DEVELOPMENT OF THE POSTEROVENTRAL

COMPLEX OF THE RABBIT THALAMUS

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UDC 599.325.1-148.112:591.3

The early appearance of the primitive posterior ventral nucleus of the rabbit thalamus and its cytological differentiation are connected primarily with the arrival of afferent impulses via the trigeminal nerve system. The corticopetal fiber system of the posterior ventral nucleus matures late, at the end of the first week of life, coinciding in time with the appearance of the positive phase of the evoked potential.

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In earlier paper I have described the development of nonspecific nuclei of the rabbit thalamus.

This article describes a study of saturation of the main specific relay of the thalamus, the posterior ventral nucleus.

EXPERIMENTAL RESULTS

My observations show that the posterior ventral nucleus is formed early.

On the 20th day of embryonic life, in the posterior part of the central pronucleus [17], a structure distinguished by the more compact arrangement of its neuroblasts appears and subsequently gives rise to the medial and lateral parts of the posterior ventral nucleus. Cells of the posterior ventral nucleus are almost indistinguishable from cells of other established pronuclei: they are neuroblasts with a small rim of basophilic cytoplasm (Figs. 1 and 2).

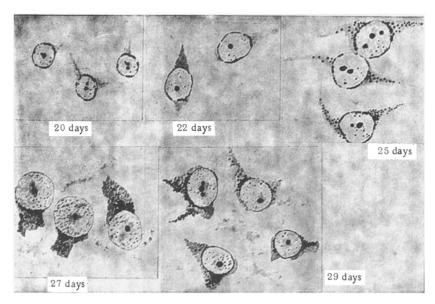


Fig. 1. Development of cells of the medial part of the posterior ventral nucleus of the rabbit thalamus. Cells drawn by means of an Abbé apparatus under the same power. Numbers given are days of prenatal life. Stained by Nissl's method.

Laboratory of General Physiology of the Central Nervous System, Institute of Normal and Pathological Physiology, Academy of Medical Sciences of the USSR (Presented by Academician P. K. Anokhin). Translated from Byulleten' Éksperimental'noi Biologii i Meditsiny, Vol. 6, No. 12, pp. 102-105, December, 1968. Original article submitted March 17, 1966.

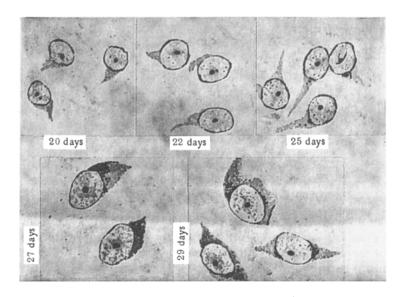


Fig. 2. Development of cells of the lateral part of the posterior ventral nucleus of the rabbit thalamus. Legend as in Fig. 1.

At this age (20-day embryos) the whole of the diencephalon, including the anlage of the posterior ventral nucleus, is penetrated by a few thin fibrils visible only under immersion. The fibrils are sharply distinguished from the diffuse massive glio-protoplasmic bands.

In 20- and 21-day embryos the glio-protoplasmic basis of the ventral medullary lamina, separating the posterior ventral nucleus from the ventral thalamus, begins to appear. At the same stage part of the medial medullary lamina, separating the developing lateral geniculate body and the posterior ventral nucleus, also begins to be formed. In the 21-day embryo the glio-protoplasmic basis of the ventromedial arcuate system, one of the most important systems of the posterior parts of the thalamus, carrying fibers of the medial lemniscus, cortico-tectal, cortico-pretectal, and tecto-pretecto-thalamic fibers in the adult, is also laid down. Connections of this system with the hypothalamus and the tectum mesencephali are known.

In the next stage (22 days) the cells of the posterior ventral nucleus have acquired a large nucleus and one or two cones of cytoplasm. This stage of embryonic life is characterized by the first appearance of neurofibrils in the cells of the posterior ventral nucleus, in the form of short bands for linear arrangements of argentophilic granules. In 25-day embryos neurofibrils are observed in all (or nearly all) cells of the nucleus as dark bands of different lengths.

The fiber system of the posterior ventral nucleus in the 22-day embryo is much more mature: long, thin glio-protoplasmic radial bands can be distinguished, forming a system connecting the posterior ventral nucleus with the cortex and subcortex, together with a thin network of single fibers running obliquely and transversely. The latter are evidently primitive afferent fibers of the ventral nucleus arriving from the mesencephalon and lower levels.

Sometimes single fragmented nerve fibrils can be seen in the radial bands. The system of single fibrils consists mainly of mature fibers.

In the 25-day fetus, masses of tigroid appear in the cells of the medial and lateral parts of the posterior ventral nucleus. In their number and size, and also in the size of the nucleus and the definition of its cytoplasm, the medial part is far ahead of the lateral. The formation of Nissl'granules evidently begins in the medial part of the posterior ventral nucleus one or two days sooner than in the lateral part, toward the 23rd-24th day of embryonic life.

In the 27-day fetus, cells of the medial and lateral parts of the posterior ventral nucleus pass into the next stage of development, the stage of diffuse tigroid. The medial nucleus, also distinguished at this age by the large size of its cells, begins to move out of the stage of diffuse tigroid: against the background of an intensely basophilic cytoplasm, a few tigroid granules appear in it. At 27 days, after staining with reduced silver, nerve fibrils can be seen in the posterior ventral nucleus and medullary laminae surrounding it.

In the 29-day fetus, mature nerve fibers in the posterior ventral nucleus are definitely more numerous than in the early fetuses, but the main mass of the system of radial fibers (corticopetal) still consists of glio-protoplasmic bands.

The same is also true of the dorsal thalamic peduncle, through which corticopetal fibers of the posterior ventral nucleus pass.

The results indicate early establishment and early differentiation of the primitive posteroventral complex. A clear heterochronism is observed in the development of the medial and lateral nuclei of the complex. It may naturally be asked with the development of which systems these facts are connected.

Afferent pathways of the posterior ventral nucleus consist of the medial lemniscus, the dorsal and ventral trigeminal tracts, and the medial and lateral spinothalamic tracts. Besides somatic afferents, these tracts also carry visceral afferents, on which grounds it has been suggested [5] that the posterior ventral nucleus be called the relay of somatovisceral sensation.

In the rabbit, as a number of investigations have shown [13, 15], only tracts beginning in the brain stem and upper parts of the spinal cord reach the thalamus. Spinal tracts terminate mainly in the rhombencephalon and mesencephalon.

Consequently, only those fibers of the spinothalamic tract which commence in the upper part of the spinal cord can reach the ventral nuclei of the thalamus.

It has been found [18] that in the rabbit the trigeminal lemniscus activates nearly the whole ventrobasal complex; only a narrow band along the lateral and ventrolateral border of the nucleus responds to tactile stimulation of other parts of the body.

In the trigeminal nerve system and also in the spinothalamic system, reticular parts can be distinguished, consisting of cell centers and conducting fibers [6, 19, 20]. In the thalamus, fibers of the reticular part of the trigeminal system (dorsal trigeminal tract) are distributed not only to the posterior ventral nucleus, but also in the medial medullary lamina, where the anterior intralaminar nuclei are concentrated. Fibers of the paleospinothalamic system also are mainly distributed here. From data in the literature [8] and personal observation [3], there is evidence of extremely early maturation of some parts of the reticular formation, including the giganto-cellular reticular nucleus and adjacent structures, receiving trigeminal afferent fibers also [7, 11, 14]. It may accordingly be postulated that the thin, sharply outlined fibrils which penetrate into the primitive thalamus of the 20-day rabbit embryo constitute the forerunner of the system connecting the thalamus with the reticular formation of the brain stem, including reticular structures of the trigeminal nerve system. Further evidence in support of this view is given by the predominant localization of these fibrils at the next stage (22 days) in the medial medullary lamina, the posterior ventral nucleus, and the parafascicular complex.

All these observations suggest that the early appearance and cytological differentiation of the primitive posterior ventral nucleus are associated primarily with afferent impulses carried by nonspecific and specific fibers of the trigeminal nerve system.

The earlier differentiation of the medial part of the posterior ventral nucleus is evidently associated with the fact that it receives a large number of trigeminal afferent fibers and is a link in the early-maturing physiological system of nutrition [9, 10].

As was mentioned above, the corticopetal fiber system of the posterior ventral nucleus matures late: even just before birth the radial bands of the posterior ventral nucleus and the dorsal peduncle of the thalamus still contain a high proportion of glio-protoplasmic bands. Growth of the corticopetal fibers of the posterior ventral nucleus toward the cortex evidently takes place only at the end of the first week of postnatal life. This can be deduced from physiological studies. For instance, experiments on kittens [10] have shown that the cortical connections of the medial part of the posterior ventral nucleus, associated with the transmission of tactile and taste impulses from the tongue, are still not mature at birth, according to the EEG findings, but become fully formed on the following day. Further evidence is given by results [1, 2] showing that the positive phase of the evoked potential due, according to Ata-Muradova, to excitation traveling along specific thalamic afferent fibers, does not appear until the 6th day of postnatal life of the rabbit. My own results agree with these findings. Judging from a quantitative criterion (changes in the nucleocytoplasmic ratio), neurons of the posterior ventral nucleus become mature on the 2nd-5th day of postnatal life.

Studies of the nucleo-cytoplasmic ratio also show that, despite considerable variations in the time of commencement of maturation, neurons of the thalamic nuclei reach the stage of maturity at the same time (2nd-5th day after birth). This fact may be important in connection with the problem of cortico-sub-cortical relationships.

Work in recent years has shown that some nonspecific nuclei of the thalamus, principally the centrum medianum, send polysensory information to the cortex, in contradistinction to the projection nuclei, which send impulses only of one specific modality [12, 16]. Some authors describe areas of the cortex receiving polysensory afferent impulses as associative, others as polysensory [4], which would seem to be more apt. In the rabbit cortex polysensory areas coincide with projection areas. Responses of different modalities can be obtained from the motor cortex. This feature, and also the fact mentioned above of simultaneous maturation of the specific and nonspecific thalamic nuclei together with, as I have suggested, their corticopetal fibers, are characteristic only of a cortex with a comparatively low level of organization and of undifferentiated thalamocortical relationships.

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