

PROLOGUE TO THE NEW ENGLISH EDITION

The retina of vertebrates

Nicolás Cuenca & Pedro de la Villa

The figure of Santiago Ramón y Cajal and his work on the organization of the nervous system and the Neuron Theory are widely recognized. His monumental work fully justifies his well-deserved title as the founder of modern neuroscience.¹ More than a century has passed since Santiago Ramón y Cajal completed his extraordinary studies on the vertebrate retina, yet his observations remain among the most accurate and visionary in the history of neuroscience. It was in the retina—a delicate, layered tissue at the back of the eye—that Cajal found both a scientific muse and an ideal model for revealing universal principles of neural organization. Cajal considered the retina an ideal model for understanding the organization of the nervous system and the transmission of nerve impulses. From his studies, he showed that visual signals pass from rods and cones to bipolar cells and then to ganglion cells. His investigations of the avian retina^{2,3} demonstrated that nerve cells connect individually, without forming continuous networks, through contacts between axon terminals and the dendrites or cell bodies of other neurons. These observations provided strong support for the Neuron Theory, which established that the nervous system is composed of individual cellular elements later called neurons. These findings contradicted the prevailing Reticular Theory concerning the general organization of the nervous system.⁴⁻⁵

¹ Ramón y Cajal, S.: *Textura del sistema nervioso del hombre y los vertebrados*, Madrid, Moya, 1899–1904.

² Ramón y Cajal, S.: “Estructura de la retina de las aves”, *Revista Trimestral de Histología Normal y Patológica*, 1 (1888): 11–16.

³ Ramón y Cajal, S.: “Sur la morphologie et les connexions des éléments de la rétine des oiseaux”, *Anatomischer Anzeiger*, 4 (1889): 111–121.

⁴ Gerlach, J.: “Von dem Rückenmark”, in *Stricker’s Handbuch der Lehre von den Geweben*, Leipzig, Engelmann, 1871, pp. 665–693.

⁵ Golgi, C.: “La rete nervosa diffusa degli organi centrali del sistema nervoso. Suo significato fisiologico”, *Archives Italiennes de Biologie*, 15 (1891): 434–463.

Inspired by the retinal organization, Cajal also formulated the principle of dynamic polarization, proposing that information flows from dendrites and the cell body toward the axon terminal. Following this idea, he not only depicted neurons and their connections in extraordinary detail, but also used arrows to indicate the direction of signal transmission, anticipating the pathways of visual information processing.

His studies on the structural organization of the retina, together with the almost prophetic predictions he made about its functions, became the foundation of retinal neuroanatomy, neurophysiology, and neuropathology. The general organizational scheme of the retina proposed by Cajal remains fundamentally valid, and in many respects his studies continue to be relevant today. His descriptions of the different retinal cell types across species, and of the ways in which these cells are interconnected, remain among the most remarkable and comprehensive ever produced.

Cajal originally published his monograph *La rétine des vertébrés* in French in 1892, in the Belgian journal *La Cellule*.⁶ Two years later, in 1894, Richard Greeff issued a German translation, *Die Retina der Wirbeltiere*, thereby introducing Cajal's work to a broad German-speaking community of anatomists and ophthalmologists.⁷ Much later, in 1972, Sylvia Thorpe and Mitchell Glickstein produced the first book-length English translation, *The Structure of the Retina*, based largely on Greeff's German edition.⁸ In the same period, Robert W. Rodieck included an independent English translation from the original French as an appendix to his volume *The Vertebrate Retina*, making Cajal's text accessible to another generation of anglophone readers.⁹ More recently, in 2021, a new Spanish translation—prepared directly from the original French edition by Nicolás Cuenca and Pedro de la Villa—made Cajal's work once again accessible to Spanish-speaking readers, offering the most complete and faithful version of *La retina de los vertebrados* published to date.¹⁰ This new English edition seeks to bring his insights to today's

⁶ Ramón y Cajal, S.: "La rétine des vertébrés", *La Cellule*, 9 (1892): 119-257.

⁷ Greeff, R.: *Die Retina der Wirbelthiere*. Wiesbaden, J. F. Bergmann Verlag, 1894.

⁸ Ramón y Cajal, S.: *The structure of the retina*, Charles C. Thomas Publisher, Illinois, 1972. Translated by Sylvia Thorpe and Mitchell Glickstein.

⁹ Rodieck, R. W.: *The Vertebrate Retina*. Freeman and Company, San Francisco, 1973.

¹⁰ Ramón y Cajal, S.: *La retina de los vertebrados*, 1st ed., eds. Nicolás Cuenca y Pedro de la Villa. CSIC. Madrid, 2021.

researchers in visual sciences, for whom the original works, published in French, German, and later in English, are now rare or inaccessible.

Cajal recognized early on that the retina was uniquely suited for uncovering the architecture of the nervous system. Using the Golgi method,¹¹ he produced drawings of individual neurons so precise that he could trace their full morphology, determine their synaptic relationships, and propose organizational principles that remain foundational today. However, beyond its scientific value, the retina held for Cajal a deeply personal significance. In his memoirs he confessed that the retina had been “the oldest and most persistent of my laboratory loves”, a tissue whose elegance and complexity captivated him from the beginning of his career. He believed that no other structure revealed its mysteries with such generosity, nor rewarded careful observation with such clarity. For Cajal, the retina was not merely an object of study — it was a lifelong intellectual companion, the place where his curiosity flourished and where many of his most revolutionary ideas first took shape.¹²

Among Cajal’s most important contributions to retinal science were:

- The confirmation of the Neuron Doctrine.
- The principle of dynamic polarization.
- The detailed classification of retinal cell types.
- The coining of the term “amacrine cells.”
- The demonstration of laminar organization.
- The proposal of convergence and divergence in retinal circuits.
- The pioneering description of Müller glia in several species.
- Early hypotheses on development and axonal guidance.

These discoveries, many made decades before tools existed to test them fully, demonstrate the depth of Cajal’s analytical imagination. His interpretations —some speculative, many prophetic— laid the conceptual groundwork for the modern fields of retinal development, synaptic physiology, and neural circuitry.

Importantly, *La rétine des vertébrés* has become one of the most cited and enduring works in the entire field of vision science. Yet, despite its profound

¹¹ Golgi, C.: “La rete nervosa diffusa degli organi centrali del sistema nervoso. Suo significato fisiologico”, *Archives Italiennes de Biologie*, 15 (1891):434–463.

¹² Ramón y Cajal, S.: *Recuerdos de mi vida*, Moya, Madrid, 1917.

influence, it is today almost impossible to read: the original editions are long out of print, scattered across archives, and seldom accessible to researchers.

For researchers who study the retina —whether in anatomy, physiology, development, clinical ophthalmology, or computational neuroscience— it remains essential reading. Its relevance has not diminished with time; rather, it continues to shape how visual circuits are conceptualized and how new discoveries are interpreted in the broader context of neural organization.

This volume also highlights another remarkable aspect of Cajal's legacy: the profound integration of science and art. His drawings of retinal neurons, made from preparations of numerous vertebrate species, are not only scientifically precise but artistically exquisite. They reveal a mind that observed, in equal measure, rigor and aesthetic sensitivity. By juxtaposing Cajal's original illustrations with modern micrographs, this edition invites readers to appreciate how observation, intuition, and artistic skill can together illuminate the hidden architecture of the nervous system.

In this volume, we present a newly prepared English edition together with high-quality reproductions of Cajal's original drawings, photographed from the preserved preparations at the Cajal Institute. Alongside these historical images, we include contemporary micrographs of retinas from multiple vertebrate species, enabling readers to compare the pioneering observations of the late 19th century with the views afforded by today's advanced imaging techniques.

This book is offered especially to students and early-career scientists. Cajal believed deeply in the creative power of youth, insisting that progress in science depends on fresh perspectives unrestrained by rigid dogma. His own journey—from modest beginnings to a Nobel Prize—reminds us that discovery springs not from resources alone but from curiosity, perseverance, and an unwavering commitment to observe nature carefully.

We hope that this edition inspires readers to look, as Cajal did, with both precision and wonder. The retina, which he once called “a true nervous center, exquisitely adapted for histological analysis”, continues to shape our understanding of how the brain constructs meaning from light. May his observations guide new generations in their efforts to reveal the hidden logic of neural circuits and the profound beauty of the visual system.



Commemorative medal of the XIV Concilium Ophthalmologicum, held in Madrid in November 1933.

This volume, from Editorial CSIC, is an English translation of the version of *La rétine des vertébrés* published in 1933 on the occasion of the XIV Concilium Ophthalmologicum, as this is the most complete version.¹³ The organizing committee of this congress decided to publish this monograph “in view of the demands of numerous colleagues who have long wished to own this classic work, which marks a historic era in the structure of the retina”. This work was updated by Cajal himself, who inserted into the text some schematic drawings taken from works subsequent to the original. We also include a chapter on *The Histophysiological Problems of the Retina*,¹⁴ published in the *XIV Concilium Ophthalmologicum*. In this previously unpublished work, he speculates imaginatively, on the basis of his anatomical studies, about the functions of retinal cells and the possible significance of their connections, since physiological techniques and studies were still very limited at that time.

Finally, to further enrich this volume, we have decided to include unpublished images of retinal cells taken by us from Cajal’s original preparations,

¹³ Ramón y Cajal, S.: *La rétine des vertébrés*, XIV Concilium Ophthalmologicum, Madrid, 1933, Tomo II-3: 1-144.

¹⁴ Ramón y Cajal, S.: *Los problemas histofisiológicos de la retina*, XIV Concilium Ophthalmologicum. Madrid, 1933, Tomo II-2: 1-8.

which we have had the opportunity to photograph thanks to the generosity of the Cajal Institute of the Spanish National Research Council. We would also like readers to be able to compare the images from the original preparations made by Cajal more than a century ago with the images obtained using current microscopy techniques. To this end, we have also included some of our own photographs of the retina of different vertebrate species (www.retinalmicroscopy.com). Finally, to further enrich this volume, we have decided to include unpublished images of retinal cells taken by us from Cajal's original preparations, which we have had the opportunity to photograph thanks to the generosity of the Cajal Institute of the Spanish National Research Council. We would also like readers to be able to compare the images from the original preparations made by Cajal more than a century ago with those obtained using current microscopy techniques. To this end, we have also included some of our own photographs of the retina from different vertebrate species (www.retinalmicroscopy.com). In addition, we have incorporated ten plates featuring Cajal's original drawings illustrating key aspects of retinal organization and function, including the visual pathways, the processing of visual information within the retina, the diversity of retinal cell types, comparative anatomy, retinal development, and the connections between the retina and the brain. These plates provide readers with a unique opportunity to appreciate both the remarkable scientific insight and the extraordinary artistic quality of Cajal's work, while highlighting its enduring relevance to contemporary visual neuroscience.