72. Three Dimensional Analysis of Neurons in the Substantia Gelatinosa Rolandi

By Yasuo Sugiura

3rd Department of Anatomy, Faculty of Medicine, Tokyo Medical and Dental University

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Using Golgi's method, many careful descriptions of the substantia gelatinosa have been published (Lenhossék, 1895; Ramón y Cajal, 1909; Szentágothai, 1964; the Scheibels, 1968; Réthyelyi and Szentágothai, 1969). These findings are principally based on the observation of single sections cut by the microtome knife transversely, sagittally or horizontally. However, it can easily be understood that, if observations are made only of single sections, it is nearly impossible to follow wholly the dendritic and axonal branches due to their vast three-dimensional expansions.

For the sake of following up dendritic and axonal trajectories, Mannen (1975) introduced a microreconstruction method which makes it possible to visualize the full extension of an individual neuron by means of Gogi-stained serial sections. In order to analyse the three-dimensional dendritic and axonal distribution of the substantia gelatinosa, lumbar segments from the two kittens aged less than 30 days have been examined by this method. This article contains the results thus obtained.

The neurons located in the substantia gelatinosa (lamina II of Rexed) can be divided into two groups according to their dendritic pattern: the outer neuron and the inner neuron which are comparable to limitrophe cell and central cell of Ramón y Cajal. Typical cases will be described (Fig. 2). The outer neuron, Cell A (Fig. 2) of which the soma (10μm×15μm in diameter) is situated in dorsal rand of this lamina sends its dendrites in ventral and dorsal directions. The mediolateral and dorsoventral extent of the ventral dendrites in a transverse plane is about 100–150μm and about 200μm, almost equal to the total depth of lamina II. The ventral dendrites show a profile like a fan which radiates in a rostrocaudal direction: its rostrocaudal extent is about 300μm, stretching out in three sections (section 99–101) (Fig. 2b, A). The dorsal dendrites, less numerous than the ventral ones, after issuing from the soma and

* Present address: 1st Department of Anatomy, Faculty of Medicine, University of Nagoya.
Fig. 1. Transverse section showing a number of cells of the substantia gelatinosa (lamina II). Arrows and
joining points of cut ends found in the confronting planes of the serial sections. The solid line and the
dotted line mark the outline of the spinal cord and the ventral border of the posterior funiculus respectively.
bifurcating in lamina I, run along the dorsal border of the substantia gelatinosa in medial and lateral directions in the transverse plane, while they extend, if viewed from a lateral aspect, in mediocaudal and laterorostral directions.

Cells B (10 μm × 10 μm) and C (8 μm × 10 μm) (Fig. 2) belong to the inner neuron of which the soma is scattered in lamina II except for its dorsal rand. In these typical cases, the dendrites issue bilaterally in ventral and dorsal directions in transverse sections. However, in the sagittal plane, these dendrites also develop remarkably in a rostrocaudal direction. Their mediolateral, dorsoventral and rostrocaudal extent are about 80–100 μm, 150–230 μm and 200–250 μm. Furthermore, in addition to these typical cases, there are many transitional forms between the outer cell and the inner cell (Fig. 1, f, m) and the variant forms among both types of cells (Fig. 1, a, b, g, h, j, k, l, p and c, d, e, i, n, o).

The axon of the gelatinosa neuron generally is very fine and bifurcates without any conspicuous tapering. In a majority of cases the axon of the outer cell runs initially into lamina I and thereafter takes either a dorsal course or a ventral course with development of a few collaterals. The axon of Cell A emerges from the bifurcating point of the dorsal dendrite (S-A distance (the distance from the starting point of the axon at the dendrite to the point where the dendrite joins the soma), 45 μm). After running laterally 100 μm, it bifurcates into two branches: a lateral branch and a medial branch. The medial branch, after taking a mediocaudal course (sections 100–101), terminates in the ventral border of lamina I while the lateral branch, running in a lateroventral direction (sections 100–101), disappears at the ventromedial border of Lissauer’s tract. Further tracing was impossible.

Some of the outer cells (Fig. 1, b) produce axons which turn back from lamina I into various laminae of the dorsal horn. However, in a few cases, the axon follows a dorsoventral course which passes through all laminae of the dorsal horn in a single section and finally enters the deeper layer of the lateral funiculus of the ipsilateral side in which it bifurcates into an ascending branch and a descending branch (Fig. 1, Cell D).

The axon of Cell B, a typical inner cell, emerges from a secondary bifurcating point of the rostral dendrites (S-A distance 65 μm). Its proximal portion, after describing a dorsalwards concave arch which is characteristic of this type, bifurcates several times. The collaterals emerging from these branchings form, on the medial side of their own dendritic tree, an axonal plexus which spreads out in three sections (88–90). One of the collaterals escaping
Fig. 2. Neurons of the substantia gelatinosa described in this paper. a: axonal and dendritic spread of these neurons projected onto a transverse plane. b: their lateral view. The numbers found to one side of the cells are the numbers of serial sections. These figures were composed from observations made at various levels.
from this plexus ascends rostro-dorsally (86-88) to end with terminal arborization in the dorsal part of lamina II. The axon of Cell C issues directly from the soma and forms an arch similar to Cell B in its proximal portion and bifurcates into two fine branchlets which run, at the same level (85), parallel to each other in a dorsal direction. One of them terminates within lamina II, but its distribution does not overlap the dendritic domain of the mother cell. The other runs into lamina I and disappears at the ventral border of the posterior funiculus. Further tracing was impossible. The soma of Cell E (10μm x 12μm) (Fig. 2) belonging to the inner neuron is located on the ventral border of lamina II and shows an atypical dendritic tree which extends slightly in a rostro-caudal direction (85-86). The axon of this cell emerges from the soma and, after running ventralwards, curves dorsalwards to gain lamina I. In the neighboring section (86) it enters Lissauer's tract and descends through this tract nearly 1200μm. Then it reenters, at the level of section 74, lamina I and runs horizontally in a medial direction. In the next caudal section, it turns back into lamina II to disappear in this level. Cell F (8μm x 8μm, S-A distance 10μm) (Fig. 2) of which the profile of the dendritic tree is similar to that of Cell E shows an axonal course limited to within lamina II and extended in only one section.

According to Ramón y Cajal, in the transverse plane, the limitrophe cell presents the anterior or lateral dendrites while the central cell provides the anterior and posterior dendrites. However, sagittal sections reveal that these dendritic branchings also extend remarkably in a rostro-caudal direction, showing a laminal arrangement separated by incoming afferent collaterals. The axons of these cells mainly enter the lateral funiculus, and partly the posterior funiculus and Lissauer's tract. These findings have been recently confirmed by Szentágothai (1964) and the Scheibels (1968). In addition, Szentágothai and the Scheibels showed by means of Golgi's method or the degeneration method that the majority of axons of the gelatinosa cells enter Lissauer's tract or the adjacent dorsolateral white matter and turn back into the dorsal horn after ascending or descending 2 or 3 segments.

The neuron examined in this study can be found in these hitherto published drawings or schematic drawings as far as the principal orientation of the dendritic tree and axonal course is concerned. In these comparisons, however, it must be kept in mind that these descriptions were drawn from single sections. The results of measurements obtained in this study suggest that, even in regard to the dendritic tree, a complete tracing would be highly difficult with single sections of less than 100μm, however the cutting plane may be
oriented. According to our findings, the dendrites of the outer cell and the inner cell are oriented according to different patterns: the ventral dendrites of the outer cell show a fan-like radiating pattern in the sagittal plane while the dendrites of the inner cell spread out bilaterally in the same plane in a rostrocaudal direction. Thus, the profiles of the dendritic tree of these cells form a sort of checkered pattern, if viewed laterally. As concerns the axonal trajectory, the tortuous axonal course of Cell E reconstructed in this study confirms the results of observations previously obtained by Szentágothai and the Scheibels. However, even in this case, it was difficult to determine whether the axon actually terminates in lamina II or it proceeds to some other final destination, passing through this lamina.

Summary. The dendritic and axonal trajectories of the neurons of the substantia gelatinosa Rolandi in the cat were followed by a three-dimensional reconstruction method with Golgi-stained serial sections. The results obtained in this study reconfirm the hitherto published descriptions and show the necessity of three-dimensional observations in neurohistological studies.

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References