STUDIES ON THE CEREBRAL CORTEX

S. RAMÓN Y CAJAL

LLOYD-LUKE

Studies on The Cerebral Cortex

[LIMBIC STRUCTURES]

by

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Translated from the Spanish

by

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PREFACE

At the turn of the century it can be truly stated that no two men had contributed more to our understanding of the function of the nervous system than Ramón y Cajal and Sir Charles Sherrington. Cajal claims our attention because of his remarkable studies on the structural interrelations of the brain stem and forebrain. In making this translation of Cajal's classic work, Dr. Lisbeth M. Kraft has given us insight into the part he played in bringing the limbic system to the fore. During the past fifty-odd years this part of the brain has come into increasing prominence. But since knowledge of structure must inevitably precede functional considerations, it is important historically that we have this account of the anatomy of the limbic cortex and its relation with subcortical structures by the greatest master of neuroanatomy the world has yet known. Dr. Kraft's translation is particularly welcome since it comes at a time when there is renewed and active interest in the functions of the medial and basal structures of the forebrain.

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Yale University,
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INTRODUCTION

On page 117 of this book, one will find a reference by Cajal to the "memorable works of Broca". In 1878, Broca demonstrated that a large convolution which he called the great limbic lobe is found as a common denominator in the brains of all mammals. He chose the word limbic to indicate that this lobe *surrounds* the brain stem. In accordance with the theory of Papez, experimentation in recent years has shown that the limbic lobe is also, physiologically speaking, a common denominator of a variety of viscerosomatic and emotional reactions in the mammal. Furthermore, it has been found that the limbic lobe and its subcortical cell stations constitute a functionally integrated system which may be appropriately designated as *the limbic system* (for terminology see *EEG Clin. Neurophysiol.*, 1952, 4: 407–418).

The knowledge of these findings is arousing increasing interest in the limbic system among students of behaviour. But aside from its academic interest, the limbic system is of great immediate practical importance because of its bearing on epilepsy. Although foreseen in the observations of several workers of the last century, it remained for present-day electroencephalography to establish that epileptogenic foci within or neighbouring the limbic cortex of the fronto-temporal region are responsible for a large proportion of seizures now classified as psychomotor epilepsy. This common form of epilepsy has protean ictal and inter-ictal manifestations, but in line with experimental findings, it is to be emphasized that it reveals itself conspicuously in viscerosomatic and emotional disturbances.

On the basis of comparative studies, Broca and others gave emphasis to the close developmental relationship between the limbic lobe and the olfactory apparatus. As a result, the inference grew that the former was predominantly concerned with olfactory function. Indeed, by the turn of the last century, authors of some textbooks had extended the meaning of Turner's term rhinencephalon to apply to the entire limbic lobe and thereby established an authoritative precedent for a concept that has since been passed on from one generation to another. It was to discover whether or not there were justifiable anatomical grounds for such an assumption that led Cajal to undertake his studies of limbic structures. He presented much evidence to the contrary. Without the support of physiologic experiment, however, neither his arguments nor the evidence of other workers could counteract the weight of tradition in this respect.

The foregoing situation illustrates how necessary it is for anatomy and physiology to proceed hand in hand with one another. But of the two, physiology is probably the less able to walk alone. There can be no adequate understanding of the function of an organ without a precise knowledge of its structure. Cajal's studies of limbic structures are important not only because they are the work of one of the world's greatest anatomists, but also because they represent the most comprehensive and precise anatomical account of the limbic system system that is available.

There can be no doubt that the process of familiarizing onself with a difficult subject is greatly facilitated if one can become acquainted with it through the medium of one's own language. In 1951, I had the good fortune to interest Dr. Kraft in translating for me the series of Cajal's papers that is included in this volume. My colleagues and I found her splendid translation so continuously helpful that it seemed a pity it could not be shared with others interested in this field. In the summer of 1952, I wrote Dr. Fulton to this effect while he was in Europe. With his usual genius for action, he called on the publishers of this volume whose quick insight into the importance and timeliness of such a translation set the stage for its publication. I wish to join Dr. Kraft in expressing deep appreciation to them for all their efforts in this matter.

In turn, it remains for me to acknowledge especial gratitude to the Foundations' Fund for Research in Psychiatry, whose grant to me for the study of the functions of the limbic system has paid for the cost of photographing the illustrations that are reproduced in this volume. At the same time, I owe great thanks to Dr. Frederick C. Redlich for his long-continued interest in supporting research in this field and for what he has done to promote the publication of this book.

Finally, I wish to express my indebtedness to Dr. Kraft not only for this translation, but also for the added education I received from the word by word re-reading and working over of the various chapters with her while there was direct reference to the Spanish text. In a number of instances where the translation led to anatomical ambiguity, the matter of interpretation or choice of word sometimes rested on me, a situation that should forewarn the reader that any notable errors in this respect are in all likelihood not hers.

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Translator's Foreword

In 1951, in anticipation of the hundredth anniversary of the birth of Santiago Ramón y Cajal, it was decided to translate into English his papers concerning the limbic cortex. These may be found in the *Trabajos del Laboratorio de Investigaciones Biológicas de la Universidad de Madrid*, Tomo I, 1901–2, on pp. 1, 141, 159, and 189. Portions of them have been available in German translation for some time. In presenting this material in English, an attempt has been made to preserve, wherever possible, the historical qualities of the original publication. Thus, for example, modern neurologists (or at least the publishers of their works) would be loath to present a bibliography constructed along the lines that Cajal has done for the present first chapter; but it was felt that to formalize the references according to today's customs would not necessarily add anything of intrinsic value. On the other hand, readers who will compare the present work with the original will discover that the body of the text has been outlined more thoroughly as to section headings than was done by Cajal. This has been undertaken solely to aid the student in finding his way about in the "labyrinthine paths" of the cortex with a minimum of effort.

The translator is deeply grateful to the following: the Real Academia Nacional de Medicina, Madrid, and the Instituto Cajal of the Universidad de Madrid for permission to publish these papers in English; Dr. John F. Fulton for his very gracious help in seeing to this publication; Dr. Paul D. MacLean for his dedicated interest and his willingness to devote long hours in poring over the manuscript; the Foundations' Fund for Research in Psychiatry for its generous support in defraying the cost of photographing the illustrations; and the present publishers for their patience with, solicitude for, and co-operation in this endeavour.

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CHAPTER I

THE STRUCTURE OF THE OLFACTORY CORTEX OF MAN AND MAMMALS*

ACCORDING to most neurologists, the central olfactory system comprises two nerve stations or foci of nerve connexions: first, the primary centre, represented by the olfactory bulb; second, the secondary centres, consisting chiefly of the pyriform lobe, and in addition, the grey matter subjacent to the superior, internal, and external olfactory roots (grey substance of the bulbar peduncle, of the frontal lobe, of the olfactory tubercle, &c.). Finally, in the third place, according to many authors, tertiary, or terminal stations are also supposed to exist, the most important of which is Ammon's horn. But, as we shall see later, the acceptance of the existence of direct communicating pathways between the primary and secondary olfactory centres on the one hand, and Ammon's horn, the fascia dentata, septum lucidum, cingulate gyrus, supracallosal striae, &c., on the other, finds its way into the field of anatomical investigation with the greatest of difficulties.

A careful study comparing the structure, position, and connexions of these centres with the corresponding ones of the visual, tactile, and acoustic systems reveals that the primary station (olfactory bulb) is the homologue of the retina (not in its entirety, but only in the inner plexiform, ganglionic, and subsequent layers), the ventral and lateral acoustic nuclei in the medulla, and the ganglia of the columns of Goll and Burdach in the same region. The second station, or sphenoidal cortex, probably represents a cortical centre of projection or sensation (in the sense of Flechsig's theory). If this homology is acceptable, then in the central olfactory system (at least in the sequence and position found in the other systems) the intermediate or thalamic station is lacking. In the optic system this is formed by the external geniculate body and the pulvinar; in the

* This work forms a part of an extensive paper entitled, *The origins and terminations of the olfactory, optic, and acoustic nerves in vertebrates*, which was presented to the Royal Academy of Medicine of Madrid in application for the Martínez y Molina prize. The extreme delay in the printing of this monograph (the manuscript and figures were submitted in June of 1901) has compelled us (with the authorization of the Academy) to publish some of the first chapters at this time.

tactile, by the lateral thalamic ganglion[1]; and in the acoustic by the internal geniculate body[2]. Some authors have presumed that there are connexions between the secondary olfactory centres and the stria thalamica, or between the columna fornicis and the thalamus. These, even if they do exist (which is still debatable), cannot be regarded as centripetal intermediate thalamic stations, but rather as reflex centres from which centrifugal tracts arise.

The present study, a continuation of earlier work[3], will be concerned particularly with the structure of the secondary olfactory centre, or sphenoidal cortex. Nevertheless, in order to make this discussion complete, and to give the reader a cohesive picture of the parts of the central olfactory system, we shall also consider in summary the olfactory bulb, anterior commissure, interhemispheric cortex, Ammon's horn, and other centres and secondary tracts that presumably connect with those centres.

I. THE OLFACTORY BULB, OR PRIMARY STATION

Since it is our plan here, as we have outlined above, to present the essential structures of the olfactory bulb, we advise the reader, who so desires, to immerse himself in the histological details of this centre as found in the fundamental monograph of Golgi[4] and our own[5], as well as in those of P. Ramón[6], van Gehuchten and Martin[7], Kölliker[8], Retzius[9], Calleja[10], and Blanes[11], most of which are based on observations of chrome silver preparations.

As is known, the olfactory bulb is the terminus of the olfactory nerve fibres which are connected with the bipolar cells of the nasal mucosa. Their termini are situated throughout the bulbar contour, and accordingly, the structure of this region is practically identical in all its radii. Only in the superior plane, where the bulb encroaches

[1] CAJAL: Contribución al estudio de la via sensitiva central y estructura del tálamo óptico. *Rev. trim. microgr.* Vol. V, 1900.

[2] CAJAL: Die Endigung äusseren Lemniscus oder die secundäre akustische Nervenbahn. *Deutsche Mediz. Wochenschrift.* 17 April 1902.

[3] See: *Revista trimestral.* Vol. IV and V.

[4] C. GOLGI: *Sulla fina struttura dei Bulbi olfactorii.* Reggio-Emilia, 1875.

[5] S. R. Y CAJAL: Origen y terminación de las fibras nerviosas olfatorias. *Gaz. sanit. de Barcelona.* October 1890.

[6] P. RAMÓN: Estructura de los bulbos olfatorios de las aves. *Gaz. sanit. de Barcelona.* July 1890.

[7] VAN GEHUCTEN ET MARTIN: Le bulbe olfactif de quelques mamifères. *La Cellule.* Vol. V, no. 2, 1891.

[8] KÖLLIKER: Über den feineren Bau des Bulbus olfactorius. *Aus den Sitzungsber. der Würzb. Phys.-med. Gesellschaft.* 19 December 1891.

[9] G. RETZIUS: Die Endigungsweise der Riechnerve. *Biol. Unters.* Neue Folge. Vol. III, no. 3, 1892.

[10] CALLEJA: La región olfatoria del cerebro. Madrid, 1893.

[11] BLANES: Sobre algunos puntos dudosos de la estructura del bulbo olfatorio. *Rev. trim. microgr.* Vol. III, 1898.

on the cerebrum, does one observe a few minor variations in arrangement.

From without inward the bulbar cortex consists of the following layers: (1) zona nervosa, or superficial olfactory plexus; (2) zone of olfactory glomeruli; (3) peripheral plexiform zone; (4) zone of mitral cells; (5) internal or central plexiform layer; (6) layer of granules and bundles of white matter; and (7) epithelial, or ependymal layer.

1. Peripheral fibrillar zone

In carmine preparations this layer appears to be plexiform. In methylene blue and chrome silver sections it is seen to have small bundles of varicose and parallel, non-medullated fibres which cross each other in a complex fashion. It is thus like a felt hat extending over almost the entire bulb, particularly over the vertex and its lateral and inferior aspects. Between the bundles numerous large neuroglial cells are found whose long processes extend into the underlying layers.

2. Glomerular layer

Beneath the aforementioned fibrillar layer lies an irregular band consisting of two or more rows of egg- or pear-shaped masses called olfactory glomeruli. These are circumscribed islands of grey matter in which the olfactory fibres of the first zone end.

The following elements enter into the composition of each glomerulus: the terminal arborizations of the olfactory fibres; the dense tufts of dendrites coming from deeper zones; certain dwarf neurones; and finally, some neuroglial elements.

(a) **Terminal nerve arborizations.**—Golgi was the first to demonstrate the interglomerular ramifications of the olfactory fibres; but, still prejudiced by Gerlach's nerve networks, he believed that some of these branches leave the glomerulus and anastomose with collateral fibres coming from axons of neurones situated in deeper zones. Our own painstaking investigations in the bulb of various mammals have proved an important point, *viz.*, that the ramifications of the olfactory fibres end freely within the confines of the glomerulus without anastomosing therein nor ever connecting with fibres coming from deeper regions.

This basic fact about the structure of the olfactory bulb has been confirmed by van Gehuchten, Kölliker, His, Retzius, P. Ramón, Calleja, Lugaro, Blanes, and others.

The terminal arborizations of the olfactory fibres within the glomerulus are delicate, varicose, and complexly entangled. Nevertheless, it is possible to see that the final branches, after tracing labyrinthine paths, end by means of a free varicosity. When the glomerulus is completely and well impregnated, one observes therein a very dense plexus of nerve fibres in which there are empty clear areas corresponding to the dwarf neurones and neuroglial cells. This intraglomerular plexus is not formed by one fibre, but rather by a group or bundle of olfactory fibres (Fig. 2, *b*).

(b) **The dendritic tufts.**—The mitral cells, and other less deeply situated elements that we shall call tufted cells, send to the glomerulus a heavy protoplasmic trunk which ends therein by means of a graceful brush or feather composed of numerous diverging and varicose rami. These also end freely and insinuate themselves in the spaces left by the arborizations described above to establish intimate and multiple contact with them (Fig. 2, *c*).

According to the results of investigations by P. Ramón, Calleja, Catois, and others, a similar arrangement is seen in lower vertebrates, indicating that Nature, when she desires to insure the dynamic relationship between two neurones, exaggerates the number of contact points to the extreme by placing next to each other extensive and intricate nervous and protoplasmic ramifications. But since the axons of three, four, or more mitral or tufted cells enter each glomerulus, there to present their final arborizations, another interesting conclusion can be drawn: that the propagation of the nervous impulse is not individual, from neurone to neurone, but rather is collective, passing from a group of nerve fibres to a group of ganglionic cells.

(c) **Dwarf neurones.**—Within the glomeruli, as well as at their periphery, a few minute stellate elements are also found. Golgi believed them to be neuroglial in character, but their nervous significance, suggested some time ago by us[12], has recently been demonstrated by Blanes Viale. He has described them in excellent detail. These elements, which Kölliker has called external (or superficial) granules, are very small, spheroidal or polygonal, and sometimes pyriform in shape. From the cell body one or more delicate dendrites arise which branch profusely over the surface and cortex of the glomerulus; in addition, a very slender axon is given off that proceeds more or less horizontally through the interstices of the glomerulus to end by terminal branches. Since the dendrites may assault one or two glomeruli, the cells are called monoglomerular or biglomerular, designations which we owe to Blanes. Nissl preparations (Fig. 1) reveal the great abundance of these minute elements and show us that their preferred position is the internal contour and intercalary spaces of the glomeruli. Within the glomeruli

[12] CAJAL: *Origen y terminación de las fibras olfativas, &c.* 1890.

only two or three nuclei are found; these might very well belong to neuroglial cells.

In view of this description, the tiny intra- and peri-glomerular cells of Kölliker (superficial granules) seem to represent cells of intra-glomerular association, by virtue of which the stimuli received by their dendrites are transmitted from the area of one glomerulus to the terminal dendritic tufts found in more or less distant glomeruli. In this way conduction, and particularly diffusion of the olfactory impulses are afforded even greater insurance. Indeed, this diffusion of the impulse seems to have been one of the primary preoccupations of Nature in establishing the olfactory pathways.

(d) **Neuroglial cells.**—These are of two kinds: endogenous, or intraglomerular, represented by stellate cells having pinnate and curled branches; and exogenous, represented here by terminal tufts of neuroglial cells found in neighbouring zones.

3. Molecular, or external plexiform zone

All the layers situated below the glomerular zone are organizations of perfection and complexity peculiar to mammals and birds; they are lacking in fish and the Batrachia, or are found in the latter in considerably simplified form. This is not true of the glomeruli which retain their basic organization in all vertebrates.

One of these organizations of perfection is the plexiform zone concentric to the glomerular layer in which the following elements are prominent: accessory dendrites of the mitral cells and of the medium, peripheral tufted cells; the terminal tufts of the granules; and the recurrent collaterals of the axons of the tufted and mitral cells. The integration of these various parts, which we shall discuss again below, creates a dense mesh in the plexiform zone which is well defined in its internal and external boundaries, and in which parallel or concentric fibres outnumber the radial ones.

4. Zone of mitral cells

This zone is so called because it is composed of one, two, or three concentric rows of large, compressed, multipolar neurones among which the mitral form predominates; however, ovoid and triangular shapes are also abundant. With Nissl's stain the body of these cells manifests a huge nucleus with one or two nucleoli and with several chromatin granules that extend into the principal dendrite (Fig. 1, 4). Among the processes seen by means of chrome silver there are: first, a strong axis cylinder coming from the deep surface of the cell body and connecting with a nerve fibre of the subjacent zone; and second, two kinds of dendrites which we shall designate primordial and secondary (Fig. 2, *e*).

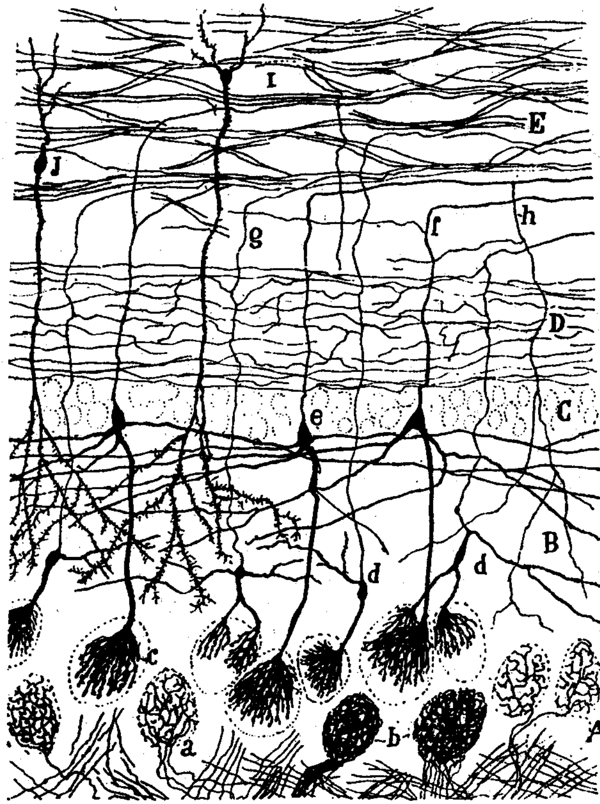

FIG. 2.—SECTION OF THE OLFACTORY BULB OF A NEWBORN CAT
A, glomerular layer; B, external plexiform layer; C, layer of mitral cells; D, internal plexiform layer; E, granular layer and white matter; *a*, terminal arborization of an olfactory fibre; *b*, glomeruli with several endings; *c*, tuft of a mitral cell; *d*, tufted cells.

The primordial dendrite, so called because it is present even in lower vertebrates and can actually be regarded as the earliest process to appear, is robust, smooth in outline, radial or peripheral in direction, and almost always single (in man and the gyrencephalic mammals). In birds, reptiles, and fish, as my brother has shown, they are often multiple; sometimes as many as four, six or more are present. In its path to the periphery this process frequently follows an oblique direction, maintains its original diameter without sending forth collaterals (except rarely), and ends in the interior of a glomerulus by a brush or tuft of free rami in intimate contact with the arborizations of the olfactory fibres as we have shown above.

The accessory dendrites are two, three, or more in number. They arise from the sides of the cell body, but sometimes from the origin of the primordial dendrite, and, dividing repeatedly, proceed to the substance of the external plexiform zone. There they unite with the processes of other cells forming the dense plexus which we mentioned earlier. Some of these dendrites are so long that they may extend as far as 0·1 mm. The final branches end freely within the plexiform layer without ever reaching the glomerular boundary.

In mentioning the plexiform zone, we stated that within it are found certain minute elements which we have designated tufted cells because they all have in common two features: a strong peripheral dendrite terminating in a tuft, and entrance into the olfactory glomeruli like the processes of the mitral cells. In Fig. 1 we have reproduced some of these elements. According to their position, they are appropriately differentiated into: internal (*c*), which remain in the plexiform zone; external (*b*), which are found at the periphery and extend to the vicinity of the glomeruli; and interstitial, which rest between the glomeruli themselves in the midst of the superficial granules (Fig. 1, *a*). The circumference of these elements decreases from within outward so that those situated near the mitral cells are almost of the same size as the latter, while the interstitial or interglomerular ones (Fig. 1, *a*) have the smaller circumference. All these ovoid, fusiform, or triangular cells have, in addition to the glomerular process, one, two, or more dendrites branching in the plexiform layer, as well as a delicate central axon that reaches the deep bulbar regions, there to turn and continue as a nerve fibre of the granular layer. Nissl preparations show that the protoplasm of the tufted cells, particularly of the external ones, contains large chromatin granules that often extend the length of the principal dendrite.

5. Internal plexiform layer, or layer of the nerve collaterals

Within the row of mitral cells one sees a narrow band, plexiform in appearance and poor in cells. Most of the collaterals of the axons of the tufted cells, as well as certain centrifugal ramifications, are concentrated here. We shall say more about its composition later.

6. Layer of granules and of bundles of white matter

Within the internal plexiform layer a broad area extending to the ependymal region begins. At the very first glance it is seen to have two distinct formations: the granules, which are small fusiform and globular cells, and the concentric bundles of white matter.

(a) Granules.—Golgi was the first to call the attention of neurologists to the existence in the olfactory bulb of some small cells, ovoid, fusiform, or triangular in shape, which are radially directed and provided with one central and several peripheral dendritic processes, none of which possesses the attributes of an axon or axis cylinder. After we had confirmed the absence of the axon (in which respect these cells are comparable to the spongioblasts or amacrine cells of the retina), we showed that the peripheral process of these elements is constant in its orientation and connexions; it is always

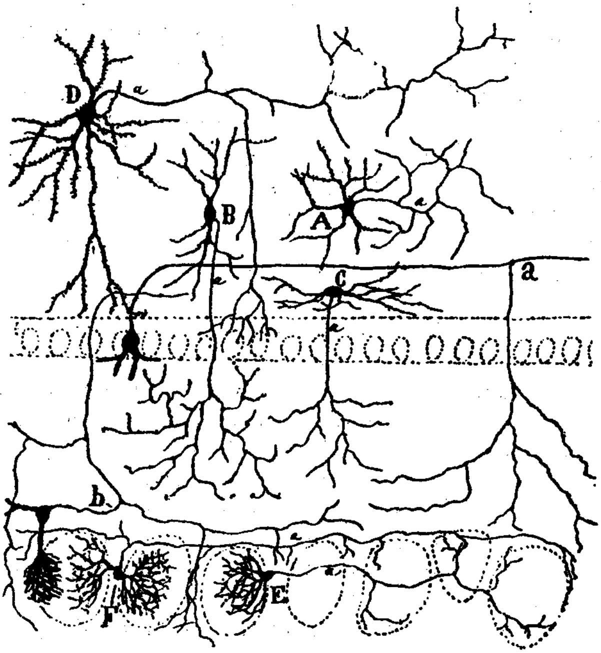

FIG. 3.—SHORT AXON CELLS OF THE OLFACTORY BULB. DRAWING CONSTRUCTED FROM OUR FIGURES AND FROM THOSE OF BLANES

A, Golgi cell; B, cell of peripheral axon; C, horizontal fusiform cell of the internal plexiform zone; D, cell of horizontal axon; E and F, periglomerular nerve cells; *a*, peripheral collateral of the axon of a mitral cell; *b*, collateral of the axon of a tufted cell.

directed toward the plexiform zone where it terminates by means of a tuft of spinose dendrites in contact with the secondary dendrites of the mitral cells (Fig. 2, *J*).

Recently Blanes, in addition to confirming this opinion, has triumphantly refuted the viewpoint of Kölliker who, relying solely on the similarity between these granules in their embryonic phases and epithelial or ependymal cells, considered them to be a kind of neuroglial cell.

Actually, as Blanes states, it is impossible to confuse these cells with neuroglia for the following reasons:

First, Ehrlich's method, which never stains the neurogliae, impregnates the granules of the olfactory bulb perfectly.

Second, the cell body is smooth, very small, and its long processes are covered with delicate short spines, whereas the body of the neuroglial cell, or of a displaced epithelial cell, is large, rich in protoplasm, and appears to be bristling with long, numerous, curly processes.

Third, the granules appear identical or very similar in all vertebrates, even in those where true neuroglial cells do not exist and where the epithelial or ependymal cells form the only supporting structure for the bulbar ventricle.*

Fourth, in the morphology of the nucleus, too, the granular cell differs from the neuroglial cell. Instead of containing, like them, a pale nucleus with a peripheral chromatin network, it has a dark nucleus wherein the chromatin is deposited in a heavy central network and in which one or more large nucleoli are found.

Even though the granules are seen singly or are scattered here and there through the layers of the white matter and in the internal plexiform zone, most of them group to form rows, islands, or clusters separated from each other by bundles of white matter (Fig. 1, 6). Nissl preparations reveal a heavy layer of granules above the mitral cells (Fig. 1, 4).

Of the polar dendrites, or processes, of the granules, the external one is thick, almost always single, and, as we have already said, proceeds to the external plexiform zone. The internal process, on the other hand, is frequently double or triple, thinner and shorter, and soon ends in a tuft of few branchlets in the interstices between the nerve fibres (Fig. 2, *J*, *I*).

The absolute constancy of the connexions between the terminal tufts of the granules' peripheral processes and the plexus of horizontal dendrites coming from the mitral cells and extending in the external plexiform layer leads us to believe that the granule, whose body and internal branches are related to centrifugal fibres, transmits some special stimulus to the mitral cells. If not morphologically characteristic, the peripheral processes might still be dynamic and functional, since the nervous impulse travels within them in a cellulifugal direction just as in true axons.

(b) **Short axon nerve cells.**—Scattered sparingly here and there in this zone a few stellate or fusiform neuronal elements are found.

* The absence of the axon is a property noted by all authors. Hill, however, ventured to contradict this viewpoint, thereby committing an error which Blanes correctly refuted. See Hill: Notes on granules, *Brain*, 1897.