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Review

How Camillo Golgi became "the Golgi"

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ABSTRACT

On April 1898 Camillo Golgi communicated to the Medical–Surgical Society of Pavia, the discovery of the "internal reticular apparatus", a novel intracellular organelle which he observed in nerve cells with the silver impregnation he had introduced for the staining of the nervous system. Soon after the discovery it became evident that this cellular component, which was also named the "Golgi apparatus", was a ubiquitous structure in eukaryotic cells. However the reality of the organelle was questioned for years and many cytologists considered the internal reticular apparatus as an artefact due to the fixation and/or metallic impregnation procedure. The controversy was finally solved in the mid-1950s by electron microscopy when the Golgi apparatus definitely acquired its dignity of being a genuine cell organelle. The designation of "Golgi complex" entered officially in the literature in 1956. Both the terms Golgi apparatus and Golgi complex are currently interchangeable. However a quick "the Golgi" and the introduction of Golgi in adjectival form are now prevalent in the blooming scientific literature on the organelle. Thus Camillo Golgi underwent his final transformation and, becoming the eponym of the organelle he had discovered, he found a way to immortality.

1. Black silhouettes

At the end of the nineteenth century Camillo Golgi, professor of General Pathology and Histology at the University of Pavia, was already internationally famous for his discoveries on the structure of the central nervous system and for his descriptions of the human malaria parasites development in the human blood [1].

Graduated in Pavia in 1865, he was trained in microscopy by Giulio Bizzozero, a Rudolf Virchow's pupil and one of the pioneer of cell biology in Italy [2]. In 1873, while he was chief physician in a hospital for chronic patients at Abbiategrasso not far from Milan, Golgi developed a method, the "black reaction" (known nowadays as the Golgi stain or the Golgi impregnation), which allowed for the first time a full view of a single nerve cell. This histological method, which is widely still in use, was based on hardening blocks of nervous tissue in potassium dichromate, followed by impregnation with silver nitrate. The final result was a precipitation of silver chromate, filling the nerve cell body and its prolongations, which could be followed and analyzed even at a great distance from the cellular soma. Thus the black silhouette of the nerve cell appears in all its morphological complexity with all its ramifications (see Fig. 1).

The great advantage of this technique is that, for reasons that are still unknown, the precipitate of silver chromate randomly but selectively stains in black only a small proportion of nerve cells (usually from 1% to 5%), and completely spares the others allowing the individual elements to emerge from the nervous puzzle.

The discovery of the "black reaction" provided the spark to a truly scientific revolution which allowed the morphology and the basic architecture of the cerebral tissue to be evidenced in all its complexity, thus contributing to the foundation of the modern neurosciences.

Aided by his black reaction method, Golgi described the complex arborisation of the dendrites, discovered the branching of the axons, analyzed several regions of the nervous system in detail and provided beautiful illustrations of them. Among the remarkable Golgi's descriptions of different brain regions, particularly important were those of the cerebellum (where he described the so called "Golgi cells"), the olfactory bulb, the hippocampus, and the cerebral cortex. Taken together these investigations provided a remarkable contribution to the advancement of the knowledge on the structural organization of the nervous system.

Meanwhile he began to elaborate a general anatomic-physiological theory of brain organization, the "diffuse nervous net", according to which the ramified axons were connected (through direct fusion or intimate contact) in a diffuse network along which the nervous impulse propagated. Actually, it dealt with an illusory network which resulted from a mistaken microscopic image created by superimposition and by interlocking of the axons of the diverse cells. Towards the end of the nineteenth century this concept

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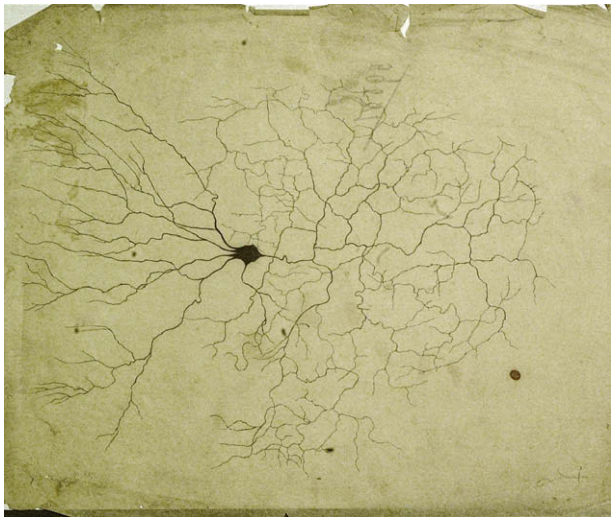

Fig. 1. Nerve cell stained with the black reaction. Drawing preserved with Golgi's papers, Museum for the History of the University of Pavia.

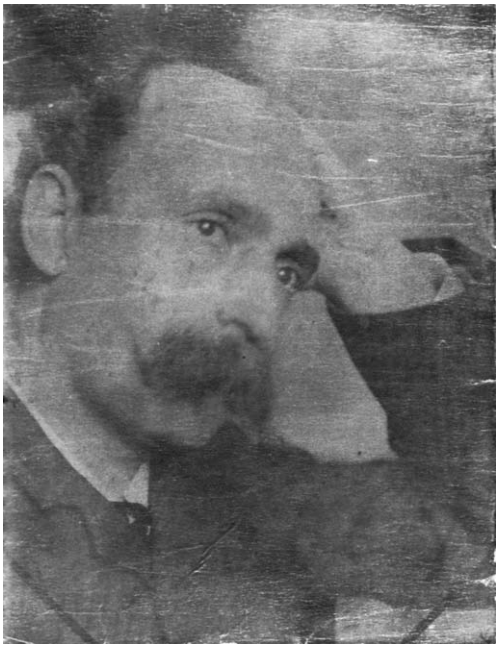

Fig. 2. Camillo Golgi around 1890. Museal System – University of Pavia.

developed in polemical opposition to the neuron theory championed by the Spanish histologist Santiago Ramón y Cajal which affirms that the nervous system is anatomically and functionally composed of individual cells, like any other tissue, and that nerve cells act to each other through points of contact subsequently named synapses by the British neurophysiologist Charles Scott Sherrington.

Since the development of the black reaction in 1873, Golgi continued to modify the chemical and physical parameters of the reagents in order to improve the selectivity and the reproducibility of the method under standard condition. The goal was however never completely reached since an element of randomness remained, and still remains, in the Golgi stain. However by 1885, Golgi was able to describe in his book *Sulla fina anatomia degli organi centrali del sistema nervoso* (*On the fine anatomy of the central organ of the nervous system*) some modifications and variants of the black reaction [3]. Particularly important was the introduction of a osmium-dichromate solution as the first immersion step of the reaction which allowed a fast staining of the nerve cells (the so called rapid variant of the method).

Very interested in infectious diseases and concerned about public health, between 1886 and 1892 Golgi temporarily abandoned neurobiological research and concentrated on studying human malaria (see Fig. 2). Not only he did worked out the cycle of development of the malaria parasite *Plasmodium* in the red blood cells, but he also discovered the temporal coincidence between the recurrent fever of the infection, and the multiplication of the parasite in human blood. Between 1893 and 1896 Golgi was mainly involved in academic and administrative commitments as elected rector of the University of Pavia. However he never lost his interest for the nervous system. In 1897 he returned in the laboratory to perform original research and started an investigation on the structure of the spinal ganglia. The topic was at the centre of Golgi's attention since the T shape of the spinal ganglion cells seems to contradict the "law of dynamic polarization" of Santiago Ramón y Cajal and Arthur van Gehuchten, one of the theoretical basis of the neuron theory.

2. A fine and elegant network hidden within the cell body

During this research Golgi noticed the occurrence of a strange reticular structure, hidden in the cytoplasm of the nerve cell body,

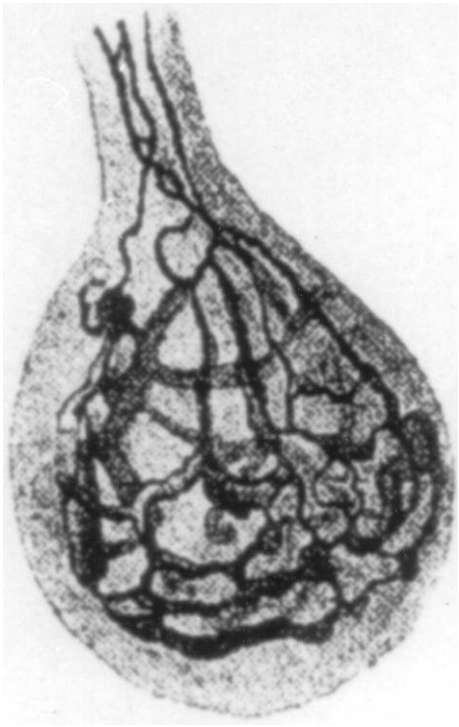

Fig. 3. First published illustration of the Golgi Apparatus. From Ref. [5].

which was clearly detached from the membrane and from the nucleus. Unfortunately this bizarre new formation was not constantly stainable. But Emilio Veratti (who in 1902 went on to describe the sarcoplasmic reticulum [4]), working in Golgi's laboratory, was able to replicate and confirm the findings in the cell body of the fourth cranial nerve. Golgi then persevered in his neurocytological research and was able to obtain very good and reproducible impregnation of the intracellular apparatus in the cell body of the Purkinje cerebellar cells of the owl *Tyto alba* (see Fig. 3).