# COMPARATIVE STUDY OF THE SENSORY AREAS OF THE HUMAN CORTEX, PP. 311-382

Published @ 2017 Trieste Publishing Pty Ltd

ISBN 9780649349944

Comparative study of the sensory areas of the human cortex, pp. 311-382 by Santiago Ramón y Cajal



Edited by Trieste Publishing Pty Ltd.
Cover @ 2017

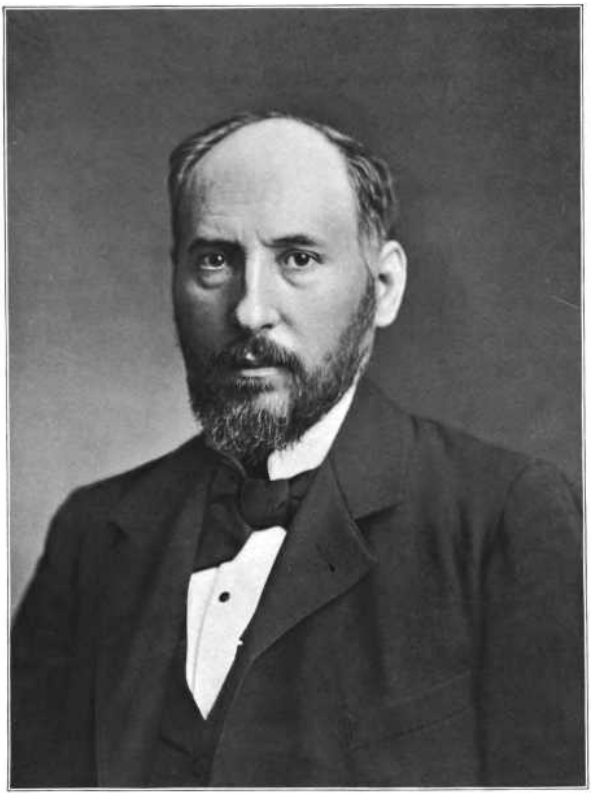


www.triestepublishing.com

SANTIAGO RAMÓN Y CAJAL

# COMPARATIVE STUDY OF THE SENSORY AREAS OF THE HUMAN CORTEX, PP. 311-382

Trieste



S. Ramon Cajal

# COMPARATIVE STUDY OF THE SENSORY AREAS OF THE HUMAN CORTEX.

By Santiago Ramón y Cajal.

In order to respond worthily to the gracious invitation with which Clark University has honored me, I ought to offer you, as was my original intention, a work of synthesis, a general summary of the present state of our knowledge of the minute anatomy of the nervous system. Unfortunately, the duties of my professorship, every day more pressing, have deprived me of the time necessary for the accomplishment of such a task, and have compelled me to moderate my ambition, and to limit it to presenting to you a modest analytical contribution to our knowledge of the microscopical structure of the sensory centres of the human cerebral cortex, a subject to which I have devoted the leisure of the past months.

This subject is so vast and so difficult that, in spite of my efforts and the time devoted to it, I have been able to clear up only a few points. Consequently, my contribution will be, to my utmost regret, a very incomplete one, treating, as it does, only the visual cortex as I have made it out in man and some of the higher mammals. I shall add, however, a few observations on the structure of other sensory regions.

This anatomical study of the sensory areas of the cortex, at the present state of our knowledge, presents points of special interest, since, as you well know, neurologists who have interested themselves in the histology of the brain are divided at present into two camps, the unicists and the pluralists.

The unicist doctrine, proclaimed by Meynert and reaffirmed quite recently by Golgi and Kölliker, supposes that all regions of the cortex possess essentially the same structure, functional diversity being due to diversity of origin of afferent or sensory nerves. This amounts to saying that cerebral specific energy of nerves is the necessary effect of the partic-

ular organization of each sense as well as of the special character of the stimuli received by the peripheral sensory surfaces, skin, retina, organ of Corti, etc.

The pluralist doctrine, upheld recently by Flechsig, without rejecting the particular influence of connections with different nerves, maintains that diversities of function result also from the particular structure of each cortical area.

It is this latter opinion, as we shall presently see, that presents a closer agreement with the observed facts. In fact, my researches tend to prove that the topographical specialization of the brain depends not only on the quality of the stimuli analyzed and gathered up by the sensory mechanisms, but also on the structural adaptations which the corresponding cerebral areas undergo; since it is very natural to suppose, even if one were to form an *a priori* judgment, that the cortical areas connected with the spacial senses sight and touch, which form exact images of the exterior world with fixed relations of space and intensity, have by accommodation to the stimuli received an organization different from that existing in cortical areas attached to the chemical senses of taste or smell, and from that which is appropriate to the chronological sense hearing, which gives only relations of succession, free from every spacial quality.

We may add that if there exist in the human cerebral cortex, as Flechsig supposes, besides the sensori-motor centres, other regions, association centres, characterized by absence of direct sensory or motor connections, it seems very natural also to associate to these important regions of the brain, with which are connected the highest activities of psychic life, a special organization corresponding to their supremacy in the hierarchy of functions.

But we must not carry to an extreme the structural plurality of the brain. In fact, our researches show that while there are very remarkable differences of organization in certain cortical areas, these points of difference do not go so far as to make impossible the reduction of the cortical structure to a general plan. In reality, every convolution consists of two structural factors: one, which we may call a factor of a general order, since it is found over the whole cortex, is represented by the molecular layer and that of the small and large pyramids; the other, which we may call the special factor, particularly characteristic of the sensory areas, is represented by fibre plexuses formed by afferent nerve fibres and by the

presence at the level of the so-called granular layer of certain cell types of peculiar form.

But, before proceeding to outline the general conclusions of an anatomico-physiological order, that result from all our researches taken together, permit me to present very briefly the facts of observation.

## Visual Cortex.

The minute anatomy of the visual cortex (region of the calcarine fissure, sulcus cornu lobulus lingualis) has been already explored by several investigators, among whom we may make particular mention of Meynert, Vicq d'Azyr, Gennari, Krause, Hammarberg, Schlapp, Kölliker, *et al.* But their very incomplete researches have been performed by such insufficient methods as staining with carmine, the Weigert-Pall method, or that of Nissl with basic anilines — methods which, as is well known, do not suffice at all to demonstrate the total morphology of the elements and the organization of the most delicate nerve plexuses. They led, however, in spite of the difficulties which stood in the way of these first analytical attempts, toward a precise differentiation of the visual cortex from other regions of the brain. At the outset two characteristic differences attracted the attention of the first investigators into the structure of the visual cortex: first, the existence of a very thick stratum of granules, subdivided into accessory strata by laminæ of molecular appearance; and, second, the presence in the intermediate layers of the cortex of a white lamina formed of medullated fibres — which lamina may be seen with the unaided eye. This lamina, appearing in cross-section as a white line, has been named, in honor of the writers who first described it, the line of Gennari or Vicq d'Azyr.

For the sake of brevity, we shall omit a detailed description and discussion of the various layers admitted by the authorities on this region; suffice it to mention in order the eight layers described by Meynert for the human cortex: First, molecular; the second, layer of small pyramidal cells; third, layer of nuclei or granules; fourth, layer of solitary cells; fifth, layer of intermediate granules; sixth, layer similar to the fourth, containing nuclei and scattered cells; seventh, deep nuclear layer; eighth, layer of fusiform cells. We may also mention the arrangement of layers recently described by Schlapp for the occipital cortex of the monkey: (1) layer of tangential fibres; (2) layer of exter-


nal polymorphic cells; (3) layer of pyramidal cells; (4) layer of granules; (5) layer of small solitary cells; (6) second layer of granules; (7) layer poor in cells; (8) layer of internal polymorphic cells.

The investigations which I have made on the human cortex as well as on that of the dog and cat, by both the Nissl and Golgi methods, have led me to distinguish the following layers: —

1. Plexiform layer (called molecular layer by authors generally and cell-poor layer by Meynert).
2. Layer of small pyramids.
3. Layer of medium-sized pyramids.
4. Layer of large stellate cells.
5. Layer of small stellate cells (called layer of granules by the authors).
6. Second plexiform layer, or layer of small pyramidal cells with arched axon.
7. Layer of giant pyramidal cells (solitary cells of Meynert).
8. Layer of medium sized pyramidal cells with arched ascending axon.
9. Layer of fusiform and triangular cells (fusiform cell layer of Meynert).

You see that we have modified current nomenclature by introducing terms which call to mind cellular morphology. For we believe that such trite expressions as "molecular layer," "granular layer," must be

FIG. 1. — Vertical section of the visual cortex of man, calcarine sulcus, stained by Nissl's method — semischematic. 1. Plexiform layer. 2. Layer of small pyramids. 3. Layer of medium-sized pyramids. 4. Layer of large stellate cells. 5. Layer of small stellate cells. 6. Second plexiform layer, or layer of small pyramids with arched axon. 7. Layer of giant pyramids. 8. Layer of medium-sized pyramidal cells with ascending axon. 9. Layer of fusiform and triangular cells.

banished once for all from scientific language, and they must be replaced by terms which point out dominant morphological characters in the nerve structures of each layer or some interesting peculiarity relative to the course and connections of the axis cylinder processes. The number of layers could be easily increased or diminished, because they are not separated by well-marked boundaries, particularly in Nissl's preparations. Thus the number of layers which I adopt is somewhat arbitrary. By distinguishing, however, nine layers, I have followed a criterion of individualization which seems to me the most convenient and suitable for my exposition of the cortex as a mechanism composed of elements at a certain level which differ in special morphological features from those of neighboring levels. Besides, the number, extent, and size of cells in these layers vary a little in the different median occipital convolutions, as does also the degree of definite nidification, according as we study the convex or concave aspect of the gyri. Our description relates generally to the cortex of the margin of the calcarine fissure, the region where structural differentiation of the visual cortex is most pronounced.

### Plexiform Layer.

The plexiform or molecular layer is one of the oldest cerebral formations in the phylogenetic series. It presents characters similar to those of the human cortex in all vertebrates except the fishes. This has been fully demonstrated by the researches of comparative histology undertaken by Oyarzun (batrachia), by myself (batrachia, reptilia, and mammalia), by my brother (batrachia, reptilia), by Eddinger (batrachia, reptilia, aves), by Cl. Sala (aves). In the visual cortex of man, the structure of this layer coincides perfectly with that which my own researches, as well as those of G. Retzius, have revealed in the motor region. The only modification which may be noted, visible even by Nissl's method, is its notable thinness in the margins of the calcarine fissure (except in the sulci, and here it appears somewhat thinned). This diminution in thickness, noted by authors generally, depends probably on the small number of medium-sized and giant pyramidal cells in the underlying layers, because it is well known that each pyramidal cell is represented in the plexiform layer by a spray of dendrites. A similar opinion has been expressed by Bevan Lewis in order to explain irregularities in thickness of this layer in different regions of the cortex