Prenatal and early postnatal ontogenesis of the human motor cortex: a Golgi study. II. The basket-pyramidal system

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Introduction

The existence in the human cortex of a cortical basket cell, a specific type of stellate interneuron with a short axon having terminal pericellular baskets has been reported recently. The morphological characteristics of these neurons, their cortical distribution and the behavior of their axons suggests a functional interaction between them and the pyramidal cells. These two types of neuron together form an intracortical basket-pyramidal system. The fact that in a single section the cortical basket cells are visualized in toto, including their dendritic and axonal trees and their terminal pericellular baskets, indicates that they are oriented in the cortex in a particular plane. These cortical basket cells can completely be demonstrated in sections cut in a vertical plane transverse to the precentral gyrus. Thus, the human motor cortex has within its predominantly horizontal pattern of neurons some that are vertically oriented.

The existence of functional vertical columns within the cerebral cortex is a relatively recent neurophysiological concept. In 1957, Mountcastle reported, for the first time, that the somatosensory cortex of the cat appears to be subdivided into a system of vertical columns extending from the pial surface to the white matter. Since then analogous functional vertical systems have been reported in the visual cortices of the cat and monkey. These reports were based on neurophysiological studies using single-cell recording techniques. The first direct anatomical demonstration of a functional vertical system (eye dependence) has been reported by Hubel and Wiesel in the visual cortex of the monkey. These authors showed that the pattern of degeneration in layer IV of the striate cortex, which resulted from a specific lesion in the lateral geniculate body, was indeed arranged in parallel stripes that alternated with zones of sparing. They demonstrated that the stripes of degeneration were eye-preference columns receiving signals predominantly from one eye while the spare zones received inputs predominantly from the other eye. They postulated that 'The striate cortex can therefore be thought of as subdivided into slab-shaped columns with walls perpendic-
ular to the surface and long narrow cross-sections determined by the fourth layer mosaic. All, or nearly all, cells in a given column thus respond more actively to one eye than to the other."

It should be pointed out that, structurally speaking, contrary to Mountcastle's concept of vertical columns, Hubel and Wiesel introduced the concept of vertical slab-shaped columns or 'vertical walls' based on the analysis of their data. The determination of the morphological substrate (neuronal profiles) within these vertical walls is of paramount importance. Colonnier has recently analyzed this problem. He suggested that the cortical organization could give rise to functional vertical columns, but that these columns are not separated morphological entities, in view of the considerable tangential overlapping. Perhaps what has not been sufficiently investigated is the possibility that the tangential fibers, most of which are derived from axonal collaterals of the basket cells (at least in the human motor cortex), could in themselves constitute spatially oriented systems. Such spatially oriented systems could be represented in the cortex, not by 'columns' in Mountcastle's concept, but rather by 'vertical walls' more in agreement with Hubel and Wiesel's observations.

The presumable location of the cortical basket cells between the afferent fibers and the efferent pyramidal cells and their vertical orientation within the cortex suggests that they could be the central neurons of an intracortical vertical system. The description of this basket-pyramidal system and an attempt to analyze its development and its structural-functional relationships, is the purpose of this communication.

MATERIALS AND METHOD

The precentral gyrus (motor area) of 3 human fetuses (gestational ages: 5, 7 and 7.5 months) and of 4 infants (ages: newborn and 2, 2.5 and 8 months) were studied. The tissue blocks obtained were vertical to the pial surface and perpendicular to the long axis of the gyrus and were 2.5 mm in thickness. The blocks were stained with the rapid Golgi method and cut freehand with a razor blade. The entire procedure used in this study is described elsewhere.

OBSERVATIONS

Prenatal and early postnatal development of the basket–pyramidal system of the motor cortex

Around the 7th month of intrauterine life a system of afferent fibers reaches the level of the motor cortex between the pyramids of lower layer III and the pyramids of layer V (ref. 6). The fibers of this system (probably specific thalamic afferent) become horizontal at that level of the cortex and constitute the external band of Baillarger. The arrival of this system of fibers marks the beginning of the development of layer IV. By 7.5 months of prenatal life layer IV is established and its peculiar stellate interneurons are recognizable as cortical basket cells. The cortical basket cells of layer IV are the first neurons of this type to appear in the motor cortex. These interneurons are
characterized even in their early stages of development by horizontal and vertical dendrites and by an axon which branches in many long horizontal collaterals. The formation of pericellular baskets around the bodies of the pyramidal cells by the axonal collaterals of the cortical basket cells is considered to be an indication of their maturity. Since pericellular baskets are not yet present at this age in prenatal life the cortical basket cells are considered to be developing but still immature at this age.

At the time of birth, cortical basket cells are found in all cortical layers (except layer I), but only those located within, above or below layer IV are considered to be mature. The horizontal axonal collaterals of these cells form pericellular baskets around the bodies of the pyramidal cells of lower layer III and layer V. The pericellular baskets around the pyramidal cells of layer V are more numerous, more complex and better developed than those formed around the pyramidal cells of lower layer III suggesting an earlier maturation of the former. The cortical basket cells of upper layer III and layer II are considered immature since pericellular baskets are not found at these cortical levels at this age. By 2.5 months of postnatal life the cortical basket cells of upper layer III have achieved maturity since few pericellular baskets were stained around the bodies of the pyramidal cells of this cortical level. The number and the complexity of the pericellular baskets of lower layer III and layer V are increased at this age by comparison with the newborn infant. The cortical basket cells of layer II are still immature, at this age, without pericellular baskets. Although cortical basket cells were stained in layer II of the motor cortex of the 8-month-old infant, no pericellular baskets were found at this cortical level. This suggests that the cortical basket cells of layer II will achieve maturity perhaps during late postnatal ontogenesis.

The development of the cortical basket cells is therefore closely related to that of the pyramidal cells. The development and maturation of the cortical basket cells parallels that of the pyramidal cells with which they establish neuronal chains. The development of the pyramidal cells of the motor cortex seems to be related to the arrival of afferent fibers at the different cortical levels. Therefore, the cortical basket cells are considered to be a special type of interneuron located between the afferent fibers and the efferent pyramidal cells of the different cortical layers.

When fully developed the cortical basket cells, as also the pyramidal cells, can be separated into several groups according to their size and cortical location (Fig. 1). There are small (layer II), medium (upper layer III), large (lower layer III) and giant (layer V) sized cortical basket cells in the human motor cortex. The development of the individual types of cortical basket cells of the different layers of the human motor cortex during prenatal and early postnatal ontogenesis can be followed in Figs. 2-5 of the preceding communication. The morphological characteristics of the mature cortical basket cells and of the pericellular baskets of the human motor cortex have been described in detail elsewhere.

Spatial orientation of the basket–pyramidal system within the motor cortex

When the structure of the cortical basket cells was first reported, their peculiar orientation within the cortex was not emphasized. The present developmental study of

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a more complete series than originally studied, and the fact that they have also been recognized in the upper cortical layers, have made their peculiar orientation more clearly evident. The inclusion of the cortical basket cells in toto within transversely oriented vertical planes of the precentral gyrus clearly establishes their topography. Since the Golgi sections were no thicker than 0.2 mm and the longest horizontal axonal collateral so far demonstrated was no longer than 1 mm, one can ascertain that these cells are located within slab-shaped vertical planes of similar dimensions extending from layers II to V. Thus, the cortical basket cells of a given vertical plane establish contacts with all the pyramidal cells of that plane. Therefore, the human motor cortex can be considered to be subdivided into parallel vertical planes ('walls') of basket–pyramidal neuronal chains, extending from layers II to V, of undoubtedly functional significance.

DISCUSSION

The human motor cortex is characterized by the marked development of pyramidal and basket cells. These two types of neuron are closely associated during the course of cortical ontogenesis and together constitute the basket–pyramidal system of the motor cortex. This neuronal system is located within the cortex in a vertical plane which is transverse to the long axis of the precentral gyrus and extends from layers II to V. It is composed of several horizontal neuronal chains formed between the cortical basket cells of the different layers and the pyramidal cells of those layers. In the human motor cortex and according to their size and cortical location, the following cortical basket cells are recognized (Fig. 1). (a) The giant cortical basket cells of layer V, which form pericellular baskets predominantly around the bodies of the pyramidal cells of this layer, but also around the bodies of the pyramidal cells of lower layer III. (b) The large cortical basket cells of lower layer III, which form pericellular baskets predominantly around the bodies of the pyramidal cells of this layer, but also around the bodies of the pyramidal cells of layer V and upper layer III. (c) The medium-sized cortical basket cells of upper layer III, which form pericellular baskets predominantly around the bodies of the pyramidal cells of this layer, but also around the bodies of the pyramidal cells of lower layer III and presumably in postnatal ontogenesis around the bodies of the pyramidal cells of layer II. (d) Finally, the small cortical

Fig. 1. Examples of small (layer II), medium (upper layer III), large (lower layer III) and giant (layer V) sized basket cells of the motor cortex of a 2.5-month-old infant. On the left side of the figure are illustrated the bodies, the axons with their collaterals and the cortical location (depth) of the basket cells depicted on the right side of the figure. The predominant horizontal distribution of the axons of the basket cells and the several horizontal strata formed by their collaterals from layers II to V are also illustrated. The figure represents a vertical section of the motor cortex transverse to the long axis of the precentral gyrus. The intracortical distribution of the axons of the different basket cells determine a slab-shaped vertical column or vertical 'wall' in which the axonal terminals establish contacts with all the pyramidal cells within that vertical 'wall'. The synaptic contacts are established by the formation of pericellular baskets around the bodies of the pyramidal cells. The pericellular baskets represented semi-schematically in this figure were found in the sections. Rapid Golgi method. Scale 100 μm.

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basket cells of layer II which presumably in late postnatal ontogenesis will form pericellular baskets around the bodies of the pyramidal cells of layer II and perhaps also around the bodies of the pyramids of upper layer III. The basket–pyramidal system of the motor cortex consists therefore of several horizontal overlapping strata of neuronal connections between the cortical basket cells and the pyramids of the different cortical layers.

The formation of the pericellular baskets (index of maturity of the cortical basket cells) during the course of cortical ontogenesis follows a sequence which parallels that of the maturation of the pyramidal cells and the formation of the cortical layers. The sequential development of the different strata of basket–pyramidal connections in cortical ontogenesis and their possible relationship to the arrival of the different afferent fibers should be investigated.

Although both the dendritic and axonal trees of the basket cells are oriented within vertical planes, the neuronal system forms between them, and the pyramidal cells become determined by their axonal distribution. It is the predominantly horizontal (tangential) distribution of the axonal collaterals of the basket cells that determines the vertical neuronal system and establishes its cortical orientation and approximate dimensions. The fact that the axonal distribution and its pericellular ending determine the basket–pyramidal system of the motor cortex is of interest and should be emphasized. In general, the attention of most investigators of the structure of the neocortex has been directed more toward the dendritic patterns of distribution than toward the axonal profiles of intracortical distribution. The human motor cortex appears to be subdivided into slab-shaped vertical planes or ‘walls’ no thicker than 0.2 mm and no longer than 1–2 mm, extending from layers II to V, which are perpendicular to the long axis of the precentral gyrus and are determined by the horizontal distribution of the axons of the cortical basket cells. The morphological characteristics of the basket–pyramidal system of the human motor cortex presented here coincide with those of the slab-shaped columns described by Hubel and Wiesel.

The structural similarities among the basket–pyramidal system of the motor cortex, the basket–Purkinje system of the cerebellum and the basket–pyramidal system of the hippocampus are also emphasized. These three systems have distinct spatial orientations and similar types of neuronal connections. The inhibitory nature of the last two systems suggests a similar type of function for the basket–pyramidal system of the motor cortex which should be investigated.

The existence in the human motor cortex of a vertical neuronal system presupposes the possibility of the existence of still others perhaps with different spatial orientations. The fact that such systems may be determined by the profiles of intracortical axonal distribution should open new avenues into the study of the structural organization of the cerebral cortex.

SUMMARY

A Golgi study is presented of the prenatal and early postnatal development of the basket–pyramidal system of the human motor cortex. The morphological charac-
teristics of the cortical basket cells, their origin and development, their orientation along vertical planes within the cortex and their formation of several strata of neuronal connections (pericellular baskets) with the pyramidal cells have been analyzed. It is concluded that the human motor cortex, as well as the sensory and visual cortices of the cat and the visual cortex of the monkey, are subdivided into vertically oriented neuronal systems of undoubtedly functional significance.

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REFERENCES
