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Miguel A. Merchán and the Cajalian influence: Pioneering auditory neuroscience in Spain

Enrique Saldaña[a,b,c,*], Fernando de Castro[d], Dolores E. López[a,b,c], Manuel S. Malmierca[a,b,c]

[a] Neuroscience Institute of Castilla y León (INCyL), University of Salamanca, Salamanca, Spain
[b] Department of Cell Biology and Pathology, Medical School, University of Salamanca, Salamanca, Spain
[c] Institute of Biomedical Research of Salamanca (IBSAL), Salamanca, Spain
[d] Instituto Cajal, Consejo Superior de Investigaciones Científicas (CSIC), Madrid, Spain

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ABSTRACT

This article traces the history of auditory neuroscience in Spain. It begins with the pioneering contributions of Santiago Ramón y Cajal, who meticulously described the organization of every region of the auditory system, from the cochlea to the cerebral cortex. His legacy continued with his disciples, Rafael Lorente de Nó, who conducted a detailed study of the cochlear nuclei, and Fernando de Castro, who later passed the baton to Jaime A. Merchán. Jaime Merchán revitalized Spanish auditory neuroscience and mentored his brother Miguel, whose contributions receive special focus.

Starting in the early 1980s, Miguel A. Merchán's pioneering research has profoundly expanded our understanding of the structure and connectivity in the central auditory system. His collaborations, both within Spain and internationally, have played a pivotal role in shaping the field. As his career progressed, his research evolved to investigate the plasticity of the auditory system, and his recent work continues to explore innovative approaches to protect and restore hearing, with significant clinical implications.

Beyond his scientific accomplishments, Miguel Merchán's influence as a mentor and administrator further highlights his enduring legacy. His contributions have not only advanced the field but have also nurtured the development of future generations of Spanish scientists, encouraging collaboration and innovation in the scientific community. His work continues to inspire emerging researchers, while his ongoing investigations into auditory system plasticity and protection hold promise for vital breakthroughs in the understanding and treatment of hearing loss and related disorders.

1. Cajal and the origins of Spanish auditory neuroscience

This paper is part of the special issue of Hearing Research published in honor of Miguel A. Merchán on the occasion of his 70th birthday. Miguel A. Merchán, now Professor Emeritus of Histology at the University of Salamanca (Spain), moved to Salamanca in 1981 to embark on an exceptional scientific journey in the best tradition of Spanish neuromorphology. Interestingly, his move to Salamanca occurred exactly one hundred years after Cajal published his first paper on the nervous system (Cajal, 1881).

Santiago Ramón y Cajal (1852–1934), the greatest Spanish neuroscientist of all time, is often considered the father of modern neuroscience. In a remarkable scientific career spanning more than five decades, he studied virtually every region of the nervous system, across a wide range of species (from insects to humans) and at various developmental stages (from early embryos to adults) (Cajal, 1899, 1904, 1909, 1911). He is internationally renowned for his groundbreaking observations on the structure of the cerebellum, spinal cord, and retina, as well as for his physiological insights, which led him to formulate original theories and principles. These include the neuron doctrine, the law of transmission by contact, the establishment of neuronal connections by the progression of the axonal growth cone, the neurotropic theory, the law of dynamic polarization of the neuron, and the mechanisms of degeneration and regeneration of the peripheral and central nervous systems. While the magnitude and brilliance of these discoveries have often overshadowed his forays into other areas of neuroscience, including auditory neuroscience, Cajal's contributions to the knowledge of the auditory system are considerably broader and more significant than is commonly

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* Corresponding author.
E-mail address: saldana@usal.es (E. Saldaña).

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recognized. This seems to be a constant theme in the work of Cajal, as contemporary neuroscientists continue to rediscover the genius of his findings (see Espinosa-Sánchez et al., 2024, for a recent example from the vestibular system).

Cajal's laboratory produced eight articles entirely focused on auditory structures. Seven of these were authored solely by him (Cajal 1900a, 1900b, 1902a, 1902b, 1908a, 1908b, 1908c). The eighth, which described the neurons of the medial superior olive and the innervation of the medial nucleus of the trapezoid body in the cat, was signed only by Isidoro La Villa, who was Cajal's student (La Villa, 1898). However, a close examination of the illustrations and writing style of La Villa's publication strongly suggests that Cajal's involvement in this study extended far beyond mere mentorship.

The number of Cajal's papers specifically devoted to auditory neuroscience does not fully capture his contributions to the field. He included valuable information on the organization of auditory structures in many publications that addressed broader brain regions, innovations in staining techniques, or critical biological issues and principles (e.g., Cajal, 1891, 1894, 1895, 1896a, 1896b, 1896c). The following example illustrates how Cajal dealt with auditory structures in investigations unrelated to acoustic processing. In a comprehensive publication on the internal structure of nerve cells (Cajal, 1896a), he presented several arguments supporting the existence of a membrane surrounding the cell, a concept that, due to technical limitations, had not been proven at the time. Cajal observed that when alcoholic solutions used to fix samples of the nervous system entered a neuron, they displaced the basophilic elements of the cytoplasm (i.e., Nissl bodies) towards one side of the cell body, where they accumulated. He suggested that this accumulation occurred because the basophilic elements found an obstacle, which is the membrane. Remarkably, the neurons chosen by Cajal to demonstrate this phenomenon were from the ventral cochlear nucleus. In the illustration accompanying this assertion, these neurons closely resemble the spherical bushy cells of the anteroventral cochlear nucleus (Cajal, 1909, his Fig. 40).

Cajal's discoveries related to the auditory system were included in his monumental work, *Textura del Sistema Nervioso del Hombre y de los Vertebrados* (Texture of the Nervous System of Man and the Vertebrates), which compiled and consolidated the results of fifteen years of groundbreaking research. This *opus magnum* was originally published in Spanish in two volumes (Cajal 1899 [Volume I), 1904 [Volume II, in two parts]), which included more than 880 original drawings. A French translation, entitled *Histologie du Système Nerveux de l'Homme et des Vertébrés* (Histology of the Nervous System of Man and the Vertebrates), was released a few years later, in two volumes (Cajal, 1909 [Volume I], 1911 [Volume II]). The French edition, personally supervised by Cajal, incorporated his latest observations and more than 130 additional illustrations.

Cajal made numerous contributions to the knowledge of the auditory system. In fact, many of his discoveries have become so widely accepted and taken for granted, that most researchers do not associate them with him. In the following paragraphs, we highlight a few selected examples of the originality and prominence of his findings with the aim of illustrating how much Cajal advanced our understanding of every part of the auditory system, from the cochlea to the cerebral cortex. Cajal's key discoveries include:

- The pioneering description of the termination of the peripheral branches of the avian vestibulocochlear nerve and their relationship with the hair cells of the acoustic and vestibular epithelia (Cajal, 1908a).
- The demonstration that the complex synaptic specializations of the anteroventral cochlear nucleus, known as the endbulbs of Held, are formed exclusively by collaterals of the ascending branch of the cochlear nerve fibers. In contrast, the descending branches give rise to thin collaterals that form delicate arrays around the neurons of the posteroventral cochlear nucleus (Cajal, 1900a).
- The identification and first description of two prominent cell groups of the superior olivary complex: the lateral nucleus of the trapezoid body (referred to by Cajal as the "outer preolivary nucleus"), and the ventral nucleus of the trapezoid body (his "inner preolivary nucleus") (Cajal, 1895, 1896c, 1904).
- The parcellation, first suggested by Held and Kölliker, of the inferior colliculus into a central nucleus surrounded by lateral and dorsal cortices. Cajal emphasized the cytoarchitectural and hodological differences between the central nucleus and the lateral cortex (Cajal, 1902a).
- The identification of different patterns of termination of the fibers of the lateral lemniscus within the inferior colliculus. While many lemniscal fibers innervate only the central nucleus, others target both the central nucleus and the external cortex (Cajal, 1902a).
- The demonstration that at least one-third of the axons of the lateral lemniscus, rather than terminating in the inferior colliculus, continue their rostral trajectory all the way to the medial geniculate body of the thalamus (Cajal, 1902a).
- The demonstration that the ascending auditory pathway makes an obligatory relay in the thalamus, with no subthalamic nuclei directly innervating the auditory cerebral cortex.
- The first comprehensive description of the neurons and axons of the human auditory cerebral cortex (Cajal, 1900b).

Cajal's descriptions were systematically reinforced by masterful drawings of his histologic slides. Fig. 1 shows an example of one of his earliest drawings of auditory structures.

Although most of the descriptions and conclusions of Cajal were later ratified by others, he occasionally incurred in mistakes. A notable example is his interpretation of the origin of the thick fibers that form the large calyces of Held in the medial nucleus of the trapezoid body. We now know that these fibers originate from the globular bushy cells of the contralateral ventral cochlear nucleus. However, Cajal concluded that they were most probably formed by collaterals of the ascending branch of the fibers of the cochlear nerve (Cajal, 1904). His conclusion was primarily based on the remarkable similarity between the endbulbs, which are formed by collaterals of the ascending branch of the fibers of the cochlear nerve in the anteroventral cochlear nucleus, and the calyces of the medial nucleus of the trapezoid body. He was also influenced by the results of experiments in which intracranial transection of the vestibulocochlear nerve led to axonal degeneration not only in the cochlear nuclei, but also in the superior olivary complex, including the contralateral medial nucleus of the trapezoid body (Thomas, 1898). Interestingly, this issue was revisited by Cajal's last disciple, Rafael Lorente de Nó (see below).

Cajal had a long scientific collaboration with his brother Pedro, who worked in Zaragoza (Spain). Pedro Ramón y Cajal (1854–1950) contributed a description of the mammalian inferior colliculus and medial geniculate body in a comprehensive study of various nervous structures in a wide range of vertebrates (Ramón y Cajal, 1894).

In the second half of his scientific career, Cajal collaborated with several investigators who followed in his footsteps, ultimately establishing the so-called *Escuela Neurohistológica Española* (Spanish Neurohistology School) or *Cajal School*. In addition to his brother Pedro, the list of these distinguished scientists includes such relevant names as Francisco Tello (1880–1958), Nicolás Achúcarro (1880–1919), Domingo Sánchez (1860–1947), Gonzalo Rodríguez Lafora (1886–1971), Pío del Río-Hortega (1882–1945), Fernando de Castro (1896–1967), and Rafael Lorente de Nó (1902–1990) (Fig. 2). These scientists produced innovative and seminal work that has been reviewed extensively elsewhere (e.g., de Castro, 1981; Nanduri et al., 2008; Puelles, 2009; Iglesias-Rozas and Garrosa, 2013; de Castro, 2019; Espinosa-Sánchez et al., 2020; Ramón y Cajal and De Carlos, 2020; Vera-Sempere, 2022; Serrano-Herrera and Espinosa-Sánchez, 2024). However, only one of Cajal's disciples made a significant contribution to the understanding of the auditory system: Lorente de Nó (Fig. 3).

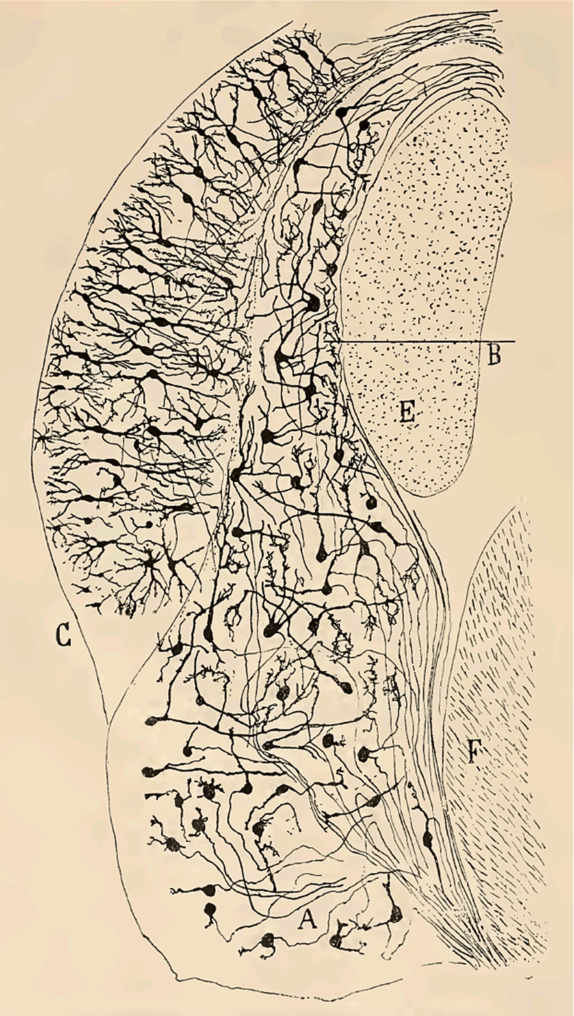


Fig. 1. One of Cajal's earliest illustrations of auditory structures. This drawing of a transverse section of the cochlear nuclei of a four-day-old rabbit faithfully depicts the principal neuron types, including globular bushy, planar multipolar, and octopus neurons of the posteroventral cochlear nucleus, and fusiform, cartwheel, and giant neurons of the dorsal cochlear nucleus. The drawing also illustrates the path followed by the axon of the main projection neurons of the cochlear nuclei: the axons of globular bushy and multipolar neurons are shown entering the trapezoid body, those of octopus neurons entering the intermediate acoustic stria, and those of fusiform neurons entering the dorsal acoustic stria. (Reproduced from Cajal, 1896, Figure 22. This drawing first appeared as Figure 22 in Cajal, 1895. It also appeared as Figure 265 in Cajal, 1904).

2. Lorente de nó and the mastery of the cochlear nuclei

Rafael Lorente de Nó was born in 1902 in Zaragoza (Spain). In 1917 he enrolled in the Faculty of Medicine at the University of Zaragoza, where he had his first contact with the field of Histology and the histological laboratory. Three years later, he moved to Madrid to continue his medical studies and, above all, to join Cajal's laboratory. Under the guidance of Cajal and his collaborators, Lorente de Nó quickly began to make substantial observations. At the age of 20, he published a remarkable article on the structure of the cerebral cortex of the mouse, entitled *La corteza cerebral del ratón: Primera contribución – La corteza acústica* (The mouse cerebral cortex: First contribution – The acoustic cortex) (Lorente de Nó, 1922). This pioneering work laid the foundation for understanding the columnar organization of the cerebral cortex and foreshadowed the description of cortical barrels (Espinosa-Sánchez et al., 2020). Ironically, while Lorente de Nó was attempting to unravel the organization of the auditory cortex, his work ended up providing an accurate and detailed description of the somatosensory cortex.

Lorente de Nó remained closely associated with Cajal's laboratory until 1929. During those years he spent several long periods in Uppsala (Sweden), where he investigated with Robert Bárány (1876–1936) on the morphofunctional organization of the eighth cranial nerve and the mechanisms underlying vestibular reflexes. One of the numerous papers he published from Uppsala contained a collateral observation that helped settle the old debate about whether the fibers of the cochlear nerve terminate in the cochlear nuclei or continue into the trapezoid body. Lorente de Nó observed a group of neurons distributed along the cochlear nerve and particularly abundant in its most distal portion, near the internal auditory meatus (Lorente de Nó, 1926). These cells were later identified as the neurons of the acoustic nerve nucleus (Harrison et al., 1962) or cochlear root neurons (Merchán et al., 1988). Lorente de Nó concluded that the fibers of the cochlear nerve do not extend beyond the cochlear nuclei. He suggested that the degeneration observed in some studies following experimental lesion of the cochlea could be explained by the unintentional damage of the most distal neurons of the cochlear nerve, which in many species occupy an intracochlear position. Interestingly, Lorente de Nó never mentioned these neurons in any of his many later studies of the cochlear nerve and nuclei.

In 1929, Lorente de Nó underwent intensive training in otorhinolaryngology, and in 1930 he worked feverishly as head of the otorhinolaryngology department in the *Casa de Salud Valdecilla*, a brand new hospital in Santander, Northern Spain (Espinosa-Sánchez et al., 2020). Frustrated by his inability to balance clinical practice with his scientific ambitions, he abandoned medicine. In 1931, he went to the United States to accept and take up a research position at the Central Institute for the Deaf in Saint Louis, (Missouri). Five years later, he moved to the Rockefeller Institute for Medical Research in New York, where he became one of the most influential electrophysiologists of the 20th century.

During his years in Saint Louis, Lorente de Nó published many of the results he had obtained in his previous laboratories. A series of three articles published in the journal Laryngoscope in 1933 was devoted to audition-related matters. The first paper described in detail the organization of the cochlear and vestibular branches of the eighth cranial nerve and presented an accurate account of the distribution of cochlear nerve fibers within the cochlear nuclei (Lorente de Nó, 1933a) (Fig. 4). This work also included a personal and somewhat controversial interpretation of the tonotopic organization of the cochlear nerve (see below). The second paper, which addressed the physiology of hearing, examined the effects of controlled lesions of the tympanic membrane on the function of the middle ear muscles and on hearing (Lorente de Nó and Harris, 1933). The third paper described in general terms the organization of the cochlear nuclei (Lorente de Nó, 1933b). Among the many original findings and ideas in this work were the parcellation of the cochlear nuclei into no less than thirteen regions, each of them innervated by every fiber of the cochlear nerve, and the identification of more than fifty neuron types. Lorente de Nó also noted that the dorsal cochlear nucleus receives centrifugal, descending projections, and that the ventral and dorsal cochlear nuclei are interconnected by bundles of intrinsic, association fibers. Additionally, he deduced the origin of the fibers that leave the cochlear nuclei through each of the acoustic striae: the fibers of the ventral acoustic stria or trapezoid body originate in the anteroventral cochlear nucleus; those of the intermediate acoustic stria or stria of Held originate in the posteroventral cochlear nucleus; and those of the dorsal acoustic stria or stria of von Monakow originate in the dorsal cochlear nucleus. Finally, Lorente de Nó speculated on the possibility that auditory information might reach the cerebral cortex with just two central synapses: He proposed that "*the peripheral organ is connected with the primary [cochlear] nuclei by the ganglionic cells. The primary nuclei are connected with the thalamic nuclei (internal geniculate body, etc.) by another direct path, finally the thalamic nuclei are connected with the cerebral cortex by a third direct path*" (Lorente de Nó, 1933b, page 347).

Between 1931 and 1938, Lorente the Nó created thousands of

Fig. 2. Postal stamp and souvenir sheet issued by *Correos* (Spain's official postal service) in 2023 as a tribute to Santiago Ramón y Cajal and the *Escuela Neurohistológica Española* (Spanish Neurohistology School). The central stamp, with a face value of 6.45 euros, features an engraved portrait of Cajal. The stamp is flanked by photographs of Cajal's main disciples.

microscopic slides to study the organization of the mammalian cochlear nerve and nuclei. At the time, he meticulously documented his observations with highly realistic drawings (Fig. 4). With few exceptions (Lorente de Nó, 1933a, b, 1937), this material remained unpublished for decades. Lorente de Nó officially retired from the Rockefeller Institute in 1972 and was then appointed Professor Emeritus at the Brain Research Institute at UCLA. It was only then that he began to consider the idea of publishing all his results on the cochlear nuclei. Two partial reports (Lorente de Nó, 1976, 1979) laid the groundwork for the book *The Primary Acoustic Nuclei* (Lorente de Nó, 1981). In this monograph, which included around 140 original illustrations, mostly drawings, he analyzed in exquisite detail the morphology and distribution of the neurons and axons of the cochlear nuclei of mammals. Lorente de Nó extended his 1933 parcellation of the cochlear nuclei into an even more complicated array of regions, some of which were further subdivided into zones or layers. He also distinguished a very large number of neuron types, which are difficult to reconcile with modern classifications derived from functional and molecular characterizations. In addition, he revised his polemical interpretation of the tonotopy of the cochlear nerve and correctly concluded that the fibers of the cochlear nerve of apical and basal cochlear origin innervate ventral and dorsal regions of the cochlear nuclei, respectively. More than forty years after its publication, Lorente de Nó's book remains as the most detailed description of any territory of the auditory system. His drawings, appreciated ever since, continue to serve as a valuable resource that stimulates contemporary research.

3. Jaime A. Merchán and the resurgence of auditory neuroscience in Spain

Fernando de Castro, along with Lorente de Nó, was Cajal's youngest disciple. His scientific work primarily focused on the peripheral nervous system, and he is renowned for the discovery of the first arterial chemoreceptors, located in the carotid body (de Castro, 1926, 1928; for a review in perspective, see de Castro, 2009). Cajal chose de Castro to compile the protocols used by the Spanish Neurohistology School and together they published the book *Elementos de Técnica Micrográfica del Sistema Nervioso* (Elements of Micrographic Technique of the Nervous System) (Cajal and de Castro, 1933), which may be considered the first manual specifically devoted to neurohistological techniques. Fernando de Castro also played a pivotal role in preserving the spirit of the Spanish Neurohistology School during and after the Spanish Civil War (1936–1939). He trained a new generation of Spanish neuroscientists, including prominent figures such as Facundo Valverde (1935–2020) and Constantino Sotelo. The last medical student that Fernando de Castro recruited to science was Jaime A. Merchán (1946–2011). Through Jaime Merchán, Fernando de Castro provided the genealogical scientific link between Cajal and contemporary Spanish auditory neuroscience (Fig. 3).

Jaime Merchán completed his medical studies and the early stages of his scientific career at the Complutense University of Madrid under the guidance of Agustín Bullón Ramírez (1912–1988), who had been de Castro's collaborator. His doctoral thesis focused on the neurobiological discoveries of de Castro (Merchán, 1973). In 1972, Jaime Merchán played a major role in the reedition of Cajal and de Castro's treatise on neurohistological techniques (Cajal and de Castro, 1972). In 1981, he moved to the newly-created University of Alicante, on the Mediterranean coast of Spain, as a full professor of Histology. His interest in the auditory system began in the 1970s, when he started to study the ultrastructure and development of the inner ear, as well as the ototoxic effects of aminoglycosides. At that time, he attracted to his laboratory three enthusiastic young collaborators, who would later become leading figures in the auditory neuroscience community: Pablo Gil Loyzaga, José Manuel ("Pepe") Juiz, and his own brother Miguel (Figs. 3 and 5). These

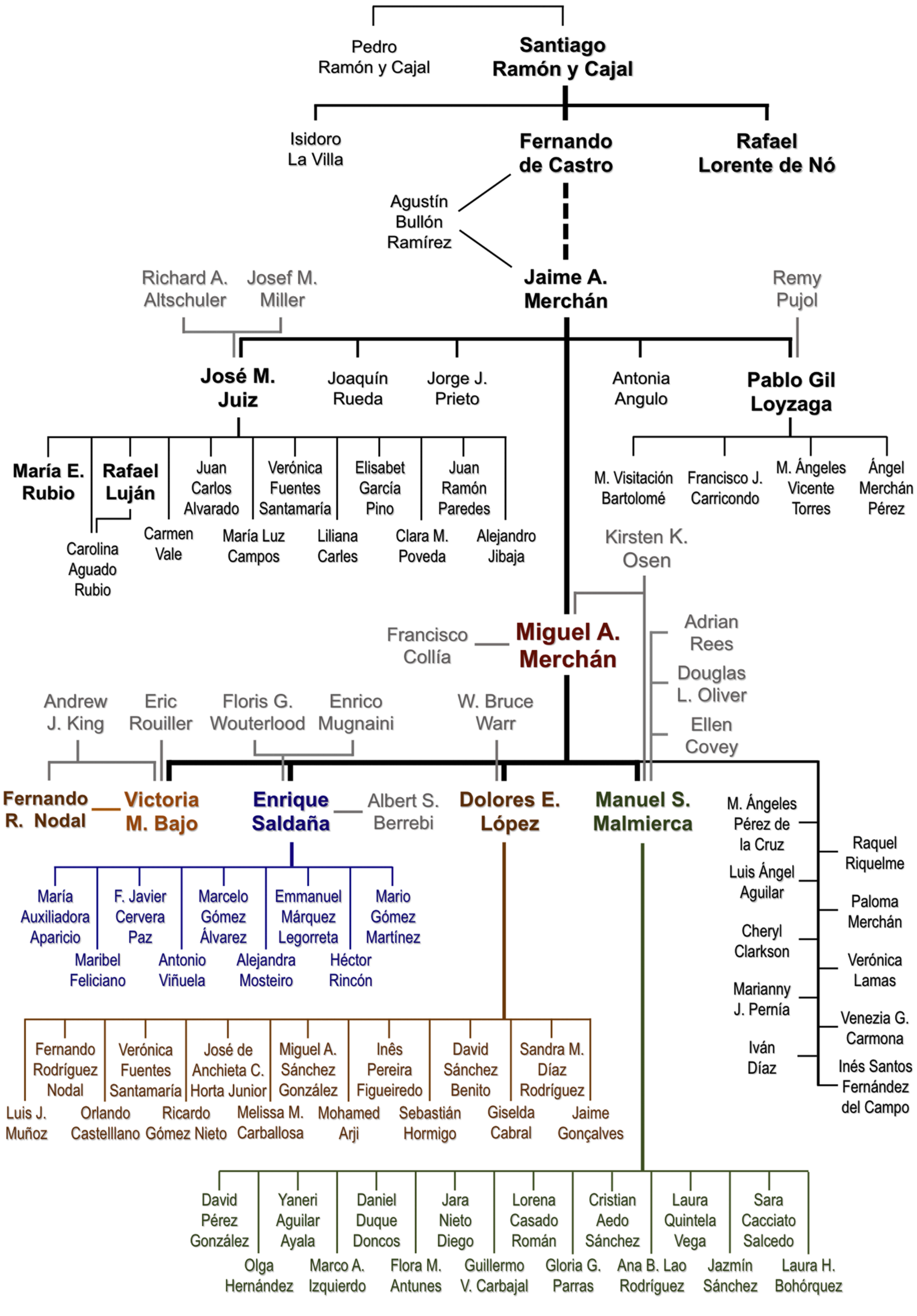


Fig. 3. Scientific genealogical tree of Spanish auditory neuroscience.

early efforts led, among other things, to a detailed description of the Hensen's cells of the inner ear (Merchán et al., 1980).

After moving to Alicante, Jaime Merchán continued a fruitful collaboration with his bother Miguel, who was establishing his own group at the University of Salamanca. This collaboration led to several papers on the innervation of the mammalian cochlear nuclei by the fibers of the auditory nerve (Merchán et al., 1985, 1986a; Angulo et al., 1990). At the same time, Jaime Merchán strengthened his laboratory in Alicante with collaborators such as Joaquín Rueda, Antonia ("Toñi") Angulo, Pepe Juiz, who had followed him from Madrid, and Jorge J. Prieto, who was his first doctoral student there (Fig. 3). Investigations during these years focused on various aspects of cochlear morphology, including ultrastructure, histochemistry, and the effects of surgical trauma, kainic acid, and hyperthyroidism (e.g., Prieto and Merchán, 1986; Rueda et al., 1987; Juiz et al., 1988, 1989; Prieto et al., 1990).

A unique, non-auditory aspect of Jaime Merchán's work was his quest for technical tips to improve the reliability of the always capricious Golgi method. He and his collaborators demonstrated that the optimal impregnation depended on the degree of chromium reduction, a parameter that could be easily assessed by measuring the rise in pH of

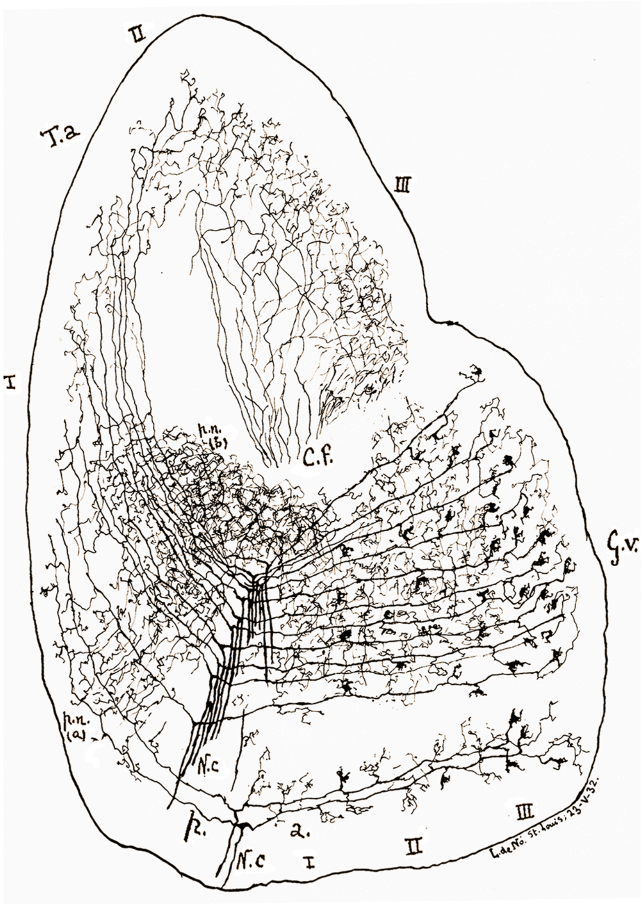


Fig. 4. Drawing by Lorente de Nó of a parasagittal section of the cochlear nuclei of a four-day-old cat. Fibers of the cochlear nerve, impregnated by the Golgi rapid method, bifurcate into an ascending branch, which spans caudorostrally the anteroventral cochlear nucleus, and a descending branch, which spans ventrodorsally the posteroventral cochlear nucleus before entering the dorsal cochlear nucleus. (Reproduced from Lorente de Nó, 1933a, Fig. 1. This drawing also appeared, with slight modifications in the labels, as Fig. 1–4 in Lorente de Nó, 1981).

the potassium dichromate solution before transferring the nervous tissue to the silver nitrate solution (Angulo et al., 1994, 1996).

After Jaime Merchán moved to Alicante, Pablo Gil Loyzaga (1954–2013) remained at the Medical School of the Complutense University of Madrid. In 1984, Gil-Loyzaga joined as a postdoctoral fellow the laboratory of Rémy Pujol, at the University of Montpellier (France), where he used histochemical and immunocytochemical techniques to analyze the distribution of several neurotransmitters in the adult and developing cochlea (e.g., Gil-Loyzaga and Pujol, 1988; Merchán-Pérez et al., 1990a, 1990b). After returning to Madrid, he formed his own research group (Fig. 3) and carried out a prolific scientific career that was abruptly cut by his premature death. Pablo Gil-Loyzaga is best known for his cutting-edge work in characterizing dopamine and serotonin as key neurotransmitters of the cochlear efferent system (e.g., Gil-Loyzaga, 1995; Gil-Loyzaga et al., 2000; Vicente-Torres et al., 2003).

Pepe Juiz completed his Ph.D. in Alicante under the supervision of Jaime Merchán. He then worked as a postdoctoral fellow at the Kresge Hearing Research Institute (University of Michigan, USA), where he joined the group of Richard A. Altschuler. Using immunoelectron microscopy, he characterized different classes of synaptic boutons in the lateral superior olive (Helfert et al., 1992) and in the cochlear nuclei (Juiz et al., 1994, 1996).

Upon returning to Alicante, Juiz continued his investigations of the auditory system. He mentored María E. ("Lania") Rubio (Fig. 3), whose doctoral thesis focused on the ultrastructural characterization of synaptic boutons in the dorsal cochlear nucleus (Rubio and Juiz, 1998; 2004). Rubio eventually pursued an outstanding career as an auditory neuroscientist in the United States, where she now runs her own laboratory at the University of Pittsburgh.

In 1998, Juiz moved to Albacete to help establish the newly created Faculty of Medicine at the University of Castilla-La Mancha, where he would later become dean. He also created his own research group, which over the years has included collaborators such as Rafael Luján, Verónica Fuentes-Santamaría and Juan Carlos Alvarado (Fig. 3). Among the many auditory issues tackled by Juiz and his group are the localization of neurotransmitters and their receptors in auditory nuclei (e.g., Campos et al., 2001; Luján et al., 2004; Caminos et al., 2007) and the pathogenesis and prevention of hearing loss induced by noise or aging (e.g., Alvarado et al., 2015, 2019; Fuentes-Santamaría et al., 2017, 2022, 2024).

4. Miguel Merchán and the Salamanca group

In 1981, at the age of 28, just one year after receiving his Ph.D. from the Complutense University of Madrid, Miguel Merchán moved to the University of Salamanca as an assistant professor of Histology. During the academic year 1981–1982, he was heavily involved in teaching at the Faculty of Medicine, but he was also determined to begin research on the organization of the central auditory system. To pursue his goal, he teamed up with Francisco ("Paco") Collía (Fig. 3), a fellow assistant professor who was particularly skilled in classical neurohistological techniques. Collía's expertise in silver impregnation methods was instrumental in the first studies to emerge from Merchán's laboratory, which dealt with the innervation of the cochlear nuclei (Merchán et al., 1985, 1986b). At the same time, Miguel Merchán sought to recruit collaborators among the medical students. In June 1982, he contacted four brilliant students nearing the completion of their second year of medical school and invited them to join his laboratory. Only one of them, Enrique Saldaña, committed himself seriously to the scientific endeavor while continuing his medical studies and became Miguel Merchán's first disciple (Fig. 3). Merchán continued this strategy in the years that followed. Among the many medical students who joined his laboratory at one time or another, two deserve special mention: Manuel ("Manolo") Sánchez Malmierca, who entered the group in 1983, and Victoria M. Bajo, who joined three years later (Fig. 3). During those years, the laboratory was also strengthened by the incorporation of Dolores E. ("Lita") López (Fig. 3), who already held a Ph.D. in Biology. Fig. 6 shows the members of Merchán's laboratory in the early years.

In the mid-1980s, the activities of the group focused on the organization of the rat cochlear nuclei. Three papers on the distribution of cochlear nerve fibers (Merchán et al., 1985, 1986a; 1986b) were followed by a foundational description of the neuron types of the ventral cochlear nucleus of the rat using the Golgi method (Saldaña et al., 1987) (Fig. 7A).

In the summer of 1987, Miguel Merchán, Collía and Saldaña attended the symposium "Auditory Pathway-Structure and Function", organized by Josef Syka and R. Bruce Masterton in Prague (Czechoslovakia), and presented their preliminary results on the organization and connections of the rat cochlear nuclei. Kirsten K. Osen, one of the most respected figures in the field, spent several hours with the young Spaniards discussing their results and generously offered to help them fully realize their potential. It was at this symposium that Prof. Osen became the scientific "godmother" of the Salamanca Group, a relationship that continues today, more than 35 years later (Figs. 8 and 13).

In the spring of 1988, Osen spent two weeks working in Salamanca. During her stay, she helped and assisted Merchán in refining the manuscript that described the first significant result from his laboratory: the rediscovery of the so-called cochlear root neurons or neurons of the acoustic nerve nucleus. This paper, published a few months later (Merchán et al., 1988), included the characterization of the root neurons

Fig. 5. Jaime A. Merchán and his young collaborators in a photograph taken at the first national meeting of the *Sociedad Española de Histología* (Spanish Society of Histology), held in Zaragoza (Spain) in July of 1979. **1.** Pablo Gil-Loyzaga. **2.** María Dolores ("Loli") Ludeña. **3.** Miguel A. Merchán. **4.** Jaime A. Merchán. **5.** José Manuel ("Pepe") Juiz.

Fig. 6. The members of Miguel Merchán's laboratory in 1986, celebrating his promotion to the rank of Full Professor of Histology at the University of Salamanca. **1.** Enrique Saldaña. **2.** Dolores E. ("Lita") López. **3.** M. Ángeles Pérez de la Cruz. **4.** Francisco ("Paco") Collía. **5.** Manuel ("Manolo") S. Malmierca. **6.** Miguel A. Merchán. **7.** María Dolores ("Loli") Ludeña (Merchán's wife).

with the Nissl and Golgi methods, the confirmation that these neurons project through the trapezoid body, and the description of their ultrastructure (Fig. 7A).

A cornerstone in the development of the Salamanca Group was establishing relationships with top-tier international laboratories (Fig. 3). This strategy, which once again benefited from Osen's assistance, had the dual advantage of fostering the training of Merchán's graduate students and postdoctoral fellows and enriching the technical arsenal of his laboratory. During a couple of predoctoral stays in the laboratory of Floris G. Wouterlood (Free University of Amsterdam, The Netherlands), Enrique Saldaña became familiar with the then revolutionary anterograde neuroanatomical tracer *Phaseolus vulgaris*-leucoagglutinin (PHA-L) (Wouterlood et al., 1990). In his doctoral work, mentored by Miguel Merchán, Saldaña used this tracer to investigate the intrinsic, commissural, and descending connections of the inferior colliculus (Saldaña and Merchán, 1992; Saldaña, 1993). He subsequently worked as a postdoctoral fellow with Enrico Mugnaini (University of Connecticut, USA) investigating the descending auditory pathway (e.g., Vetter et al., 1993; Saldaña et al., 1996). This work led to the surprising discovery of direct projections from the auditory cerebral cortex to the first relay stations of the auditory pathway (Feliciano et al., 1995).

Manolo S. Malmierca conducted much of his doctoral work in Osen's laboratory (University of Oslo, Norway) (Fig. 3). There, in collaboration with Theodor W. Blackstad, he applied state-of-the-art three-dimensional reconstructions to analyze the laminar organization of the central nucleus of the inferior colliculus (Malmierca et al., 1993). He then went on to work with Adrian Rees (University of Newcastle upon Tyne, UK) as a postdoctoral fellow (Fig. 3). During his time with Rees, Malmierca became well-versed with electrophysiology and published several

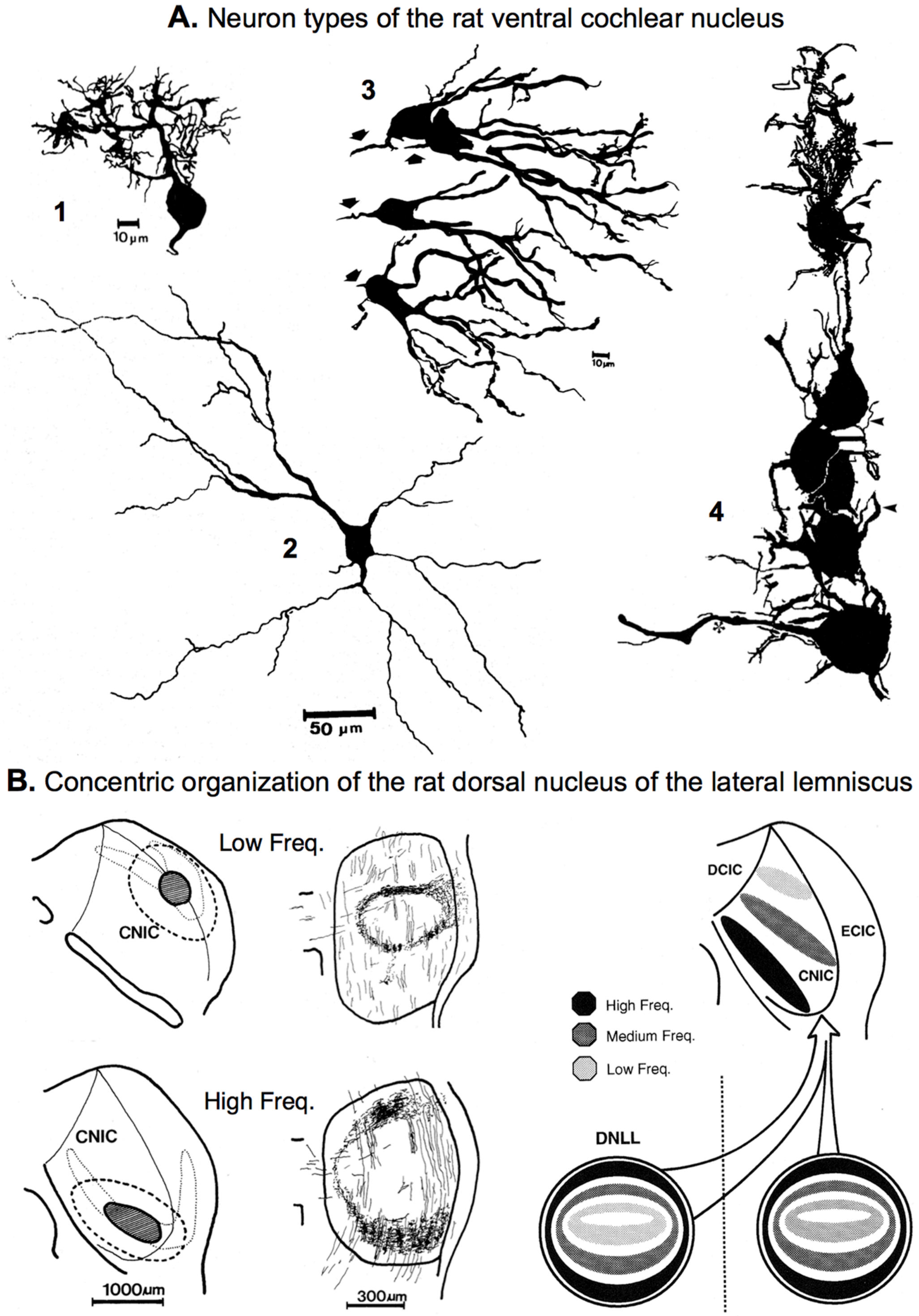


Fig. 7. Representative examples of Miguel A. Merchán's scientific achievements. **A.** Early drawings of neuron types of the rat ventral cochlear nucleus impregnated by the Golgi method. 1. Bushy cell with several tufts of dendritic appendages. (*Adapted from* Saldaña et al., *1987, Fig. 2B*). 2. Large multipolar neuron. (*Adapted from* Saldaña et al., *1987, Fig. 4A*). 3. Group of typical octopus neurons in the posteroventral cochlear nucleus. (*Adapted from* Saldaña et al., *1987, Fig. 6B*). 4. A cluster of aligned cochlear root neurons of the intranuclear portion of the cochlear nerve. (*Adapted from* Merchán et al., *1988, Fig. 10*). **B.** Injection of the bidirectional neuroanatomical tracer biotinylated dextran amine (BDA) into the central nucleus of the inferior colliculus (CNIC) revealed the concentric tonotopic organization of the dorsal nucleus of the lateral lemniscus (DNLL). (*Adapted from* Merchán et al., *1994, Figs. 5A, 5D, 6A, 6D, and 11*).

papers on the organization and function of the guinea pig inferior colliculus (Malmierca et al., 1995, 1996; Le Beau et al., 1996, 2001).

In the early 1990s, Lita López spent a year at the Boys Town National Research Hospital (Omaha, Nebraska, USA) investigating with W. Bruce Warr the projections of cochlear root neurons (López et al., 1999) (Fig. 3). This stay laid the foundation for a fruitful collaboration with Michael Davis (Yale University, New Haven, Connecticut, USA), which led to the demonstration that cochlear root neurons are an essential component of the circuit mediating the acoustic startle reflex (Lee et al., 1996). Additionally, in collaboration with Donald G. Sinex at Arizona

Fig. 8. Photograph taken on November 10, 1996, after the formal ceremony in which Kirsten K. Osen was conferred the degree of Doctor Honoris Causa at the University of Salamanca. From left to right: José Manuel ("Pepe") Juiz, Victoria ("Vicky") M. Bajo, Kirsten K. Osen, Miguel A. Merchán, Manuel ("Manolo") S. Malmierca, Enrique Saldaña, and Dolores E. ("Lita") López.

State University (USA), López obtained the first electrophysiological data on cochlear root neurons (Sinex et al., 2001).

Miguel Merchán also supervised the Ph.D. thesis of Victoria M. Bajo (Fig. 3), which focused on the cytoarchitecture and connections of the rat dorsal nucleus of the lateral lemniscus (Bajo et al., 1993). She then moved to the University of Lausanne (Switzerland) to join the group of Eric M. Rouiller. During her postdoctoral work, Bajo combined anatomical and electrophysiological experiments to investigate the dorsal nucleus of the lateral lemniscus (Bajo et al., 1998) and various corticofugal pathways (e.g., Bajo et al., 1995; Jacomme et al., 2003). Of the four initial young collaborators of Miguel Merchán, Bajo was the only one who did not eventually return to Salamanca. After a short stay in Salamanca following her time in Switzerland, Bajo joined the group of Andrew J. King at the University of Oxford (UK), where she remains today. Over the last two decades, her work, often in collaboration with Fernando ("Fertxo") R. Nodal (her husband and a former Ph.D. student of Lita López) (Fig. 3), has resulted in numerous studies that combine morphological, electrophysiological and behavioral approaches to address important questions about auditory functions, with an emphasis on cortical functions (e.g., Bajo and Moore, 2005; Bajo et al., 2007; Homma et al., 2017). She has also conducted groundbreaking work demonstrating the role of the auditory cortex in learning (Bajo et al., 2010, 2019).

After their stays abroad, Enrique Saldaña, Manolo Malmierca and Lita López returned to the University of Salamanca to establish their own laboratories and develop independent scientific projects. Saldaña concentrated on the morphological characterization of mammalian auditory nuclei and their connections. For example, he has extensively studied the connections of the superior olivary complex in rodents (e.g., Saldaña and Berrebi, 2000; Saldaña et al., 2009; Viñuela et al., 2011; Saldaña, 2015; Gómez-Alvarez and Saldaña, 2016; Felix et al., 2017; Gómez-Martínez et al., 2023, 2025; Rincón et al., 2024). Many of these studies were carried out in collaboration with Albert ("Al") S. Berrebi (West Virginia University, USA) (Fig. 3). Saldaña has also discovered several brain nuclei, including the ventral tectal longitudinal column (Saldaña et al., 2007; Marshall et al., 2008; Aparicio et al., 2010), the dorsal tectal longitudinal column (Aparicio and Saldaña, 2014), and the semilunar nucleus of the lateral lemniscus (Gómez-Martínez et al., 2023). Furthermore, he has characterized the scarcely known pretectothalamic lamina, formerly known as the limitans nucleus of the thalamus (Márquez-Legorreta et al., 2016).

With the dedicated collaboration of Orlando Castellano, Ricardo ("Richard") Gómez Nieto, José de Anchieta de Castro Horta-Júnior and Sebastián Hormigo (Fig. 3), Lita López has focused on two main scientific projects. The first investigates the anatomical substrate of the acoustic startle reflex and the related phenomenon of prepulse inhibition (e.g., Nodal and López, 2003; Gómez-Nieto et al., 2008a, 2008b, 2014a, 2014b, 2020; Horta-Júnior et al., 2008; Hormigo et al., 2015). The second applies a wide variety of morphological, electrophysiological, pharmacological, molecular, proteomic and bioinformatic tools to explore the characteristics of the cochlea and the brain of a rodent model of audiogenic epilepsy: the hamster GASH/Sal (e.g., Fuentes-Santamaría et al., 2005; Barrera-Bailón et al., 2013; Carballosa-Gonzalez et al., 2013; López-López et al., 2017; Muñoz et al., 2017; Díaz-Casado et al., 2020; Sánchez-Benito et al., 2020; García-Peral et al., 2023).

Manolo Malmierca spent his first years in Salamanca as an independent researcher exploring the connections and electrophysiological features of the rat central auditory system (e.g., Malmierca et al., 2002, 2003, 2005; Hernández et al., 2005). At the turn of the century, with the help of his student and now disciple, David Pérez González, and in collaboration with Ellen Covey (University of Washington, USA) (Fig. 3), he shifted his attention to the ability of certain auditory neurons to detect novel stimuli (Pérez-González et al., 2005). This led to an extensive investigation along the mammalian auditory pathway of the phenomenon called stimulus-specific adaptation (Malmierca et al., 2009; Antunes et al., 2010; Antunes and Malmierca, 2011; Duque et al., 2012; Ayala and Malmierca, 2013; Duque and Malmierca, 2015; Nieto-Diego and Malmierca, 2016). In recent years, this groundbreaking work has significantly influenced our understanding of predictive coding theories (e.g., Malmierca et al., 2015, 2019; Parras et al., 2017; Carbajal and Malmierca, 2018; Casado-Román et al., 2020; Pérez-González et al., 2021, 2024; Lao-Rodríguez et al., 2023, 2024;

Quintela-Vega et al., 2023; Carbajal et al., 2024; Gong et al., 2024; Hockley et al., 2025). Malmierca has balanced his scientific activities with relevant administrative responsibilities: from 2016 to 2024, he served as director of the Neuroscience Institute of Castilla y León (INCyL) at the University of Salamanca; he is the current president of the Spanish Neuroscience Society (*Sociedad Española de Neurociencia [SENC]*) and recently assumed the role of editor-in-chief of Hearing Research.

The preceding paragraphs highlight the legacy of Miguel Merchán through his first direct collaborators and disciples (Fig. 13), but what about his own contributions? He has concentrated his efforts in two complementary paths. On the one hand, he has consistently demonstrated a strong and generous commitment to scientific administration. On the other hand, he has maintained an uninterrupted dedication to scientific research.

Five different activities illustrate Miguel Merchán's role as an administrator. First, in 1991, alongside Pepe Juiz, Donald A. Godfrey and Enrico Mugnaini, he organized in Salamanca the NATO Advanced Research Workshop "The Mammalian Cochlear Nuclei: Organization and Function", which brought together leading experts and firmly established the city as a key hub in auditory neuroscience. Second, in 1994, he organized in Salamanca the first National Workshop on the Neurobiology of Hearing. The meeting was followed in 2001 by a second edition organized by Pepe Juiz in Albacete (Fig. 9). Third, in 1998, Merchán founded the INCyL at the University of Salamanca and became its first director. The prominence of hearing-related research at the INCyL grew when Enrique A. López-Poveda joined the Institute in 2003. Since then, López-Poveda has become a towering figure in audiology and psychoacoustics. Fourth, in 2001, Merchán and Malmierca organized in Salamanca the International Symposium on the Central Auditory System "Inferior Colliculus: From Past to Present", once again uniting renowned experts in the field (Fig. 10). Lastly, in 2009, the University of Connecticut launched its "Neuroscience in Salamanca" study abroad program, a yearly event co-directed by Douglas L. Oliver and Manolo Malmierca. This program, which includes the five-week Neurobiology of Hearing course, has served as a platform for prestigious auditory scientists to train and inspire younger generations.

Miguel Merchán's scientific activities have evolved significantly over the years. His work of the 1990s, often in collaboration with his first disciples, addressed primarily morphological issues. Particularly noteworthy are his contributions to the knowledge of the anatomy, neurochemistry and connections of the nuclei of the lateral lemniscus (Figs 7B, 11) (Bajo et al., 1993, 1999; Merchán et al., 1994; Merchán and Berbel, 1996; Malmierca et al., 1998; Riquelme et al., 2001), as well as his

Fig. 9. Group picture of meeting attendees at the *II Taller Nacional de Neurobiología de la Audición* (Second National Workshop on the Neurobiology of Hearing). This meeting was held in Albacete (Spain) in February 2001 and brought together de auditory groups of Alicante (led by Jaime A. Merchán), Salamanca (led by Miguel A. Merchán), and Albacete (led by José Manuel Juiz). **1.** Jaime A. Merchán. **2.** Joaquín Rueda. **3.** Miguel ("Mikel") A. Sánchez González. **4.** Jorge J. Prieto. **5.** José de Anchieta C. Horta Junior. **6.** José Julio Cabanes. **7.** Raquel Cantos. **8.** Valentín Ceña. **9.** Enrique A. López Poveda. **10.** Juan Ramón Martínez Galán. **11.** Joaquín Jordán. **12.** Carmen Ruiz. **13.** Antonio Viñuela. **14.** Carmen Vale. **15.** Xavier Blaizot. **16.** María Luz Campos. **17.** Olga Hernández. **18.** Alino Martínez Marcos. **19.** María del Mar Arroyo Jiménez. **20.** Elena Caminos. **21.** Ximena E. Caeiro. **22.** Carlos de Cabo. **23.** Enrique Saldaña. **24.** Manuel G. Forero. **25.** Miguel A. Merchán. **26.** Ana Moscoso. **27.** Verónica Fuentes Santamaría. **28.** Pilar Marcos. **29.** Carmen ("Carmina") Díaz Delgado. **30.** Rafael Luján. **31.** María Auxiliadora ("Auxi") Aparicio. **32.** Ignacio ("Nacho") Plaza. **33.** José Manuel ("Pepe") Juiz. **34.** Luis A. ("Lucho") Aguilar.

Fig. 10. Group picture of meeting attendees at the international symposium "Inferior colliculus: From past to future", held in Salamanca (Spain) in May 2001. **1.** Zoltan M. Fuzessery. **2.** Diana L. Coomes. **3.** Laura M. Hurley. **4.** Christine V. Portfors. **5.** Thomas Park. **6.** Donald G. Sinex. **7.** David McAlpine. **8.** Jeffery A. Winer. **9.** Genene Holt's husband. **10.** Enrique Saldaña. **11.** Bradford J. May. **12.** Victoria M. Bajo. **13.** A. Genene Holt. **14.** Jesko Verhey. **15.** Douglas C. Fitzpatrick. **16.** Christoph E. Schreiner. **17.** Douglas E. Vetter. **18.** Ellen Covey. **19.** Ranjan Batra. **20.** Brett R. Schofield. **21.** Liang Li. **22.** Fernando R. Nodal. **23.** Carl L. Faingold. **24.** Constantine Trahiotis. **25.** Carl Faingold's wife. **26.** Albert S. Feng. **27.** Antonio Viñuela. **28.** Dan H. Sanes. **29.** Jian Wang. **30.** Shigeyuki Kuwada. **31.** Craig K. Henkel. **32.** Ricardo A. Velluti. **33.** Shu Hui Wu. **34.** Philip H. S. Jen. **35.** Tom C. T. Yin. **36.** Dexter R. F. Irvine. **37.** Benedikt Grothe. **38.** Leonard Kitzes. **39.** Jack B. Kelly. **40.** Nobuo Suga's wife. **41.** Sandord C. Bledsoe. **42.** Philip H. Smith. **43.** Nobuo Suga. **44.** Nell B. Cant. **45.** Albert S. Berrebi. **46.** Donald M. Caspary. **47.** Alan R. Palmer. **48.** Veronika Neuert. **49.** Jorge J. Prieto. **50.** Dolores E. López. **51.** Josef Syka. **52.** Randy J. Kulesza Jr. **53.** Adrian Rees. **54.** Miguel A. Merchán. **55.** Unidentified. **56.** Atilio Falconi. **57.** Douglas L. Oliver. **58.** Kevin A. Davis. **59.** Aage R. Møller. **60.** George G. Pollak. **61.** Manuel S. Malmierca. **62.** José de Anchieta C. Horta Junior. **63.** Ignacio Plaza. **64.** Gerald Langner. **65.** Luis A. Aguilar. **66.** Ana Moscoso. **67.** Olga Hernández. **68.** Norberto García Cairasco. Attendees not shown in the picture include María-Auxiliadora Aparicio, Philip X. Joris, Raymond Meddis, Russell L. Snyder, Carmen Vale, and Jeffrey J. Wenstrup.

description of the inhibitory neurons of the rat inferior colliculus (Merchán et al., 2005). In the years that followed, he began a long-lasting collaboration with Pepe Juiz to investigate the plastic changes in the auditory system induced by cortical lesions or hearing deprivation (Fig. 12A) (e.g., Clarkson et al., 2010a, 2010b, 2010c, 2012; Lamas et al., 2013, 2017; Pernía et al., 2020). More recently, Merchán has shifted his focus to exploring the protective effects of electrical stimulation of the auditory cortex (Fig. 12B) (e.g., Colmenárez-Raga et al., 2019; Díaz et al., 2021; Carmona-Barrón et al., 2023; Fernández del Campo et al., 2024, 2025; Fuentes-Santamaría et al., 2024). This are some of his students and trainees of the last twenty-five years: Raquel Riquelme, Cheryl Clarkson, Verónica Lamas, Marianny J. Pernía, Venezia G. Carmona, Iván Díaz, and Inés Santos Fernández del Campo. Most of the experiments carried out in Merchán's laboratory during the last three decades have benefitted from the tireless and expert technical assistance of Ignacio Plaza (Fig. 13).

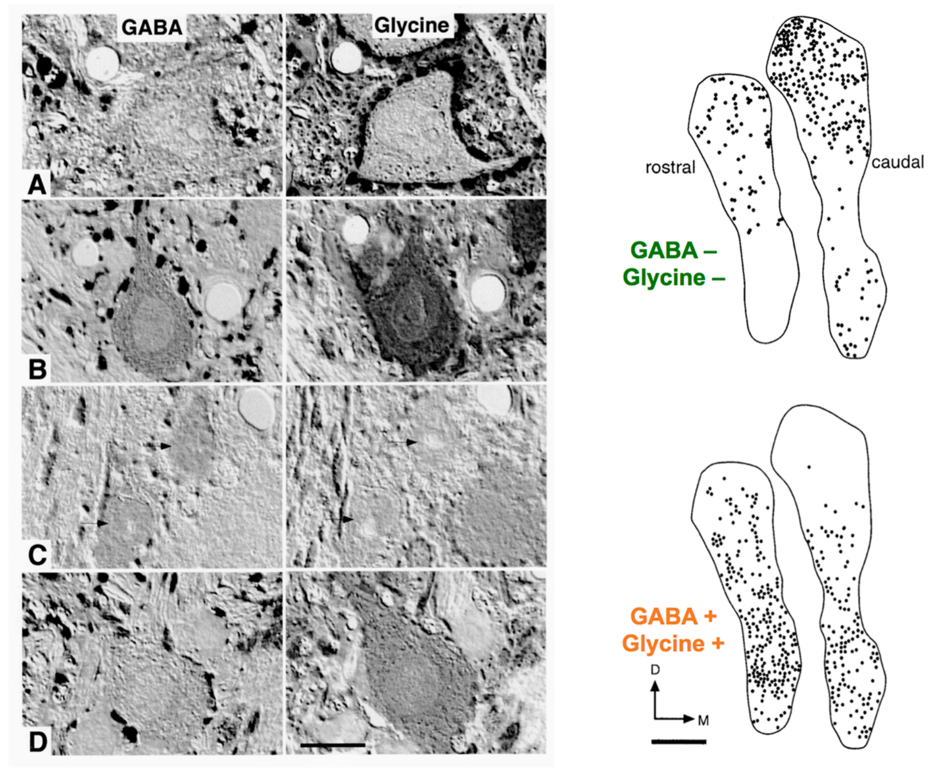
In 2016, Miguel Merchán, together with Javier DeFelipe and Fernando de Castro (the grandson of Cajal's disciple), published the book "Cajal and de Castro's Neurohistological Methods" (Merchán et al., 2016). This is an updated version, and the first in English, of the classic technical book first published by Cajal and de Castro in 1933 and promoted by Jaime Merchán in 1972. With this publication, Miguel Merchán made a true technical treasure available to an international readership worldwide and retraced the path to the Cajalian origins of Spanish neuroscience, thus coming full circle.

5. Concluding remarks

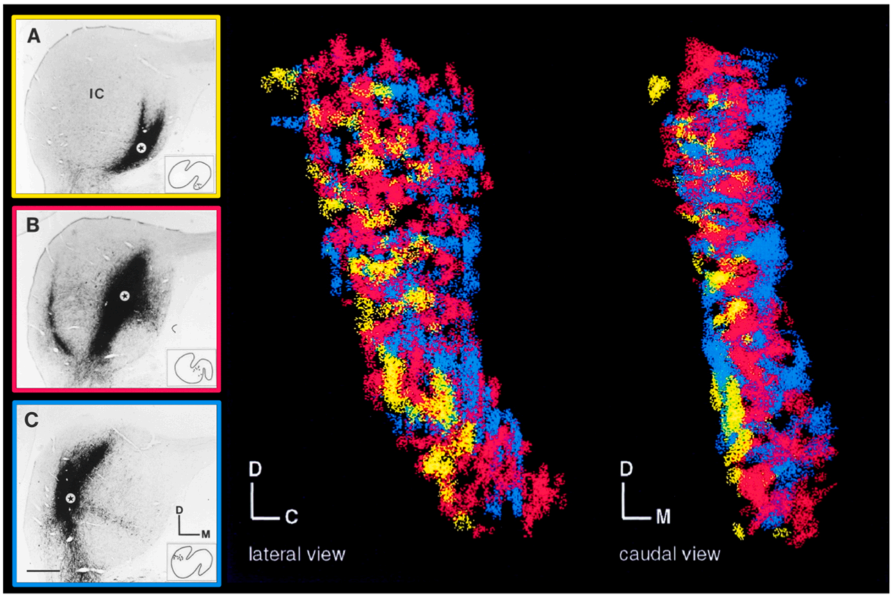
This paper offers an in-depth account of the scientific journey and profound contributions of Miguel A. Merchán and his collaborators, with particular emphasis on the field of auditory neuroscience. Beginning in the early 1980s, Merchán's pioneering work has significantly advanced our understanding of the anatomy, neurochemistry, and intricate connectivity of key structures within the central auditory system, such as the cochlear nuclei, lateral lemniscal nuclei, and inferior colliculus. His collaborations, both within Spain and internationally, have been instrumental in shaping the research landscape of auditory neuroscience.

As his career has evolved, so has his research, expanding to explore plasticity in the auditory system after cortical lesions, as well as the potential therapeutic effects of electrical stimulation on auditory processing. His most recent work continues to push the boundaries of understanding how to protect and restore hearing, a field with profound clinical implications.

Beyond his scientific achievements, Merchán's role as a mentor and administrator stands as a testament to his far-reaching influence. His legacy is defined by his groundbreaking contributions to the field, his unwavering commitment to nurturing the next generation of Spanish



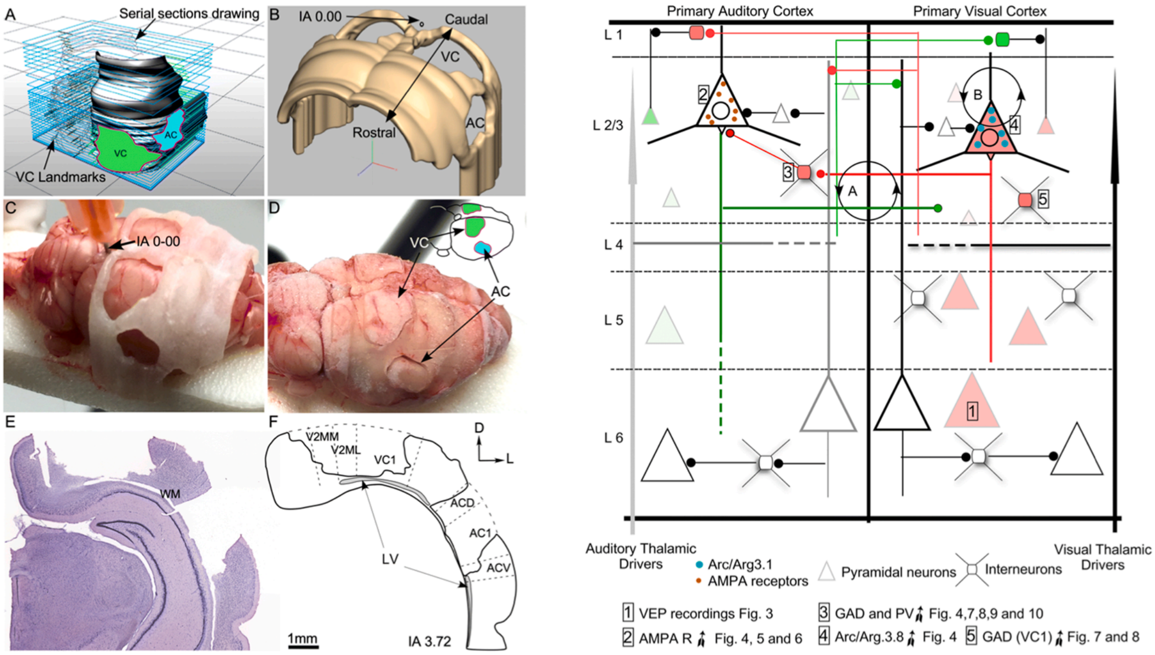
A. Inhibitory neurons of the rat ventral nucleus of the lateral lemniscus



B. Tonotopic organization of the cat ventral nucleus of the lateral lemniscus

Fig. 11. Representative examples of Miguel A. Merchán's scientific achievements. **A.** Immunostaining of adjacent semithin sections with antibodies against GABA or glycine revealed the chemical heterogeneity of the rat ventral nucleus of the lateral lemniscus. Presumably excitatory neurons (weakly immunoreactive for both GABA and glycine) are abundant in the dorsal third of the nucleus (more recently identified as the intermediate nucleus of the lateral lemniscus [e.g., Gómez-Martínez et al., 2023]). In contrast, inhibitory neurons (strongly immunoreactive for both GABA and glycine) predominate in the ventral two-thirds of the nucleus. (*Adapted from* Riquelme et al., *2001*, *Figs. 4*, *8A and 8D*). **B.** Injection of the bidirectional neuroanatomical tracer biotinylated dextran amine (BDA) into the central nucleus of the inferior colliculus (CNIC) in the cat revealed a complex, mosaic-like tonotopic organization within the ventral nucleus of the lateral lemniscus (VNLL). The yellow, red, and blue clusters of labeled elements in the VNLL (right panel) were produced by tracer injections into the high-, middle-, and low-frequency regions of the CNIC, respectively (left panel). (*Adapted from* Malmierca et al., *1998*, *Figs. 3A-C and 10*).

A. Cross-modal reaction of auditory and visual cortices after long-term bilateral hearing deprivation in the rat



B. Compared to transcranial alternating current stimulation, transcranial temporal interference stimulation decreases neural

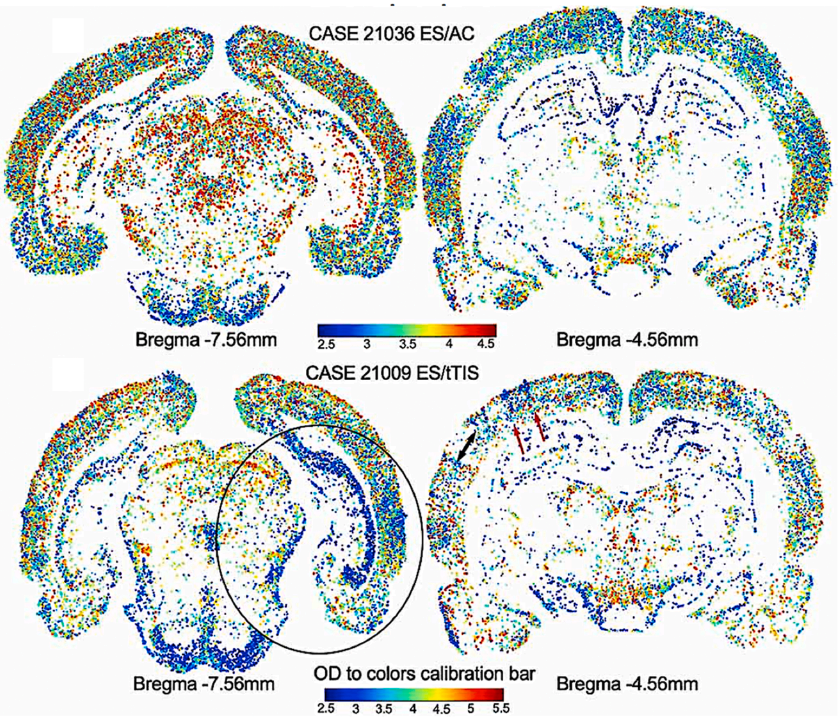


Fig. 12. Representative examples of Miguel A. Merchán's scientific achievements. **A. Left panel.** Three-dimensional mold of the rat brain designed to enable precise extraction of separate samples from the auditory and visual cortices. (*Reproduced from* Pernía et al., *2020*, *Fig. 2*). **Right panel.** Working hypothesis explaining the cross-modal reaction between the auditory and visual cortices after long-term hearing loss. (*Reproduced from* Pernía et al., *2020*, *Fig. 11*). **B.** Maps of the optical density of c-fos immunostained sections of the brains of rats exposed to a single session of either alternating current stimulation (upper row) or temporal interference stimulation (lower row). (*Reproduced from* Carmona-Barrón et al., *2023*, *Fig. 5*).

Fig. 13. Picture taken during the symposium "The Roots of Auditory Neuroscience in Spain: From Past to Future", organized as a tribute to Prof. Miguel A. Merchán on the occasion of his 70th birthday and held in Salamanca in June 2023. At almost 95 years of age, Prof. Osen, the scientific "godmother" of the Salamanca Group, traveled from Norway to Spain for the event. From left to right: Victoria ("Vicky") M. Bajo, Enrique Saldaña, Miguel A. Merchán, Kirsten K. Osen, Manuel ("Manolo") S. Malmierca, Dolores E. ("Lita") López, and Ignacio ("Nacho") Plaza (Merchán's longtime technician).

scientists, and his leadership in fostering scientific collaboration and innovation. His work continues to inspire and guide emerging researchers, and his ongoing investigations into the plasticity and protection of the auditory system hold the potential to uncover critical insights into hearing loss and associated disorders. The path he has blazed ensures the strength of Spanish auditory neuroscience for years to come.

6. Addendum

This article provides an overview of auditory neuroscience in Spain, tracing its roots from the pioneering work of Cajal to the significant contributions of Miguel A. Merchán and his academic lineage. Numerous other researchers based in Spain, though not directly connected to Cajal, have also made substantial advances in our understanding of the auditory system over the past few decades. Notably, considerable progress has been made in the study of inner ear development, both under normal and pathological conditions, by scientists such as Isabel Varela Nieto (*Consejo Superior de Investigaciones Científicas [CSIC]* and Autonomous University of Madrid), Fernando Giráldez (University Pompeu Fabra, Barcelona), Thomas C. Schimmang (CSIC and University of Valladolid), and Matías Hidalgo Sánchez (University of Extremadura, Badajoz). Special recognition is also due to Carles Escera (University of Barcelona), who has employed cognitive neuroscience tools to elucidate the mechanisms of auditory and speech perception, attentional control, and certain neurodevelopmental disorders, using mismatch negativity.

CRediT authorship contribution statement

Enrique Saldaña: Writing – review & editing, Writing – original draft, Conceptualization. **Fernando de Castro:** Writing – review & editing, Writing – original draft, Conceptualization. **Dolores E. López:** Writing – review & editing, Conceptualization. **Manuel S. Malmierca:** Writing – review & editing, Conceptualization.

Declaration of competing interest

None.

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Data availability

No data was used for the research described in the article.

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