

# Agustín González, an Inspirational Leader in Spanish Comparative Neuroanatomy

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## Introduction

It is our pleasure to open this Festschrift dedicated to our mentor Prof. Agustín González (Fig. 1) on his retirement after more than 40 years of academic work at the Universidad Complutense de Madrid. Agustín is a key figure in the field of comparative neuroanatomy, essential to understanding the evolution of this field in Spain and beyond over the last decades. This special issue collects a rich number of contributions by collaborators, pupils, and colleagues from all over the world, reflecting the impact of their achievements and the respect and admiration of the entire international community. The volume also serves as a homage to Prof. Luis Puelles, an occasional collaborator of Agustín and another giant of Spanish neuroscience.

In this commentary, we summarize Agustín's work as a researcher, teacher, mentor, and member of the scientific community. We also consider the broader impact of

Agustín's activity, primarily when it comes to its ability to influence others. As alumni from his laboratory, we do this from a very personal point of view, reflecting on our imperfect memories of the time we spent together. We wish that this imperfect historical glimpse on Agustín's professional career will bring a smile to the face of the many colleagues who have worked with Agustín over the past few decades and inspire those who have not personally known him.

## Researcher

Agustín started working on comparative neuroanatomy while he was still an undergraduate student of Biology at Universidad Complutense de Madrid (Spain). He joined the Department of Microscopic Morphology (later renamed Department of Cell Biology) to work with Alfredo Carrato and Margarita Muñoz, who later directed his doctoral thesis. As a student, Agustín was fascinated

A complete list of publications of Agustín González, included those cited in this commentary, can be found as a separate item in this special issue.



**Fig. 1.** Prof. Agustín González. This picture was provided by Agustín González, so we have his explicit consent for publication.

by the evolution of the nervous system, so he initially chose amphibians as an experimental system because they represent the first group of tetrapod vertebrates that successfully conquered the terrestrial environment. His first studies focused on the characterization of several structures of the rhombencephalon and mesencephalon, including the cerebellum, interpeduncular nucleus, and oculomotor nucleus in the frog.

During his predoctoral period, Agustín began a close relationship with the Dutch school of neuroanatomists that lasted during his entire career. At that time, Dutch neuroanatomists were pioneering many of the techniques that were subsequently used worldwide for the study of brain connectivity, and Agustín soon realized that these methods were going to be critical for his research. He first visited the Department of Anatomy and Embryology at the University of Nijmegen, where he learned to use the enzyme horseradish peroxidase as a retrograde tracer to study neuronal connections with Hans ten Donkelaar. Using this approach, he described for the first time the detailed connectivity of the cerebellum and several other mesencephalic and rhombencephalic structures in amphibians [González et al., 1984; González and Muñoz, 1987a, 1987b].

After finishing his doctoral studies, Agustín returned to the Netherlands, this time to the Department of Anatomy and Embryology at Vrije Universiteit in Amsterdam. There he joined the group of Anthony Lohman to investigate the connectivity of the striatum in the gecko, his first experimental study in reptiles [González et al., 1990]. This period was to have a great impact on Agustín's subsequent career, not only because he would learn to combine immunohistochemical approaches with the tracing

of axonal connections, but also because it is during this period that he became fascinated by the telencephalon, the structure that exhibits the greatest variation among tetrapods.

On his return to Madrid, already as an Associate Professor in Cell Biology at Universidad Complutense de Madrid (Spain) when he was only 23 years old, Agustín decided to focus his efforts on characterizing the catecholaminergic system in amphibians. In collaboration with Wil Smeets, this research program led to the identification of the structure homologous to the substantia nigra and ventral tegmental area of mammals in several groups of amphibians [González and Smeets, 1991; González et al., 1994; González and Smeets, 1994; González et al., 1995a] as well as the characterization of a primitive locus coeruleus in this group of vertebrates [González and Smeets, 1993; Marín et al., 1996].

The identification of the dopaminergic innervation of a telencephalic structure homologous to the mammalian striatum in amphibians reignited a debate about the evolution of the basal ganglia in vertebrates. Ever since Pedro Ramón y Cajal described the corpus striatum in the frog [reviewed in Triarhou and del Cerro, 2008], it had been assumed that the complex organization of the basal ganglia arose with the appearance of amniotes during evolution (reptiles, birds, and mammals). In a series of studies exploring the connectivity, neurochemistry, and development of the basal ganglia [Marín et al., 1997a, 1997b, 1997c, 1997d, 1997e, 1998a], Agustín determined that many of the main characteristics of the mammalian basal ganglia, including the existence of dorsal and ventral striatopallidal systems, dopaminergic afferents from the midbrain, and efferent connections to premotor structures such as the superior colliculus, were also present in modern amphibians. These results revealed that elementary basal ganglia structures were already present in the brain of ancestral tetrapods and that they were organized according to a general plan shared today by all extant tetrapods [Marín et al., 1998b].

More recent studies from his laboratory have revealed additional conserved features of the basal ganglia of amphibians. For example, he described the expression of DARPP-32 in projection neurons of the striatum [López et al., 2010] as well as the existence of interneurons in this structure that follow a developmental program shared with mammals [González et al., 2002b]. The exploration of neural systems from a developmental perspective has been a constant in Agustín's research, critical for the identification of conserved and derived features in the organization of the vertebrate brain.

Agustín mapped numerous other neurochemical systems in the amphibian brain, including neuropeptidergic [González and Smeets, 1992; Tuinhof et al., 1994; González et al., 1995b; González and Smeets, 1997; González et al., 1998; Muñoz et al., 2001; González et al., 2003; López et al., 2006a, 2006b, 2007; Domínguez et al., 2008; López et al., 2016], cholinergic [Marín et al., 1997f; Marín and González, 1999; González et al., 2002a; López et al., 2002; Sánchez-Camacho et al., 2006], and nitrergic [Muñoz et al., 1996b, 2000; González et al., 2002c; López and González, 2002; Moreno et al., 2002] neuronal populations, as well as those defined by the expression of specific calcium-binding proteins [Morona et al., 2006; Morona and González, 2008, 2009, 2013]. There are few other laboratories in the world that have managed to characterize the organization of the brain in a group of vertebrates with such a level of detail and insight.

In collaboration with Hans ten Donkelaar and Margarita Muñoz, Agustín also explored the somatosensory system of amphibians. Combining tract tracing and immunohistochemistry, they characterized the dorsal column nucleus and the lateral cervical nucleus of amphibians as well as the homologue of the mammalian spino-cervicothalamic system [Muñoz et al., 1995, 1996a, 1997]. Through these studies, Agustín described the ascending tracts by which sensory information from the peripheral nerves is transmitted to central nuclei, providing evidence that the organization of the three main ascending sensory channels shares many features in the brain of both anamniotes and amniotes. In addition, Agustín characterized the descending pathways modulating spinal cord neurons in amphibians, including for example the main catecholaminergic projections [Sánchez-Camacho et al., 2001a, 2001b, 2002].

The amygdaloid complex is another major telencephalic structure that has been thoroughly characterized by the laboratory of Agustín González. Focusing primarily on anurans, they described the main subdivisions of the amphibian amygdaloid complex based on their developmental origin (pallial versus subpallial), connectivity and chemoarchitecture [Moreno and González, 2003, 2004, 2005a; Moreno et al., 2012b]. As in amniotes, the amphibian amygdala is strongly connected with the olfactory and vomeronasal systems and is the origin of important hypothalamic projections. Altogether, their findings on the organization of the anuran amygdaloid complex support the idea that a basic plan is shared by tetrapods in which fundamental features can be distinguished [Moreno and González, 2006].

Agustín's work also shed light on the organization of the rest of the forebrain and not only in amphibians, but also concerning the anamniote/amniotic transition. Using the expression of developmental regulatory genes and other markers in combination with tract tracing methods, he defined the boundaries of the amphibian pretectum and its three anteroposterior domains [Morona et al., 2011, 2017], the rostral and caudal progenitor domains of the thalamus, progressively specified and compartmentalized during pre-metamorphosis [Bandín et al., 2015; Morona et al., 2020], and the main components of the alar and basal domains of the amphibian hypothalamus [Domínguez et al., 2013, 2014], as well as some elements of its connectivity [Moreno and González, 2005b]. These studies revealed that the diencephalon and the hypothalamus of amphibians are organized according to a general plan shared with amniotes, although some differences exist [Domínguez et al., 2015].

To characterize more precisely the evolutionary changes in vertebrates, Agustín extended the spectrum of experimental techniques used in his laboratory and expanded his studies to include different genera of fishes. First, he started with the lungfishes, the closest living representatives of Sarcopterygii to tetrapods. Initially, in collaboration with Glenn Northcutt, they used this model to describe the main telencephalic subdivisions and, for the first time in a non-tetrapod, the brain centers and connections involved in processing vomeronasal information [González and Northcutt, 2009; González et al., 2010; Morona et al., 2018]. In other studies, he defined the neurochemical organization of the brain, including catecholaminergic [López et al., 2017, 2019a], serotonergic [López and González, 2015], cholinergic [López et al., 2012], and nitrergic [López et al., 2019b] systems. These studies revealed that the neurochemical systems in the brain of Actinopterygii and Sarcopterygii are more complex than previously thought and share many features with amphibians and amniotes.

In parallel to his study of the connectivity and chemoarchitecture of the amphibian brain, Agustín developed a research program focusing on the expression of transcription factors in the developing and adult brain. In addition to characterizing the expression of *Nkx2-1* in the development of the subpallium and the origin of telencephalic interneurons [González et al., 2002b; Moreno et al., 2018], Agustín investigated the expression of several genes of the LIM family, in collaboration with Sylvie Retaux [Moreno et al., 2004, 2005, 2008a]. More recently, he also explored the expression of several members of the Pax family of transcription factors to define multiple re-

gions of the amphibian brain during development and in the adult [Moreno et al., 2008b; Bandín et al., 2013; Joven et al., 2013a, 2013b; Bandín et al., 2014] and extended some of this work to the brain of reptiles [Moreno et al., 2010, 2012a]. Altogether, these studies strengthened the homology of multiple areas of the amphibian brain with the corresponding brain structures in amniotes and clarified the homology of less precisely characterized regions.

### Teacher and Mentor

Agustín's career as a university teacher started very early and advanced in parallel to his research activity for nearly 40 years. This allowed him to recruit undergraduate students from early stages, who would eventually continue their work as graduate students in the lab. Perhaps related to his love of cinema and other forms of performing arts, Agustín was a very effective and extremely engaging teacher – in the classroom, he was a showman. Agustín knows how to tell a story and he does it very well, so when it came to teaching, he always prepared well and put the necessary emphasis on all the important elements of the stage: the aesthetics of the slides, the projection of the voice, the ability to build interest around important concepts with well-planned transitions, etc.

Agustín spent a large part of his teaching career on laboratory demonstrations on many different subjects imparted by the Department of Cell Biology, so most graduates in biology at the Universidad Complutense have been Agustín's students at some point. He did this because above all he enjoyed the contact with his students and the freedom of learning that practical lessons allowed. He also had what seemed like endless amounts of energy, which during high teaching season would effectively translate very often on eight straight hours of demonstrations.

In recent times Agustín also took over the subject of cellular neurobiology, much more directly related to his research. As part of this subject, he introduced in the course work the concepts of the prosomeric model originally proposed by Luis Puelles and John Rubenstein. In addition, although Agustín always exhibited a strong intolerance for management positions – or any kind of job in which internal politics were important for that matter –, during the last years of his career he accepted to become the director of the PhD program in biology at the Universidad Complutense. So, one way or another, most graduate students in this program have interacted with Agustín during the last years of his career.

Agustín was also a remarkable teacher as a mentor to his pupils. He was completely hands-on and guided new lab members through all the important steps, from experimental design to surgeries to microscopy and documentation. Although he consistently gave detailed direction, he also allowed a lot of freedom to his students and encouraged them to learn from the usual mistakes of inexperience. Despite being a very prolific scientist, Agustín always had the patience to wait for his pupils to come up with the first draft of any paper. He had a very basic but effective method for writing papers: he would begin by writing the main ideas in separate pieces of paper, which he would eventually order by juggling them around over his desk. We essentially learned to write papers using this approach to organize and connect our ideas.

Agustín managed his laboratory with great care. Although he was allergic to university politics, he had an amazing capacity to oversee his group and always found the time to deal with problems by giving everyone their own space and dedicated attention. He managed frustrations, egos, and complicated personal situations with great ability and consistently gave credit to those who earned it. Not being a natural-born leader, he nevertheless managed to create a consistently good atmosphere in his laboratory. Part of his success was his ability to relate with his pupils not only through science but also through many of his other passions, from cinema to music to languages and arts.

Agustín also provided great opportunities for the personal and professional development of his pupils. He encouraged them to attend meetings to present their research, both nationally and internationally. Agustín was strongly anti-hierarchical, and he consistently treated even the most junior student like veterans, introducing them to other members of the scientific community at the first opportunity.

### In the Scientific Community

Agustín is very well known in the community of comparative neuroanatomists, not only because of his extensive work but also because he is an extremely relatable and social person. He attended national and international meetings with great regularity, in no small part because it fed his passion for travelling around the world. If you were to ask anybody in the scientific community about Agustín, they will consistently say that “he is a good guy” – we think that's saying a lot about a person.



Agustín developed an extraordinary number of very successful national and international collaborations. Many of these collaborations were driven by his interest in investigating the brain of other groups of vertebrates. For example, we collaborated with Manuel Pombal (“Peque”) to investigate the brain of lampreys, Isabel Rodríguez-Moldes and Ramón Anadón on multiple groups of fishes, Glenn Northcutt and his wife Mary-Sue on lungfishes, Hans ten Donkelaar and Wil Smeets on reptiles, etc. He also developed collaborations to enable new approaches in his lab, such as his work with Philip Vernier on dopamine receptors or with Sylvie Retaux on the expression of transcription factors. All these collaborations not only were extremely productive from a scientific point of view but also led to lifelong friendships. Agustín is very hard not to like!

Agustín and Luis Puelles – the two scientists celebrated in this special issue of *Brain, Behavior and Evolution* – were among the founding members of the Pedro Ramón y Cajal Club of Comparative Neurobiology, which has promoted this field of research in Spain over the past 20 years. Agustín likes to tell the anecdote of how the Pedro Ramón Club was born on a bar napkin during a post-meeting dinner, which he often thought more productive than the meeting itself, during the 1995 meeting of the Spanish Society of Neurosciences (SENC) in Valladolid. Since then, the club has not stopped meeting any year as a satellite of the SENC meetings, with Luis as president of the club and Agustín as its secretary. This is probably the only not strictly scientific job that Agustín has ever had – due to his phobia of bureaucracy, management, and university politics – and he enjoyed it greatly because it allowed the entire community of Spanish comparative neuroscientists to meet regularly.

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## Beyond

The legacy of Agustín’s work in the field of comparative neurobiology is unmeasurable. He revolutionized our understanding of the organization of the amphibian brain and generated a comprehensive framework in which to comprehend how the brain of primitive vertebrates evolved during the colonization of the terrestrial environment and the anamniote/amniote transition. Beyond this, he created a school that will continue to extend his legacy in the best tradition of Spanish neuroanatomy.

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## Conflict of Interest Statement

The authors have no conflicts of interest to declare.

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## Author Contributions

O. Marín and N. Moreno wrote the commentary.

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