ORIGIN OF THE PERICELLULAR BASKETS OF THE PYRAMIDAL CELLS OF THE HUMAN MOTOR CORTEX: A GOLGI STUDY

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INTRODUCTION

The identification of a distinct histological structure with a specific function is the most significant objective in the study of the nervous system. This objective, unfortunately, has been met on only a few occasions. Perhaps the best known and the one which best illustrates this objective has been the discovery of the inhibitory function of the basket cells of the cerebellum and the hippocampus. Cajal established for the first time the histological structure of these neurons and of their connections. In 1888 (refs. 3, 7) he described, in Golgi preparations, the pericellular baskets of the Purkinje cells and their origin from stellate neurons with short axon, the basket cell, located in the molecular layer. In 1893 (Refs. 4, 7) he also described, in Golgi preparations, the pericellular baskets of the pyramidal cells of the hippocampus and their origin from stellate neurons with short axon, the basket cell, located in the stratum oriens. The morphological characteristics of the basket cells of the hippocampus were later described in greater detail by Lorente de Nó. These two systems have a similar structure consisting of an intrinsic stellate neuron characterized by the termination of its axon in an intricate axonic plexus around, and in contact with, the soma of several large neurons of projection, thus forming a distinct pericellular basket. This peculiar structure is today associated with inhibition in the cerebellum and in the hippocampus.

Cajal also described a third type of basket around the cortical pyramidal cells of the visual and the motor cortices of infants. He compared them, structurally, with the baskets of the cerebellum and the hippocampus. He suggested that the most likely origin of these baskets were the stellate neurons with horizontal axons encountered in layers III–V of the cortex. With an ingenious method (chronically isolated slabs of neocortex in which only their vascular supply is maintained) Szentágothai has been able to prove that the axo-somatic contacts are mainly contributed by cortical neurons with short axons. He suggested that the pericellular baskets formed around the pyramidal cells are derived from stellate neurons with axons not longer than 1–2 mm in length. Cajal further suggested that perhaps afferent axons may also contribute to the formation of the baskets but concluded that more investigations were needed.
before any definite conclusion could be drawn. The possibility that the baskets of the pyramidal cells may represent a component of a cortical inhibitory system has been already suggested. This possibility is further supported by the electron microscopic studies of the type of axo-somatic contacts in pyramidal cells of the cortex.

Except for two original drawings of Cajal of the baskets of the pyramidal cells of the motor cortex of man, the available information about them remains incomplete in such areas as: the structure of the baskets, their location and distribution, and the type of terminal contact which they make with the soma of the pyramidal cells. More importantly, little is known about the distribution and structural characteristics of the cortical stellate neurons which participate in their formation. The present communication reports the observations made in Golgi preparations of the human cerebral cortex concerning the structure and the distribution of the pericellular baskets of the pyramidal cells. It also describes the morphological characteristics of the cortical stellate neurons which form the baskets.

MATERIAL AND METHOD

The motor areas (area 4) of the cerebral cortex of a 7-month fetus, a premature infant, a newborn, a 2-month-old infant and an 8-month-old infant have been studied. Several tissue blocks from the motor cortex of these infants were obtained between 1 and 3 h after death. All infants died in cardio-respiratory failure. The blocks obtained measured approximately 2.5 mm in thickness, 10 mm in length and 5 mm in width. All the blocks were stained by the rapid Golgi method according to the following procedure: immersion during 5 days in a fresh 0.25 % osmic–dichromate solution; immersion for 2 days in a fresh 0.75 % silver nitrate solution; immersion for 2 days in a fresh 0.25 % osmic–dichromate solution; and immersion for 2 days in a fresh 0.75 % silver nitrate solution. The tissue blocks were washed (1 min) in distilled water between solutions. The blocks were cut by free hand with a razor blade, cleared with oil of clove and mounted with a Damar-xylene solution. 20–24 sections, 150–200 μ thick, were obtained from each block. A total of 380 sections were prepared and studied.

OBSERVATIONS

7-month fetus. The motor cortex of this infant was characterized by its embryonic stage of development and did not disclose pericellular baskets. Only pyramidal cells were found in this cortex, some localized deep in the cortex and thus establishing the first indication of the layer V. The other pyramidal cells were distributed throughout the superficial cortical regions without a clear lamination. No stellate cells were found in the cortex of this infant.

Premature infant. The motor cortex of this infant was well developed and all its cortical layers and cell types were recognized. The pyramidal cells were distributed throughout the cortex with two distinct concentrations in layers III and V. Typical stellate cells were found among the bodies of the pyramidal cells. The terminal portions of the axons of these stellate cells became so fine that they failed to be properly
impregnated by silver and could not be followed. Probably because of this no pericellular baskets were found in this infant.

8-month-old infant. The motor cortex of this infant was characterized by its extraordinary complexity of axonic fibers and dendrites. Pericellular baskets were seen on rare occasions. Any attempt to follow the fibers which form them to the cell of origin, through the complexity of this cortex, failed to give clear and positive results. Typical stellate cells were also found among the bodies of the pyramidal cells but, again, to follow their axons to their termination was a difficult if not an impossible task in this complex cortex.

Newborn and 60-day-old infants. The motor cortices of these 2 infants proved to be optimal for the detailed analysis required for this study. Pericellular baskets were abundant and the complexity of the cortex, at this age, permitted an accurate analysis of their location, structure, terminal type of contact with the soma of the pyramidal cells and, more importantly, their origin from typical stellate cells with short axon.

The human motor cortex at this age (first 2 months of extrauterine life) is well developed. It measures 2000 μ thick and is organized in the following manner: layer I: 150 μ; layer II: 250 μ; layer III: 500 μ; layer IV: 250 μ; layer V: 300 μ; layer VI: 500 μ. Although the motor cortex is classically identified and characterized by the lack of a clearly defined layer IV (granular layer), in this study layer IV is considered at a cortical depth ranging between 950 and 1200 μ from the surface pia. This is based on the observation that typical stellate neurons with short axon appeared to concentrate more frequently at that cortical depth than in any other cortical region. They concentrate above the bodies of the giant pyramidal cells of layer V and below the bodies of the large pyramidal cells of lower layer III. The stellate cells appeared at that cortical depth in small groups of several neurons (Figs. 6, 7), but failed to constitute a clearly defined layer. The bodies of the large and giant pyramidal cells of the motor cortex appeared at cortical depths ranging from 800 to 1400 μ. This particular distribution of the pyramidal cells in the motor cortex and their abundance also explains the absence of a clearly defined layer IV such as the one which characterizes the primary, visual, auditory and sensory areas of the cortex.

Location and distribution of the cortical baskets

In Golgi preparations of the human motor cortex at this age (first 2 months of extrauterine life) pericellular baskets are found frequently. They are located at a cortical depth ranging between 800 and 1400 μ from the surface pia. They coincide in location and cortical distribution with the bodies of the large and giant pyramidal cells of the lower layer III and layer V respectively. In spite of this general cortical distribution, the baskets appear to concentrate in two main locations or cortical depths at 900 μ and at 1400 μ from the surface pia. These two locations of the baskets indicate two clearly different populations of them. Those located around the 900 μ cortical depth are smaller, roughly triangular in shape and depict a very simple structural organization. The baskets located around the 1400 μ cortical depth are larger, triangular or fusiform, with apical and basal prolongations and they have a rather complex

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Figs. 1 and 2. Pericellular baskets of layer V of the motor cortices of a newborn and of a 60-day-old infant respectively. Cortical basket cells (arrows) appeared invariably associated with the baskets. The structure, fiber composition and shape of the baskets are clearly seen. Notice the abundance of horizontal axonic fibers among the baskets. There is an appreciable increase in the total number of baskets, in their complexity and in horizontal fibers between birth (Fig. 1) and 2 months of age (Fig. 2). Rapid Golgi method, scale 100 μ.

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Fig. 3. Detail of the fibrillar constitution of a basket of layer V of the motor cortex of a 60-day-old infant. The photomicrographs represent 6 different levels of the same basket to show its intricate structure, the fusiform dilatations of the fibrillae and the terminal round heads of some. The fusiform dilatations and the terminal heads are considered to represent synaptic contacts with the soma of the pyramidal cell. Rapid Golgi method.
structure. The distribution of the cortical baskets in two main populations is best seen in the motor cortex of the newborn infant. At 2 months of age this double cortical distribution is less apparent due to an increase in size and complexity of the baskets and to an increase in their total number. At this age the cortical baskets are found throughout the general cortical distribution of lower layer III and layers IV and V. The limits of layer IV become less apparent at this age also. The baskets are more abundant around the giant pyramidal cells of layer V than in any other cortical region.

Structure of the cortical baskets

The delicate and fine structure of the cortical baskets can be easily obscured in Golgi preparations by overstaining, the presence of silver precipitates, and the overlapping with other structures. It is only in certain good Golgi preparations in which the baskets are stained and can be thoroughly analysed. For reasons which remain unknown the cortical baskets are stained only in those Golgi preparations where the pyramidal cells which they surround are not stained. On the other hand, when the pyramidal cells are well stained the baskets are not distinguishable.

At low microscopic magnification the cortical baskets appeared simply as localized roughly triangular concentrations of axonic terminals clearly distinguishable from the surrounding structures. At medium microscopic magnification (Figs. 1, 2) the baskets are seen to be formed by a concentration of many incoming axonic terminals reproducing the morphology of the bodies of the pyramidal cells around which they are formed. At high microscopic magnification the incoming fibers approach and enter into the baskets from all directions. They branch in several short and fine fibrillae which constitute the basket itself. The incoming axons are seen after giving off the fine fibrillae to a basket to continue their path into other baskets or other cortical regions. On a few occasions an incoming axon terminates solely in a given basket. The baskets of the lower layer III are relatively simple in their structure. The baskets of the layer V are quite complex structures characterized by apical and basal prolongations which appear to involve the first portion of the apical and the basal dendrites of the giant pyramidal cells. Some large baskets have also another prolongation which, by its location, appears to involve the first portion of the axon of the giant pyramidal cell (Fig. 3). At this very high microscopic magnification the fine fibrillae which constitute the basket are best seen. The fibrillae terminate by small round heads ("bouton-terminaux") of approximately 1–1.5 \( \mu \) in diameter (Fig. 3). The fibrillae have also many fusiform dilations which resemble contact "en passant" of approximately 1 \( \mu \) in diameter (Fig. 3). A schematic representation of a large basket (layer V) around a giant pyramidal cell is shown in Fig. 4.

Origin of the baskets: the cortical basket cells

In Golgi preparations of the motor cortex the baskets appeared to be associated invariably with a distinct stellate neuron with short axon, the cortical basket cell (Figs. 1, 2). They are medium-sized stellate neurons distributed at a cortical depth ranging
Fig. 4. Schematic representation of a large pericellular basket around the body of a giant pyramidal cell of the human motor cortex, demonstrating the incoming axons, the fibrillar constitution of the basket and the terminal heads and fusiform dilatations of the fibrillae. The apical, basal and axonal prolongations of the basket are also demonstrated.
Fig. 5. Camera lucida drawing of a basket cell from the motor cortex of a newborn infant. It demonstrates beautifully the two types of dendrites, the distribution of the axon, and the axonic collaterals forming baskets around the pyramidal cells of the layers III and V, which characterize the histological structure of the basket cells of the human motor cortex. Several incoming axons are seen establishing axo-spinodendritic synapses (S). T, horizontal axonic fibers.

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Fig. 6. Camera lucida drawing of a group of cortical basket cells to demonstrate their structural characteristic and cortical location. The horizontal axonic (T) fibers of these neurons were cut and, therefore, their termination is missing. Several axonic collaterals (c) arising from the horizontal fibers terminate in the pericellular baskets. (Motor cortex of a 60-day-old infant.)

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Fig. 7. Camera lucida drawing of the two cortical basket cells to demonstrate the length of two complete horizontal axonic (T) fibers of one of them. These fibers measure approximately 1000 μ in length and give many axonic collaterals (c) for the baskets around the pyramidal cells of lower layer III and layer V. The cortical location of the neurons is represented in microns from the surface pia. The structural characteristics of the basket cells are clearly demonstrated. The slight oblique position of the basket cells and of the pericellular baskets are reflections of the curvature of the cortical convolution (insert). (Motor cortex of a 60-day-old infant.)

from 850 to 1400 μ from the surface pia, among the bodies of the large and the giant pyramidal cells of the motor cortex. In spite of this general cortical distribution they appeared to be more abundant at a cortical depth between 950 and 1200 μ from the surface pia establishing a poorly defined layer IV (Figs. 5–7).

The cortical basket cells of the human motor cortex (Figs. 5–7) are distinct neurons characterized by both the distribution of their dendrites and the behavior of their
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axon. Several dendrites, mainly vertical and horizontal, radiate from the body of the neuron. The vertical dendrites (Figs. 5–7) are a prominent feature of the cortical basket cells. The superior vertical dendrite crosses layer III and terminates in layer II. The inferior vertical dendrite crosses the layer V and terminates in layer VI. Both of these dendrites may measure up to several hundred microns in length. The horizontal dendrites cross the cortex at the same cortical depth as that of the neuronal body and are shorter than the vertical ones. The dendrites of the cortical basket cells are thin, long and moderately covered by dendritic spines. Perhaps the most significant and distinctive structural characteristic of these cells is the behavior of their axon (Figs. 5–7). The axon may be ascending or descending, depending on the location (cortical depth) of the neuron. It branches almost immediately after arising from the neuronal body into several horizontal fibers of great length at different cortical levels. These horizontal fibers may measure up to 1000 µ in length or more. From these horizontal fibers many ascending and descending axonic collaterals arise which terminate in the pericellular baskets. Either they terminate in the basket by branching into fine terminal fibrillae or, after giving off terminals to a basket they continue to other baskets. The same basket cell can enter into the formation of baskets around the pyramidal cells of lower layer III as well as around the giant pyramidal cells of layer V (Fig. 5). A single basket cell participates in the formation of many pericellular baskets. The soma of the cortical basket cells has clearly distinct spines.

DISCUSSION

The present communication confirms original observations made by Cajal in 1899. To those it adds new information concerning the structure, the distribution and the origin of the baskets of the pyramidal cells of the human motor cortex.

The basket cell found in the human motor cortex is structurally similar to the basket cells of the cerebellum and the hippocampus. It is a stellate neuron with short axon characterized by its long vertical and shorter horizontal dendrites, by its cortical location and by the behavior of its axon. The dendrites of the cortical basket cell are thin, long and moderately covered by spines. The cortical basket cells are distributed from lower layer III to layer V. However, they are more abundant in layer IV where they are found in small groups representing perhaps the neuronal elements of this poorly defined layer of the motor cortex. The axon of the basket cell is its most distinctive characteristic. It branches in several long horizontal fibers at different cortical levels. Many ascending and descending collaterals arise from the horizontal
### TABLE I

**MORPHOLOGICAL CHARACTERISTICS OF THE BASKET CELLS**

<table>
<thead>
<tr>
<th>Location</th>
<th>Type</th>
<th>Axon</th>
<th>Dendrites</th>
<th>Distribution of dendrites</th>
<th>Receptive neuron</th>
<th>Function</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cerebellum</td>
<td>Stellate short axon</td>
<td>Horizontal fibers with collaterals</td>
<td>With spines</td>
<td>Same regional distribution as dendrites of Purkinje cells&lt;sup&gt;3,7&lt;/sup&gt;</td>
<td>Purkinje cell*</td>
<td>Inhibitory (2)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>terminating in many baskets</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Hippocampus</td>
<td>Stellate short axon</td>
<td>Horizontal fibers with collaterals</td>
<td>With spines</td>
<td>Same regional distribution as dendrites of pyramidal cells of hippocampus&lt;sup&gt;7,11&lt;/sup&gt;</td>
<td>Hippocampal pyramidal cell*</td>
<td>Inhibitory (1)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>terminating in many baskets</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Motor cortex</td>
<td>Stellate short axon</td>
<td>Horizontal fibers with collaterals</td>
<td>With spines</td>
<td>Same regional distribution as apical &amp; basal dendrites of large &amp; giant pyramids</td>
<td>Neocortical pyramidal cell*</td>
<td>Unknown, perhaps inhibitory</td>
</tr>
<tr>
<td></td>
<td></td>
<td>terminating in many baskets</td>
<td></td>
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* Projective neurons.
fibers and terminate in fine fibrillae in the pericellular baskets. The fibrillae of a basket contact the soma of the pyramidal cell probably by its terminal heads and by its fusiform dilatations thus establishing axo-somatic synapses. The fibrillae also make contacts with the first portions of the axon, the apical and the basal dendrites of the pyramidal cells.

The same cortical basket cell can enter in the formation of baskets around the bodies of the large and the giant pyramidal cells of the lower layer III and layer V respectively. This indicates perhaps that the baskets around these two types of pyramidal cells belong to the same cortical system. A basket is formed by the axonic collaterals of many basket cells, and a single basket cell enters in the formation of many baskets.

Typical basket cells are already found shortly before birth in the motor cortex, and possibly the baskets are being formed at that age also. At the time of birth the motor cortex has well developed basket cells and the baskets are abundant, more so in layer V than in lower layer III. At 2 months of age the baskets have increased considerably in structural complexity and in total number. The basket cells at this age show the rich arborization of their axon. This age represents the best time for a detail analysis of the structure of the basket cells and of the pericellular baskets. The structural complexity of the motor cortex of older infants makes any detailed analysis of the baskets themselves and of their origin from typical stellate neurons nearly impossible.

The structural similarities of the basket cells of the motor cortex, the cerebellum and the hippocampus (Table I) give further support to the hypothesis that the baskets of the cortical pyramidal cells are perhaps part of an inhibitory system.

While the possibility that afferent axons may also contribute to the formation of the baskets of the cortical pyramidal cells has not been confirmed in the present study, it has also not been ruled out. Undoubtedly, more investigations are needed.

A few words about the rapid Golgi method appear to be in order. The clarity, completeness and elegance of this method in demonstrating the finer structure of the central nervous system have not been surpassed by any of the neurohistological methods available today. It is because of this that the rapid Golgi method, in spite of its occasional failure and capricious nature, should be encouraged in the study of the structure of the nervous system. The knowledge derived from such Golgi studies facilitates a better understanding of the structure and gives a frame of reference for ultrastructural and neurophysiological studies.

SUMMARY

A Golgi study of the structure, distribution and origin of the pericellular baskets of the pyramidal cells of the human motor cortex is presented. This study has disclosed the presence in the motor cortex of a distinct type of stellate neuron which forms pericellular baskets around the bodies of the pyramidal cells of the lower layer III and layer V. These cortical basket cells are characterized also by their long horizontal and vertical dendrites. They are distributed from layers III–V, but they concentrate more
commonly in layer IV of the motor cortex, perhaps representing the neuronal elements of this poorly defined cortical layer. The structure of the pericellular baskets is described in detail. It is suggested that the cortical basket cell here described may represent an inhibitory neuron of the human motor cortex.

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