cells of other nonspecific nuclei and of the early-maturing specific nucleus, the posterior ventral. Heterochronism in maturation of different parts of the reticular nucleus is associated with its functional heterogeneity.

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The problem of cortical-subcortical relationships is becoming increasingly pressing and is being tackled from different points of view. The study of development of cortico-subcortical relationships in ontogenesis is of particular interest, because the ontogenetic approach enables the functional relationships between structures to be explained [4, 5]. In 1962, M. M. Kurepina [7, 8] published her studies of human fetuses in which she examined the histogenesis of the thalamic nuclei. She distinguishes several generations of cells which form definite nuclear complexes of the thalamus, differing in shape, cell size, stage of development, and function.

In this paper we describe maturation of nonspecific thalamic nuclei differentiating from the ventral part of the thalamus — the reticular nucleus and the nucleus reuniens. Since the main differences in the tempo of development of these structures are observed in the early stages of cytological differentiation, we shall concentrate our attention on prenatal ontogenesis.

EXPERIMENTAL METHOD AND RESULTS

Series of brain sections from rabbits at different stages of pre- and postnatal life were studied using the methods of Nissl, Golgi and its modification, Peters, Boeke-Bielschowsky, Zurabashvili, and also Chalkley's method for calculating the nucleoplasmic ratio. A major part of the description of the material is devoted to preparations stained by Nissl's method, because they were most demonstrative in establishing the time of appearance of particular stages of neuronal differentiation.

The reticular nucleus differentiates in early stages of development. In the 20-day embryo it lies like a shell along the ventro-lateral border of the thalamus, separating it from the internal capsule and the hypothalamic and subthalamic structures.

In the 20-day fetus the cells of the reticular nucleus consist of relatively undifferentiated neuroblasts: the nucleus is darkly stained, the intranuclear chromatin is dispersed into granules, and some of them lie near the nuclear membrane (Fig. 1). Very little basophilic cytoplasm is present, sometimes forming a small cone, but more frequently it cannot be identified. Cells stained by Golgi's method have the appearance of bipolar neuroblasts.

In the 20-day fetus the reticular nucleus is crossed by the broad glial-cytoplasmic bands of the thalamostriatal bundle, joining the nuclei of the anterior region of the thalamus with the subcortical structures and, in later stages, with the cortex also. Solitary nerve fibers are found in the glial-cytoplasmic bands. Besides those in the glial-cytoplasmic bands, other solitary nerve fibrils are occasionally found (not in every section) in the reticular nucleus, and are evidently axons of the early-maturing cells of the bulbar reticular formation.

Laboratory of General Physiology of the Central Nervous System, Institute of Normal and Pathological Physiology, Academy of Medical Sciences of the USSR, Moscow (Presented by Academician P. K. Anokhin). Translated from Byulleten' Eksperimental'noi Biologii i Meditsiny, Vol. 66, No. 9, pp. 108-113, September, 1968. Original article submitted April 1, 1967.

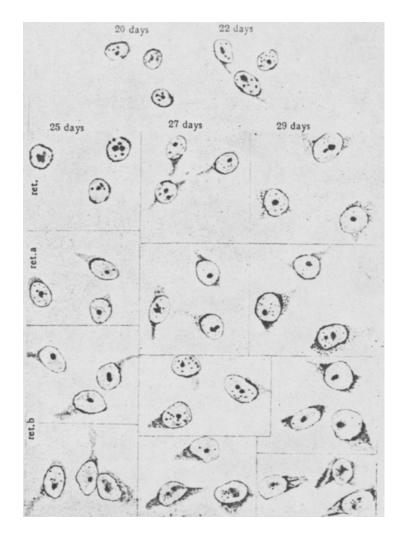


Fig. 1. Development of cells of the reticular nucleus of the rabbit thalamus. Horizontal rows represent different parts of the reticular nucleus: ret.) oral portion; ret.a) caudomedial portion; ret.b) caudolateral portion; vertical rows represent days of prenatal life. Stained by Nissl's method, cells drawn by means of an Abbe drawing apparatus at the same magnification. Ocular 20, objective 40.

In the 22-day fetus, with the completion of primary architectonic differentiation, the nucleus can now be divided into an oral part (ret.) and a caudal part, while in the latter the medial (ret. a) and lateral (ret. b) parts can be distinguished [17]. The caudal part differs from the oral in the greater maturity of its cells. The number of mature fibrils in the glial-cytoplasmic band of the reticular nucleus is only slightly greater than at the preceding stage.

In the 25-day fetus, the above-mentioned parts of the reticular nucleus are clearly distinguishable by the degree of development of their cells: cells in the oral part of the reticular nucleus (ret.) at this age are least developed. In the most lateral corner of ret. b, in the region where this part joins the internal medullary lamina, the most mature cells of the reticular nucleus are found (bottom row in Fig. 1). A few separate tigroid granules can be seen in these cells in the 25-day rabbit fetus (ret. b lat.).

The same heterochronism of development of cells in various parts of the nucleus persists also in the later stages of prenatal ontogenesis.

Since it is difficult by the use of morphological methods only to determine the precise time of maturation of a neuron, which was necessary for comparison with physiological data, we used a quantitative method: calculation of the nucleoplasmic ratio. This ratio is known to be constant in mature neurons.

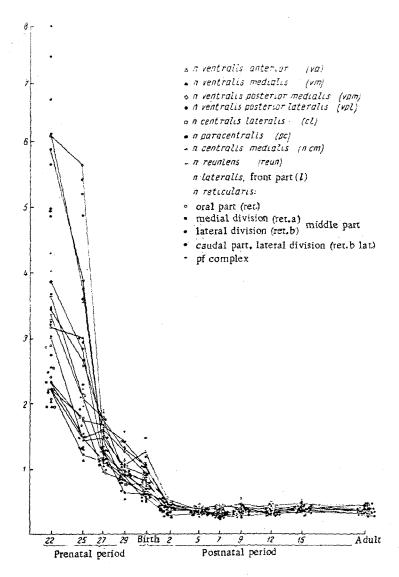


Fig. 2. Changes in nucleoplasmic ratio in cells of specific and nonspecific thalamic structures of the rabbit during ontogenesis. Abscissa, age in days; ordinate, nucleoplasmic ratio.

It is clear from Fig. 2 that the wide dispersion of the curves reflecting nucleoplasmic ratios of cells in different parts of the reticular nucleus in 22- and 25-day fetuses is replaced in the last prenatal days by an extremely close arrangement. By the end of the prenatal period all parts of the reticular nucleus are approximately equally developed as regards their nucleoplasmic index. As Fig. 1 shows, development of neurons of the reticular nucleus continues even after birth of the animal. Cells of the reticular nucleus mature simultaneously with cells of the other thalamic nuclei until the 2nd-5th day of postnatal life.

The nucleus reuniens is architectonically differentiated in the 22-day rabbit fetus. Neurons of this nucleus have passed through the same stages of development as neurons of the reticular nucleus. The beginning of the transition period from neuroblast to neuron is observed in the 26-day fetus. Just like the reticular nucleus, the nucleus reuniens reaches maturity in the first days of postnatal life.

The functional importance of the reticular nucleus of the thalamus has not yet been explained.

On the basis of results obtained in many investigations [1-3, 6, 9, 12-15] demonstrating numerous connections between the reticular nucleus, on the one hand, and nonspecific structures of the thalamus and the cortex, on the other hand, several authorities regard the reticular nucleus as a collector of nonspecific thalamic fibers and the final stage of the corticopetal nonspecific pathway [11, 13].

According to Scheibel and Scheibel [16], axons of cells of the reticular nucleus bifurcate and run only in the caudal direction: toward specific and nonspecific structures of the thalamus and mesencephalon (of 100 axons investigated only 4 ran in an oral direction, and 3 of these terminated in the basal ganglia). These workers accordingly deny the role of the reticular nucleus as a station on the pathway of nonspecific fibers to the cortex, and they consider that the reticular nucleus is reponsible for the reverberation of excitation in closed systems of different lengths, so that it may be a modulator of thalamo-corticothalamic activity.

The material at our disposal makes us skeptical of the categoric nature of the conclusion drawn by these workers, because we found axons of cells of the reticular nucleus running in a rostral direction. Axons running rostrally were more commonly observed from cells of the reticular nucleus located near the anteroinferior thalamic peduncle. We therefore consider that Chow's view [10], that the cells of the reticular nucleus are heterogeneous, some of them possibly sending their axons centripetally, the others centrifugually, is more probable than the hypothesis of Scheibel and Scheibel.

The results described in this paper demonstrate early formation of the reticular nucleus of the thalamus. However, cytological maturation of most cells of the reticular nucleus begins later than in the case of cells of other nonspecific nuclei, and of the early-maturing specific nucleus, the posterior ventral. A possible explanation of this fact is that the reticular nucleus is a structure playing a part in the activity of other nonspecific thalamic nuclei and, consequently, its development follows that of the parafascicular complex and the anterior intralaminar nuclei.

Heterochronism of maturation of different parts of the reticular nucleus has been established (the cauodolateral division of the nucleus possessing the most rapid rate of growth), and this is undoubtedly associated with functional heterogeneity of the nucleus.

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