MORPHOPHYSIOLOGICAL CORRELATES OF EVOKED POTENTIALS IN RABBIT SENSORIMOTOR CORTEX DURING POSTNATAL ONTOGENESIS

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Ontogenetic investigations are being used increasingly to study special neurophysiological problems and, in particular, to analyze the electrical activity of different parts of the brain (Hunt and Goldring, 1951; Scherrer and Oeconomos, 1954; Marty, Contamin and Scherrer, 1959; Purpura et al., 1960; Carmo, 1960). Differences in the rate of maturation among interrelated systems provide a dynamic mechanism for development of appropriate behavior of the embryo or newborn animal to characteristic features of their environment.

A special conception of development has been evolved on the basis of systematic research in P. K. Anokhin’s laboratory and introduced into the literature under the name of “systemogenesis” (Anokhin, 1948, 1964). During the last few years we have studied the regularities governing maturation of the synaptic systems of different functional importance and located in different layers of the neocortex.

A very convenient phenomenon for the study of the asynchronous development of cortical structures in ontogenesis is the evoked potential, the functional significance and composition of which has gradually become clearer. Several writers have studied the evoked potential in ontogenesis (Hunt and Goldring, 1951; Scherrer and Oeconomos, 1954; Marty, Contamin and Scherrer, 1959; Purpura et al., 1960). However, these workers did not relate the characteristics of the primary evoked potential with either the evolutionary principles of asynchronous growth of cortical structures or the existing theories of the nature of the evoked potential (Eccles, 1951; Roitbak, 1955; Chang, 1960; Bishop and Clare, 1953).

Yet it has been found that the ontogenetic approach can help to elucidate some aspects of the nature of the evoked potential. For example, the positive and negative components of the evoked potential have been shown to differ in their origin and to be elicited by different subcortical structures. It is precisely with this difference in origin of the positive and negative components, and their different physiological properties, that the earlier ontogenetic appearance of the negative component is associated.

This last fact is not in harmony with generally accepted views of the origin of evoked potentials, and it thus provides a basis for proposing a new hypothesis of their origin (Anokhin, 1960, 1961; Ata-Muradova, 1960; Anokhin and Ata-Muradova, 1964).

The differences in physiological properties of the negative and positive components are also dependent on their different origins, such as the increased sensitivity of the negative component to the action of urethane (Ata-Muradova, 1963), of heat (Ata-Muradova, 1964), and of γ-aminobutyric acid (Ata-Muradova, 1963), and the lower lability of the negative component than of the positive (Anokhin, 1964, etc.).

For these reasons we have undertaken a morphophysiological investigation of those ascending pathways which might account for the early appearance of the negative
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component. Since this component arises in the plexiform layer, the problem actually amounted to a search for the tracts ascending specifically to this layer. For this purpose, immediately after birth the negative component was recorded at the point of maximal activity, and the cortex at exactly this point was then investigated histologically. Vertical serial sections through all the layers of the cortex were studied. In this way it was possible to determine accurately the maturation of the ascending fibers at precisely the point of interest, i.e., a very restricted point (1 mm²) at which the isolated negative component of the evoked potential first appeared.

METHOD

Young rabbits from a few hours to 30 days of age were used, as described previously (Ata-Muradova, 1960). The morphological investigations consisted of an analysis of the general pattern of the cytoarchitectonic differentiation of the cortex, assessment of the degree of maturity of its constituent elements and identification of the ascending pathways. Preparations were stained using P. E. Snesarev's modification of Nissl's method (see Vall, 1947).

The degree of differentiation of the individual neurons was studied by the Golgi-Cox and Golgi methods. In both cases small pieces of brain tissue were fixed with bichromate solution in darkness for a long time. The general picture of the ascending afferent pathways of the cortex was revealed by A. D. Zurabashvili's (1951) method. The degree of myelination of the conduction pathways was studied by Sokolinskii's modification of Spielmeyer's method (see Vall, 1947).

RESULTS

In newborn rabbits an evoked primary response is recorded in the sensorimotor cortex in the form of a single negative spike with a long latent period (100–200 msec) and with a course of considerable duration—up to 60 msec (Ata-Muradova, 1960; Anokhin, 1964). On the 6th–8th day the negative spike may be preceded by a positive component.

The fact that the negative component of the evoked response appears first on the surface of the cortex can only mean that the recorded synaptic discharge takes place immediately beneath the electrode, i.e., in layer I of the cortex only. In fact, introducing the electrode deeper into the cortex fails to reveal any deep negativity suggestive of the presence of excitation at a deeper point (Scherrer and Oeconomos, 1954). Our previous experiments in which the negative component was analyzed during heating and during application of various substances to the surface of the cortex (Ata-Muradova, 1963a, 1963b; Ata-Muradova and Chuppina, 1964) also prove conclusively the superficial origin of the negative component. The possibility of surface excitation is thus the only acceptable explanation.

Accordingly, in the morphophysiological investigations were guided by the assumption that conducting structures ascending directly to layer I of the cortex must exist at birth, and that the synaptic structures on which these conducting fibers could terminate in this layer must already be mature.

The first notable fact in the study of the degree of cellular differentiation is that the distribution of the cells in the cortex of the newborn rabbit is extremely dense (Fig. 1). According to Flexner and Baxter (1955) in cortex of a newborn rabbit cells constitute from 14% to 15% of the cortical substance, compared with only 1.1% of the same volume in the adult animal. Along with this great density of packing of neuronal elements in the newborn rabbit, a sharp subdivision of the cortex into discrete layers may be observed. According to Pentsik (1940) and Troitskaya (1955) the stratification of the cortex is well advanced by the 20th day of prenatal development, and by the 25th day the areal differentiation of the sensorimotor cortex can be discerned.

Conversely, the cells of layers III-IV of the cortex in a newborn rabbit are not yet fully differentiated. They are uniformly round in shape, indistinguishable in type, and have large, round nuclei surrounded by a thin rim of cytoplasm. The distribution of the Nissl substance scattered diffusely throughout the cell body and the pattern of the nuclear chromatin indicate that the cells are not fully differentiated. At birth