

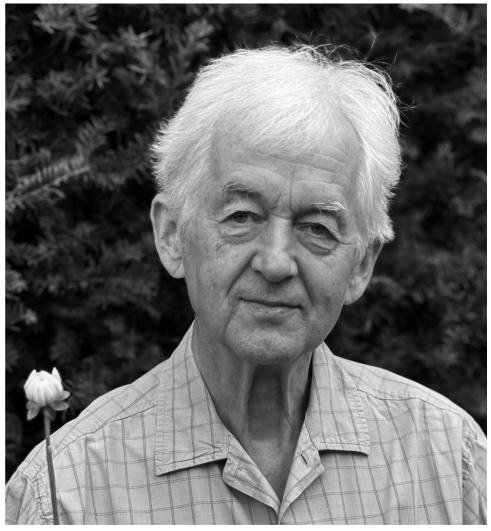
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Peter Somogyi

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Loránd Eötvös University, Budapest, Hungary (Biology, 1969–1975)
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Visiting Research Student, Department of Pharmacology, Oxford, UK (1973–1974)
Junior Research Fellow, 1st Department Anatomy, Semmelweis Medical School (1975–1983)
Research Fellow, Department of Human Physiology, Flinders Medical School, Adelaide, Australia (1983–1985)
Associate Director to Director, Medical Research Council Anatomical Neuropharmacology Unit, Department of Pharmacology, Oxford University, UK (1985–2015)
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Charles Judson Herrick Award of the Association of American Anatomists (1984)
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Elected Fellow of the Royal Society of London (2000)
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Elected Fellow of the Hungarian Academy of Sciences (2004, resigned 2020)
Elected Fellow of The Medical Academy of Sciences, London (2006)
Elected Member of The German National (Leopoldina) Academy of Sciences (2006)
Elected Member of the Academia Europaea (2009)
The Feldberg Prize and Lectures, Germany, Feldberg Foundation, London, UK (2009)
Sanford L. Palay Prize (USA), *Journal of Comparative Neurology* and Cajal Club (2010)
The Brain Prize, Grete Lundbeck European Brain Research Foundation, Copenhagen (2011)
Hungarian State Award of the Middle Cross for Services to Science (2011)
Honorary Doctorate, Loránd Eötvös University, Budapest (2013)
Elected Member of the European Molecular Biology Organisation (EMBO) (2014)
Honorary Doctorate, The University of Zurich, Switzerland (2014)

Peter Somogyi has explored the synaptic organization of the mammalian brain, including the cerebral cortex, the basal ganglia, the thalamus, the cerebellum, and the brain stem. He sought to define the location of interactions among distinct cell types operating cooperatively in space and time, what he called the chronocircuits of the brain. He introduced a cell-type definition based on the quantitative distribution of postsynaptic subcellular domains of GABAergic cortical neurons; and he discovered and named the axo-axonic cell, the bistratified cell, and others. With his colleagues, he identified the brain state and behavior-dependent spike timing of more than 15 distinct types of GABAergic neuron in relation to the frequency and phase of network oscillations in the hippocampal formation. He also defined the high-resolution subcellular location of pe- and postsynaptic neurotransmitter receptors in relation to synaptic release sites. He maintains that explanations of normal and pathological events in the brain can only come from the rigorous definition of the neuronal circuits that underlie these events.

Peter Somogyi

Prologue: Becoming A Neuroscientist—A Very Unlikely Event

I consider myself extremely lucky to be still around and have access to facilities, microscopes, and literature, and to be in the company of wonderful colleagues in the University Department of Pharmacology as well as spend time with my three children and seven grandchildren. As I look back, my life and continued presence seem very unlikely. Indeed, most of my school and university mates are no longer around. I could have passed away several times; the closest call was when as a student after a cryptic sport injury I was lying on the floor of a hospital, neglected and unconscious with mistreated sepsis, just as my wife, Klara, came to visit and saved me at 21—one undeniable advantage of marrying a charismatic schoolmate at the age of 20. Apart from luck, I was also blessed with exceptional determination, reacting to numerous adverse events in my life with the instinct that there "must be a way," which sometimes worked and at other times did not. Growing up in poverty in Soviet Union–occupied, corrupt Hungary ruled by a Communist Party, as a people we learned how to wriggle around senseless regulations and restrictions. In terms of scientific development, I also had exceptional luck in meeting great human beings and scientists who saw something in me that was worth supporting. Exceptional teachers carried me on their shoulders from first year primary school right through postdoctoral years.

As I look back on 60 years of scientific exploration from the time when I prepared my first observational report on a multiyear homemade nestbox study of breeding birds for a national biology competition as a high school pupil to my last microscopic observation this week, I feel truly fortunate. I treasure two aspects of scientific experience: the occasional emotional thrill of the unexpected observation or insight and the stimulating company of colleagues with whom to share observations and thoughts. As a biologist and nature lover, I keep repeating "this is worth living for" whenever I experience the wonders of the natural world. I prepared to become a zoologist from childhood and explored interwoven animal communities of recognizable species. Later, unconsciously, I transferred the view of the functioning of ecosystems to the exploration of neuronal networks. I have sought to *define the location of interactions* among distinct cell types operating cooperatively in space and time, in what I call the *chronocircuits* of the brain. I maintain that explanations of normal and pathological events in the brain can only come from the rigorous definition of the neuronal circuits that underlie these events.

Family and Childhood

The lives of my parents were completely turned upside down by World War II. They lived in East Hungary bordering the Soviet Union, and as the Soviet army invaded, they lost everything, the house, the garden, the poultry, and the friendly pig. My father, Pal Somogyi, was in the Hungarian army retreating on foot toward the West in front of the Soviet army, avoiding being caught and pushed forward by the Germans until he ended up in a U.S. prisoner-of-war camp in Austria. He eventually escaped and walked back to Hungary, joining my mother at her parent's village, Ölbő in Western Hungary. They moved to the town of Szentendre in central Hungary where two of my father's siblings were growing vegetables on a small island in the river Danube. When they arrived with my older sister at an abandoned former servants' farmhouse, they started life by collecting straw to sleep on. I grew up in this house, which had no running water, but we had our own well, and had an outside pit loo, some distance from the house, a most uncomfortable facility in the harsh −20 degree Celsius winter realities of the 1950s.

My father had limited schooling, but was exceptionally talented, so he had been promoted in the military of the fallen regime and could have had a promising future. In postwar Eastern Block Hungary, however, where many were jailed or hanged for little or no reason, he was afraid of being prosecuted. Therefore, he changed his identity, avoided meeting anyone from his past, and abandoned all ambition to make it in society. He lived in fear, which eventually wore him down and he became a bitter man. His spirit was broken. Nevertheless, he survived after most of his stomach was surgically removed because of an advanced ulcer, but as a result, he could eat only a little bit at a time. In addition to the farmwork of growing vegetables and flowers for market, he took a job as an unskilled laborer, sleeping little, working three shifts on alternate weeks, in a paper factory, where nobody asked about his past. He spent his working life moving heavy bales of wastepaper to and from the vaults and machines until retirement. He was incredibly strong and thin. He lived out his creativity by growing plants, experimenting with conditions and new varieties for which he traveled all over the country. He read the farming and gardening periodicals; he could have been a brilliant scientist. As the farm developed, we constructed huge glass and polyethylene tunnel greenhouses, inventing parts, making glass frames from scratch. The whole family worked day and night with our mother and three siblings under his instructions. It was relentless labor seven days a week. Twice a week on market days, my younger brother and I were woken at 4 a.m., and we pulled a wooden cart packed with produce to the market; we had to sell everything by the time school started at 8 a.m. We handled what seemed to us lots of money from the sales, which we had to hide, and after school taking the cart home, we

were allowed the reward of an ice cream. Our parents worked six days a week doing shift work in factories that started at 6 a.m.

My mother, Gabriella Kotanczi finished high school and was also a very intelligent, warm-hearted person, who dedicated her life to us, the four surviving children—the first-born daughter Katalin died suddenly at home at three years old, probably of meningitis. To generate income, my mother also went to work in a factory making cement building materials such as pipes and floor tiles. She worked in a water-logged, cold hall polishing tiles, eight hours a day in extremely unhealthy conditions and eventually contracted tuberculosis, which she tried to ignore until she became critical. After hospital treatment, she was sent to a sanatorium for many months while our older sister looked after us. We learned responsibility, solidarity, and loyalty and had more duties on the farm while looking after our schooling. Our mother survived and recovered, but she could not continue in the factory floor and was given a job as an administrator of a worker's hostel for migrant workers from other parts of the country. She coped well and was much loved by the young workers for whom she acted like a mother. She retired with distinction and continued the farm work that my work-addicted father could not abandon, even when all the children had left.

The rural environment was incredibly stimulating next to the Danube, which occasionally flooded our farm on a small island and only a stone's-throw away. I remember picking tomatoes from a boat with my father. In the summers, my friends, my brother, and I constructed from greenhouse glass frames hideaway huts in a hillside jungle next to the farm and slept there while the weather permitted, even at school times, but we had meals in the house with the family. We fished when my younger brother and neighborhood kids were off work and proudly prepared the mostly small fish catch for frying. Even when I was in high school and started dating my future wife, Klara, I took my freshly caught fried fish to impress her and her parents. Strange to think that this behavior must have been a kind of nuptial present ritual, but of course it all felt very showy at the time. We made dugout canoes from decaying tree trunks, swam in the river, or skated on it when it froze over, and in general lived a high-risk, challenging existence that probably made us innovative. Sadly, each year some children were lost in the town to drowning.

Schooling, Matriculation, National Service, and Starting University

School was easy for me in Szentendre, as I tended to be in the top few of each class and tried to minimize the effort and time spent on homework. By the time I started first grade at age six, I could read and write as I learned it by following my older sister's homework. I was good at reciting

poems and had to perform in class and on the annual school closing award ceremonies. From the earliest I can recall, I had an insatiable interest in animals, anything that moved. We kept pigs, goats, all kinds of poultry and rabbits for eating, and several dogs and cats. The goats provided the milk, and from the age of four or five, my younger brother and I had to look after the feeding of the goats and ensuring that they did not harm the vegetables. Goats are highly intelligent, crafty animals well versed in hierarchy and human psychology. They knew exactly when we were not paying attention and were off to mischief. We had to keep the unruly ones on long chains and walk with them for grazing. In the summers, while our parents worked away in the factories, we were farmed out to my grandmother, who lived far away in a truly rural farming village without any paved road, Ölbő, and ran a self-supporting farming existence with her son next door. They kept cows and every imaginable animal, ducks, geese, guinea fowl, turkey, pigeons, and pigs, the latter as the main source of cooking fat and meat. My uncle was passionate about animals and perhaps because he had no children, he loved to explain to us their behavior, development, and personalities. If there is any genetic inclination for loving animals, then I must have shared those genes with him. He was the village tailor and kept constantly singing canaries and goldfinches in his workshop while he worked the sewing machine.

My mother and particularly my godparents noticed my interest in animals, and they bought me books from a very early age, which I treasured and kept copying out the pictures into collections of drawings. The most impressive multivolume book I got for one Christmas was by the German naturalist Alfred Edmund Brehm, his *Life of Animals*, a systematic treatise of the animal kingdom, which I still have. In my primary school years, I met two eccentric nature lovers, who greatly influenced my life. György Jusztusz was an ex-army officer beekeeper, who kept about 50 hives on my parents' farm and gave us jobs to help monitoring the honey intake and ensuring that the bees had drinking troughs. He worked as a bus conductor and loved wild animals, spending some nights in the forest just watching the behavior of whatever appeared in the evening or at dawn. He knew the forest like the palm of his hand for miles and miles and recognized the individual foxes, deer, wild boar, and the various birds. He took me with him initially just for an evening walk then later as I grew to stay overnight sleeping on hunter's platforms or on the ground. It was magical.

The other naturalist, Sandor Urban, was a biology teacher from a nearby village, who knew birds well and reported his observations to the Ornithological Institute in Budapest. He also ran a farm with lots of animals, lived with his old mother and had a large orchard of hundreds of fruit trees that he populated with homemade bird nest boxes of every variety. He introduced me to nesting behaviors and timings, and I helped him to repair and clean the boxes several times a year. We also made

bird-watching walks along the Danube, and he introduced me to ornithologists at the institute. Under all these influences, I decided to become an ornithologist, and from early on, I was making my own observations and reporting. At our farm, I made nest boxes from scrap wood and even from cement water pipes, and was taking notes of species, egg-laying times, hatching and fledging successes, or the inevitable losses to predators, poisoning, and disease. At the age of thirteen, encouraged by my high school biology teacher, Roza Benedeczky, I wrote up my notes and results on breeding birds and submitted it to a national competition, achieving sixth place in the country. The award meant that I did not have to take the admission exam in biology for university courses that included biology.

The bird nest box operation expanded even further when I met the father of a high-school mate Edit Madas. Dr. Laszlo Madas was the director of a large state forestry organization, the Pilis Park Forest Company, in the area where we lived, the Danube Bend. I persuaded him to get nest boxes made for birds, which we placed with Sandor Urban and friends in colonies in the forest. By my high-school years, I was also conducting birds-of-prey surveys in these mountains with my schoolmate and future wife, Klara, Molnar, mapping and numbering nests, monitoring breeding results, and climbing to nests to put aluminum rings on the leg of the chicks for monitoring in the national survey; I kept this up also in university years. Already as a high-school pupil, I was attending some of the monthly meetings of the Zoological Society in Budapest, where great zoologists were lecturing about their collecting explorations around the world. Encouraged by scientists at the Ornithological Institute, I submitted a small result of the birds-of-prey surveys and gave a short 10-minute talk that was published as an abstract, my first scientific output with a hand-drawn map of nest sites of highly endangered species, such as the saker falcon and black kite (Somogyi, 1971).

These activities kept me in touch with ornithologists in the institute, which I visited regularly for advice and to marvel at their work. One person in particular, Egon Schmidt (1931–2023), liked me and treated me like a son, taking me out on field trips; we became friends. His main project was the distribution and feeding patterns of owls, which he used to monitor small mammalian prey distribution from the regurgitated food pellets. During my high-school years, I collected pellets for him mainly from barn owls living in church spires, which was risky business as climbing into the dirty neglected spires with often rotten stairs and ladders was challenging, and we had to be ingenious to get up into the bell towers. Most priests have never been up in the spires and never realized what risks we took; we needed all the diplomatic skills and good-looking certificates of authorization to gain entry. Again, luck was on my side: We had no serious accidents. I learned to identify small mammals such as different species of mice, voles, and shrews as well as small birds based on the skulls and teeth

patterns and helped Egon in his work. This assistance resulted in my first scientific authorship on a full paper (Schmidt et al., 1970) reporting small mammal distribution in the Danube Bend, written in German by Egon.

High-school graduation and a successful university entry exam was followed by my one year of brutal national military service, far away from home and from Klara, who enrolled in a course of medical laboratory technician training in Budapest. We were rarely allowed home from the army, and Klara could visit only twice during the year. The entire purpose of the army service was subordination and patriotic indoctrination against Western imperialists, who were allegedly plotting to occupy us and defeat our "benevolent" protector, the Soviet Union. We were trained in an army base specially set up for future university graduates who were supposed to become reserve officers, which eventually I managed to avoid. We were constantly humiliated and threatened that we would not be allowed to start university if we did not obey the many senseless orders. I suppose the way of all armies is to instill blind obedience to some degree, but such training did not go well with my personality, and I suffered a lot.

Eventually, the year passed, and I could return home, back to farm duties in Szentendre. I was determined to leave my family and managed to get a bed in the student dormitory of Loránd Eötvös University in Budapest, along with seven other students in a room furnished with four bunkbeds. It was a riotous community, a Mongolian, a Bulgarian, a Russian, a Ugandan, and us four Hungarians, all in different courses, which was enriching. One of the Hungarians was Jozsef Somogyi (no relation), who became a lifelong friend and later colleague at Budapest and Oxford. The room was not conducive to studying, or anything other than socializing, there was very little privacy, and several girlfriends would stay for the night, which was against the rules, but not strictly enforced. There were a few crowded study rooms, and those interested in studying were using every corner of the building, even the communal bathrooms. Lifelong friendships and intimate relationships formed, and we found Budapest an exciting place.

In socialist/communist Hungary, education was a high priority, and the state provided a means of existence for high-achieving students with disadvantaged backgrounds. I was accepted for a small scholarship and received free accommodation in the dormitory and three meals a day. In addition, visiting my parents at weekends and helping on the farm, I came back loaded with food for the week. For any luxuries, such as the odd book, a movie, or camping gear, I did odd jobs, the most memorable being as a crew member on a dustbin lorry at nights in a harsh winter when the usual crews left for the more lucrative snow-clearing jobs. Some of the crew members were hardened criminals exploiting us students, but it paid well and did not last long, and we did not think about risks. Now the memories feel romantic.

Notably, my zoology professor, Janos Balogh, encouraged me to orient toward insects, as he was a world expert on soil mites, which he collected all over the tropics of the world, bringing hundreds of thousands of invertebrates preserved in alcohol and kept in jars. As a first-year student, I spent my weekends and summer selecting the raw collections into groups of animals and the ones of interest to Professor Balogh even into insect families. These jars contained large numbers of species unknown to science, and the diversity, forms, and colors of the tropical creatures were just amazing. I made several enthusiastic attempts to specialize in some groups, also following the examples of more senior students, but eventually I gave up my childhood dream to become a zoologist. The decisive factor could have been that I lacked confidence that I could become a great zoologist on my own without an outstanding teacher to work with, and none of those I met provided the inspiration I craved. In retrospect, I probably underestimated the power of individual initiative and originality while overestimating the need for the guidance of a supervisor.

Marriage and a Most Unlikely Life-Changing Event: Student Internship in Oxford

I met my future wife, Klara Molnar, in high school. We were in the same class from the age of 15, but only truly discovered each other when we turned 17 after a school trip to Budapest. Soon enough, we fell in passionate love, so much so that one of my teachers warned me not to risk my promising studies and potential university future for some transient passion.

As a medical technician trainee in Budapest, Klara could not afford renting a room. However, a kind elderly couple allowed her to use a bed in their flat; she could not stay there during the day. So, our relationship flourished mostly around the university, and we went to the countryside in the weekends with a tent, where we surveyed nesting birds, as I intended to become a zoologist. At the end of my first university year in 1970, we decided to get married without any material basis for family life. We prepared for a traveling honeymoon and with two friends went to a registry office, got the papers signed, had a meal with them, and with our rucksacks embarked on a month of hitchhiking to Poland. The first afternoon, we did not get far; it was terribly hard to find a suitable hitchhiking spot out of sprawling Budapest, so by the evening, we had to bite the bullet and go by train to my sister's house in North Hungary that was in the direction of Poland. She was not amused when we turned up with rucksacks, and although our parents knew that we went traveling, we did not tell them about the marriage, as we thought marrying would not make sense to them, when four more years of studies awaited me without any income. We hitchhiked around Poland easily, warmly supported by the hospitality of

the Polish people and made it from the Carpathian Mountains in the south to the Baltic Sea in the north, our first experience of both high mountains and the sea.

By accident, we stumbled on a bird migration monitoring camp with huge walls of mist nets and scientists trapping and banding birds migrating along the Baltic coast, a program called *Actio Baltica* highly developed in Poland. We stayed with them for a week; it was exciting to learn both the recording system of measurements and the identification of species, ages, physical conditions, and energy status of individual birds. We took lots of photographs, and soon after I gave an account of our Polish experience back in Hungary, my friends established *Actio Hungarica* supported by Polish ornithologists. In subsequent years, driven by wanderlust in our early 20s, we worked hard and saved as much as we could for a summer escape on hitchhiking tours in naturally exotic places and meeting wonderful people in Mongolia, Romania, Bulgaria, Finland, Turkey, and Egypt. In Mongolia, hitchhiking on the steps for lorries transporting goods on dirt tracks, Klara and I also collected flies for a student friend, Dr. Laszlo Papp, who already specialized as a zoologist and was an expert on flies developing in animal dung. There was no shortage of that in a country with a hundred or more grazers for each human resident. We collected more than a hundred thousand flies, mostly small ones, killed them with cyanide and returned them in glass vials; Laszlo identified 43 species and 9 genera new to science, naming one after Klara (Nimosina clarae) and one after me (Norrbomia somogyii, now renamed, Copromyza somogyii).

In my second undergraduate year, I had a crisis of scientific direction and went to see my high-school biology teacher for advice, who introduced me to her husband, Dr. Istvan Benedeczky (1931–2020), a cell biologist at the Department of Pathology, Semmelweis Medical School in Budapest. Istvan invited me to see his work. He was an expert electron microscopist and had just come back from Oxford where he spent a research year as a Wellcome Trust visiting Fellow at the Department of Pharmacology. There he worked on exocytosis from adrenal chromaffin cells with David Smith, a young lecturer, who became his friend. I was captivated by the fine structural detail of cells and subcellular organelles and accepted his invitation to study in his lab in my spare time at university, which turned out to be most of the time. Soon I could carry out perfusion fixation of rodents, prepare specimens for electron microscopy (EM), cut sections, and take the images with all the accompanying darkroom work of developing negatives and printing.

Istvan was a warm-hearted and very cultured person who enjoyed and knew about classical music, literature, poetry, and our history; he became a father figure with whom I could share all aspects of my life. We remained lifelong friends until his passing during the Covid-19 epidemic. My project was to capture in EM images the effects of insulin treatment on chromaffin

cell secretion, which we studied in golden hamsters and rats. For reasons that are not clear to this day, it was very easy to see secretory granule exocytosis in hamsters (Benedeczky and Somogyi, 1975), but not in rats, even when the extruded dense core of the chromaffin granule was recognizable in the extracellular space in rats. I achieved no breakthrough in this project, but the technical difficulties of producing good fixation was excellent training. Later on, it was extremely rewarding for me that after his retirement, I could host Istvan with his wife, Roza, who was my high-school biology teacher, as a visiting scientist in Oxford in 1993. We completed a project on the identification of a calcium-storing compartment in the axon initial segments of cortical pyramidal cells, the cisternal organelle, associated with axo-axonic GABAergic synapses (Benedeczky et al., 1994).

To be able to achieve this, two decades earlier while still an undergraduate, I had to get to Oxford from Hungary, which was behind the Iron Curtain. For a student to study in the West was unheard of in 1972 when I applied for an exit permit. Istvan told me that as I had learned everything that he could teach me, he recommended me to David Smith for further research training. David duly sent an invitation letter covering travel and subsistence on a small scholarship from the J. H. Burn Trust. Formally, in the fifth year of my biology course at Loránd Eötvös University, we were supposed to do mostly a research project with few seminars until the final exams. I put together an application asking permission to do my project in Oxford, and the dean was sympathetic as I was known to be a top student. However, he warned me that there is simply no mechanism to process my application, and the Ministry of Education could not even accept it from the university for evaluation. The Cold War was still on in 1972. Frustrated, I was becoming an agitated caged beast, complaining to everybody about the denial of such an opportunity including a friend from high school whom I accidentally met on the street in Budapest. She told her father, Dr. Laszlo Madas, about my plight, who was the director of Pilis Park Forest Company for whom I did the bird nest box projects, and therefore he knew me personally. Members of the upper echelons of the Hungarian Socialist Worker's Party who ruled the country often hunted for deer and wild boar in the forest, and Laszlo had to accompany them. As it happened, in a few days after he learned about my plight, the Minister for Education arrived for a hunt and Laszlo teased him of why they would not let me go to Oxford, as he knew how brilliant I was supposed to be. To his credit, the minister got a message the next day to the university to submit my application, which was processed with high priority, including the application for a passport and a single permit to leave. As I was married, I insisted that the application for passport and leave was also processed for Klara.

The scholarship started in September, and I got my permit in mid-September, so I left, hoping that Klara's would follow. Her application was rejected after I left, a formality to reduce the chances of emigration. We

were not especially valuable, but if we had emigrated illegally the officer granting the permit would have faced investigation. Klara was pregnant with our first child, and the separation was a great emotional burden. When she stopped working, she moved back to her parents and gave birth to our son, Balazs, while I was in Oxford; I could not return to Hungary and continue in Oxford later, as only one exit permit was allowed; it was a difficult decision. She kept applying for an exit visa again and again and eventually was allowed to join me for the last month in Oxford, but our son had to stay behind with the grandparents. Such were the paranoid controls of the system. I met our son at six months, when we returned, but still had no place to live as a family.

In 1973, back when I was preparing for the possible visit to Oxford and while I was waiting for the exit permit, David and Istvan agreed on a research project that involved the electron microscopic localization of acetylcholinesterase (AChE) in chromaffin cells of the adrenal medulla. Previously, David discovered with Ian Chubb, then his doctoral student, that depolarizing *ex vivo* superfused ox adrenal glands with potassium, or upon stimulating them with ACh receptor agonists, a soluble AChE isoenzyme appeared in the perfusate, along with adrenalin and noradrenalin stored in the chromaffin secretory granules. A secreted AChE was most surprising, as AChE was supposed to be a membrane protein. Could AChE be also present in the chromaffin granules? The answer needed high-resolution subcellular localization of AChE. In the absence of antibodies, the enzyme could be localized at high resolution by its hydrolytic activity, which survived tissue fixation. As it happened, the world's top EM AChE histochemist was a Hungarian scientist, Professor Peter Kasa, at the University of Szeged, a town 200 km from Budapest. Dr. Kasa agreed to receive me for training, while carrying on with my studies. I commuted to Szeged sometimes by costly and slow trains, but mostly by taking the much faster but riskier route of hitchhiking. Professor Kasa was an inspiring teacher and allowed me to carry on in his lab even when he was not present. To progress as fast as possible, I carried specimens and reagents in vials back to Istvan's lab, even continuing with dehydration for embedding on the road. By the time I arrived at Oxford, I could localize AChE at motor endplates in the muscles and in the adrenal glands of rodents.

As I arrived at Oxford, I was determined to make a good impression on David Smith and Ian Chubb, but my English was so poor that they struggled to understand me. I enrolled in English evening classes and a kind teacher, Mary Blaschko, the wife of Dr. Hugh Blaschko who was originally a refugee from nazi Germany and was also David Smith's doctoral supervisor at the department, helped me to improve my communication. Mary and Hugh became lifelong friends. The project was exciting; with Ian we drove to the slaughterhouse to collect ox adrenals, which were removed for us, still warm, as soon as the animal was killed. Ian had to

cool his ox adrenal glands for perfusion in the lab, whereas I had to cut mine into minute pieces for immediate immersion fixation for EM while preserving enzyme activity. We achieved spectacular fine structural preservation, and I could conclude that the chromaffin granules did not contain AChE enzyme activity. However, there was plenty of it along the plasma membranes inside the rough endoplasmic reticulum, the Golgi apparatus, and most significantly in smooth surfaced tubules and vesicles along the plasma membrane, which we suggested were the source of secreted AChE upon depolarization of the cell. By about eight months after arrival, with the wonderful support of David and Ian, I was writing a manuscript, which, along with two papers by Ian and David, was published in the *Proceedings of the Royal Society* (Chubb and Smith, 1975; Somogyi et al., 1975), my first paper of many with David Smith. In 2025, we celebrated the 50th anniversary of our first publication (see the section "The David Smith Lectures in Anatomical Neuropharmacology at Oxford").

I continued to work with Ian on the EM of AChE in sympathetic ganglia and had a go at biochemical assays of AChE and Western blotting but had to realize that I was not accurate enough to match Ian's standards in biochemistry. The year of 1973–1974 was a turbulent time in British politics, with the great miner's strike, protests, police brutality, students occupying the university's administrative buildings, more protests, and general chaos that eventually led to the fall of the Heath government. Coming from stagnating, authoritarian Hungary, I found it all most refreshing. I also took the opportunity to work well-paid night shifts in a printing factory, as electricity rationing to industry created night-shift work, but little appetite for such jobs from locals. The 11 months passed quickly, I managed to complete the first manuscript, and when Klara arrived for the last month, we again set off on a hitchhiking tour with a tent and rucksacks from Oxford to the northern coast of Scotland and back, developing a better understanding of the country, the people, and the weather.

Returning to Hungary, first I had to complete my university degree. I missed the time of final exams and graduation, and this resulted in further dormitory life, but as a student in my final year, I got a room with only one other student. I graduated in biology in 1975 with a degree equivalent to a master's degree in science with distinction. The experimental data and papers from Oxford provided the results for submitting a thesis for a university doctoral degree in cell biology, which I obtained in 1977 from Loránd Eötvös University. A parallel major challenge and responsibility was to progress with building our unfinished little house, which we had started with Klara's father in the village of Leanyfalu in 1971, next to his house. He was a roof maker and knew every aspect of simple house building and could also connect to plumbers and electricians for jobs we could not do ourselves. Klara's father was a Hungarian Sekler immigrant from Transylvania, which is now part of Romania, a small man with unmatched

energy, physical and mental strength, and determination. Starting with nothing, working day and night, he built their own house, bought orchard land from income from multiple jobs, and gave each of his four children a plot next door to build on. I started digging the foundations by pickaxe and shovel after we told our parents that we had married earlier. Our friends and mates came to help together with family members. We slowly laid the foundations and hired bricklayers for the more skilled jobs. By the time I got my permit to leave for Oxford, the walls were up. Klara's father put the roof on in late 1973 to protect it from winter rains and frost. It remained there with bare walls to greet us when we returned from Oxford in 1974.

From Simple Beginnings, the Power of Serial Section EM

After graduation in early 1975, I wanted to work in the world-renowned First Department of Anatomy of Semmelweis University Medical School, where Professor Janos Szentagothai was professor and head. Professor Szentagothai was an exceptionally inspirational charismatic scientist, who unusually in the 1960s was allowed to travel abroad and receive not only Eastern but also Western visitors; he lectured in English, French, and German, the latter being his native language (Gulyas and Somogyi, 2013). I knew him personally from my undergraduate years, as I invited him to our student science club for a seminar and attended some of his anatomy lectures. In addition to a comprehensive vision of the functioning of the human body and mind, he was also a talented landscape painter, and he designed and painted his anatomical illustrations with great imagination. His atlas with Professor Ferenc Kiss of the human body appeared in many languages. But there was a problem; there was no vacancy for a fresh graduate even with a year of research in Oxford behind him, and thus I was told to wait until someone left, but—understandably, nobody in their right mind would want to do that.

So, I was waiting while working as an unskilled laborer on building sites with my father-in-law and taking any odd job, such as digging holes for trees in people's gardens. We already had a son, and Klara was at home with him receiving only a small maternity stipend. As we did not yet have family accommodation of our own, Klara stayed with her parents, and I stayed wherever I could, while also working on our half-finished little house under the supervision of Klara's father. Indeed, it was a family venture, both of our families helped when they could. This went on for about six months after graduation and was wearing me down with fear that I would never be a scientist.

Finally, in October 1975, I got my first paid employment as a junior research assistant in the Hungarian Academy of Sciences research group of the First Department of Anatomy at Semmelweis University Medical School in Budapest. In the few years I spent there, I had the good fortune

of meeting some of the inspiring great figures of 20th-century neuroscience, such as Sir John Eccles, Rodolfo Llinas (see volume 5), Sanford Palay, and Constantino Sotelo, just to name a few. I was commuting from the countryside where we lived, which took 3.5 hours each day, unless I got a lift hitchhiking by the road to Budapest. About two-thirds of the days when I tried to hitchhike, I was successful, and, out of nostalgia, I still maintain the habit whenever I am in Leanyfalu traveling to Budapest until a scheduled bus arrived. Even now, about fifty percent of the time I get a lift and meet interesting people and learn about their diverse views and lives; my latest lift was in 2025. It amuses me when they ask what I do and why I ask for a lift and I tell them that I am a brain scientist and just going to the Academy of Sciences or the university to meet colleagues.

For my first assignment of a scientific project, I was placed in the group of Dr. Jozsef Hamori, who was a pupil and close associate of Professor Szentagothai, running the EM laboratory and assisting Professor Szentagothai's research. He was a very experienced electron microscopist and was interested in neuronal development. I learned from him to recognize the different cell types, subtle structures, and different synapses. But it turned out that our personalities were largely incompatible and, despite his talent for detail, I could get no inspiration from him. Although I tried my best to fit in, our daily life was increasingly fraught, and the stress may have contributed to my duodenum ulcer. Nevertheless, I accepted the first task that he and Professor Szentagothai were keen to bring to conclusion but eluded all previous attempts. How many basket cells converge onto a single Purkinje cell in the cerebellar cortex? They thought that through serial EM sectioning it should be just a matter of perseverance to follow all axons arriving to a Purkinje cell back to their parent basket cell bodies. This would have required the three-dimensional reconstruction of at least 1 mm^3 of cerebellar cortex from tens of thousands of 70 nm thick epoxy resin sections, for which neither the technology nor the computing power existed. Even though I could cut serial sections, pick them up and photograph a few serially, I soon realized that the task could not be accomplished—only very recently have technologies been developed by large consortia and institutions to approach this scale of EM reconstruction (e.g., the Allen Institute for Brain Research).

I laid out my arguments for the impossibility of the project in an open meeting of the department, which generated a stunning silence, as in a highly conservative hierarchical department open criticism of the professors was unusual. However, I also prepared an alternative proposal, to serially reconstruct the axon initial segment of Purkinje cells and test how many basket cell collaterals forming the unique structure of the pinceau, a highly branched brush-like termination of axon collaterals, were making synaptic junctions, which was controversial at the time. This required only a few hundred serial EM sections, and although the collaterals could

not be traced back to the parent basket cells, I determined that the average number of synapses was 2.9 in the rat and 3.5 in the cat on the axon initial segment; most of the dozens of basket cell axon collaterals surrounding it never reached its membrane (Somogyi and Hamori, 1976). Decades later, the pinceau was shown to be a nonsynaptic electrical field inhibitory device, unique in the brain. At the time, the huge effort of day-and-night serial sectioning and photographing, developing the negatives, and printing them appeared to be a colossal waste of time, but a collateral reward was that I learned to recognize the axon initial segment from its fine structural characteristics even in my dreams.

Discovery of the Axo-Axonic Synaptic Termination of the GABAergic Chandelier Cell

When I arrived at Professor Szentagothai's department, he had just received copies of an all-embracing review, which he wrote with Michael Arbib, "Conceptual Models of Neural Organisation" (Szentagothai and Arbib, 1974), in which they attempted to provide a summary of the principles of mammalian brain organization, from synapses through neuron types to the principles of computations that the circuits executed. This attempt was well ahead of its time, and it foreshadowed the need for a multidisciplinary analysis of complex networks. The strength of the chapter was the anatomical detail of the circuits, summarizing decades of Professor Szentagothai's work, which I found captivating, and I decided this was what I wanted to do with my life, tracing neuronal circuit organization from synapse to synapse. There were obvious weaknesses in the actual data that were available by the late 1970s in most anatomical studies. A key problem was that the analyses were done separately on two scales: the light microscopic examination and identification of cell types by Golgi impregnation on the one hand, and the electron microscopic detail of the origin and location of synapses on the other. Correspondence was indirectly inferred from separate observations. Intracellular labeling of single neurons or axons following electrophysiological recording was very rare and difficult in mammals. Some scientists recognized the need to study the synapses of the neurons visualized by Golgi impregnation following electron microscopic sectioning (Blackstad, 1965), but this was technically challenging and not attempted in our department. I decided to have a go at it in the hope that if I could impress Professor Szentagothai, I might become an independent scientist working on the cerebral cortex rather than on the cerebellum. The technique that I attempted involved producing Golgi-impregnated tissue suitable for EM, which required osmium tetroxide treatment and epoxy resin embedding of sections onto glass slides for light microscopic selection, followed by removing tiny (~1 mm^2) areas from the large sections and reembedding them into epoxy cylinders

for EM sectioning. The Golgi impregnation produced Ag_2CrO_4 crystals in the cells, which are slightly water soluble, so the sections needed to be cut and floated on dilute Ag_2CrO_4 solution without contaminating them. Eventually, after a lot of suffering and long nights and weekends at the bench, as I had to keep the project secret in case it was stopped, I managed to overcome the difficulties and could obtain EM images of even single axonal boutons and dendritic spines that I had first preselected in the light microscope (Somogyi, 1978).

In the review by Szentagothai and Arbib (1974), there was a previously unpublished observation on a cortical neuron in the cat visual cortex, the *chandelier cell*, named by Szentagothai based on the shape of the axon. The main axon branched profusely and gave radially (from pia to white matter) oriented terminal segments of rows of boutons like the candlesticks on a chandelier. From his separate EM examination of pyramidal cells with Jozsef Hamori, Professor Szentagothai predicted that each terminal segment innervated the apical dendrite of a pyramidal cell, which was full of so-called "inhibitory and symmetrical" synapses of unproven origin. To test directly if the chandelier bouton rows formed synapses on apical dendrites, I Golgi impregnated blocks of rat visual cortex and luckily recognized the axon clouds of the chandelier cells, which according to the departmental dogma did not exist in rodents. In the darkness of the EM room, my first successful EM viewing of the impregnated axons remains one of those very intense emotional thrills that I have experienced only rarely of the unexpected insight in science. Instead of synapsing on apical dendrites, the terminal segments followed axon initial segments, which I recognized immediately based on my previous project on Purkinje cells. The electron dense membrane undercoating is the signature feature and defining criterion of the axon initial segment, which is now understood to result from the ankyrin G anchor of voltage-gated sodium channels. The specimens were not optimal, the Ag_2CrO_4 crystal did not cut well and often spread out of the bouton membrane, and it needed great luck and the tilting of the EM grid in the microscope to identify the synaptic gap in the junctions, but eventually I succeeded. Even without the synapses, it was clear that each presynaptic axo-axonic terminal segment wrapped around an axon initial segment, which I proved to originate from pyramidal cells.

After printing the images, I showed them to Professor Szentagothai, who immediately grasped the potential significance of the discovery, and we discussed that whatever the axo-axonal synapses did, they did it simultaneously on large populations of pyramidal cell action potential generation. But he could not accept that chandelier cells were not innervating apical dendrites and suggested that the interneuron that I identified in the rat was a different cell type. In his view, the axo-axonic terminal segments that I studied were much simpler rows of varicosities than the complex three-dimensional tubes of boutons of his chandelier cells in the

cat. He suggested the name of "axo-axonal interneuron" and encouraged me to write it up immediately, which I did adding his name as an author to the handwritten manuscript with illustrations. Professor Szentagothai corrected and rewrote parts of the short paper, also in longhand, and took his name off as an author, telling me that "this is your discovery, I am happy that it happened here," and my second paper on the central nervous system appeared as a single-author short communication (Somogyi, 1977), but not without an initial rejection and long arguments with referees and the editor who did not believe the unexpected result.

Selective synaptic termination of a cortical interneuron on the axon initial segment meant that all the numerous other interneuron types were likely to be selective for targets to some degree, which I continued to explore for the next 50 years. I renamed the axo-axonal interneuron as the "axo-axonic cell" (Somogyi et al., 1979), a term that is used less frequently, possibly because the "chandelier cell" name sounds more romantic. Having proved the exclusive axon initial segment innervation also in cat and monkey (Somogyi et al., 1982a), after a few years, Professor Szentagothai also accepted that the axo-axonic interneuron and his chandelier cell were the same cell type. With my graduate student Tamas Freund, we proved directly by combined Golgi impregnation and EM immunocytochemistry that the boutons contain glutamate decarboxylase (Freund et al., 1983), the enzyme synthesizing GABA, and we later demonstrated GABA in the cell bodies (Somogyi et al., 1985) in cat hippocampus. With David Smith and others, we demonstrated highly developed pyramidal cell axon innervation in the monkey hippocampus CA1 area (Somogyi et al., 1983a; figure 1), with up to 30 synapses from one axo-axonic cell to a single pyramidal cell, still the highest number of proven synapses between any two cortical neurons anywhere in the cerebral cortex (Somogyi et al., 1983b). Zoltan Kisvarday, another graduate student, and David Smith also demonstrated axo-axonic cells in the human neocortex (Kisvarday et al., 1986a). Subsequently, with Eberhard Buhl, a postdoctoral fellow at Oxford, we provided direct evidence by *in vitro* paired intracellular recordings in hippocampal slices that axo-axonic cells acted through GABA-A receptors (Buhl et al., 1994).

Much later, with talented colleagues we also recorded the firing patterns of axo-axonic cells in the hippocampus *in vivo* during different networks states (Klausberger et al., 2003; and see below). Because of its easily recognizable axonal form and selective genetic marking (Paul et al., 2017), the axo-axonic chandelier cell has become a favorite object in cortical circuit and behavioral research, appearing in thousands of papers and revealing new surprises every week. However, the critical question of why the cortical pyramidal cell requires a unique GABAergic innervation on the axon initial segment independent of the estimated 20–30 other distinct GABAergic inputs that they receive from other interneurons has mostly

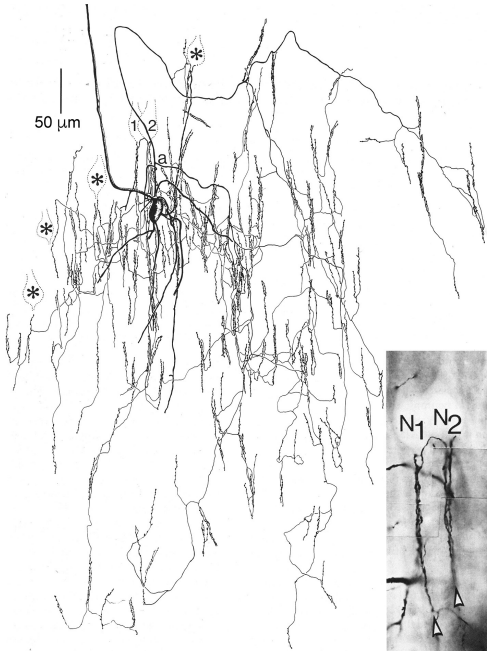


Fig. 1. Axo-axonic GABAergic neuron in the monkey hippocampal CA1 area. My partial reconstruction from a single 70 micrometer thick Golgi-impregnated section. Few dendrites are shown. The main axon (a) gives many collaterals with vertical terminal bouton rows each surrounding the axon initial segment of a pyramidal cell (some outlined, asterisks). Two pyramidal cells (1, 2) and their associated axon innervating cartridges (arrowheads) are shown in the light micrograph inset, lower right. Electron microscopic analysis showed that a terminal cartridge could give up to 30 synapses to a single axon initial segment and on average three axo-axonic cells converged onto each pyramidal cell axon (data in Somogyi et al., 1983a).

eluded explanation. For me, the most elegant study, alas *in vitro*, was carried out on dentate gyrus granule cells, which also receive dense axo-axonal innervation (Buhl et al., 1994; Han et al., 1993). Rojas et al. (2011) showed that GABA-A receptor activation on the axon initial segment depolarizes the firing threshold (i.e., more excitation is needed to evoke spikes), but does not affect the input resistance of the postsynaptic cell, whereas activation of GABA-A receptors on the soma lowers input resistance and shunts excitatory inputs, but it does not affect firing threshold. This way, the firing threshold of the postsynaptic cortical glutamatergic neurons has an independent control from the regulation of somato-dendritic input integration by GABAergic neurons. This reminds me of the pinceau of Purkinje cells, and how lucky I was in exploring the bases of two unique axon initial segment inhibitory mechanisms: electrical field inhibition of Purkinje cells by basket cells and GABA-A receptor mediated selective synaptic inhibition of cortical glutamatergic neurons by axo-axonic cells.

Synaptic Connections of Identified Neurons: From Golgi-Impregnated Neuronal Forms to the Definition of Cell Types

The visual cortex was the favorite cortical area in the 1970s because of the influence of the seminal discoveries of Stephen Kuffler, David Hubel (see volume 1), and Torsten Wiesel. I also first studied the visual cortex, and the discovery of axo-axonic cells clearly demonstrated the power of analyzing synaptic connections of neurons first visualized at the light microscopic scale. Gradually, I realized that synaptic connections reflected in neuronal form alone were insufficient to predict the position and role of neurons in the network and instead a multifaceted characterization of cell types was needed. Having added neurochemical and physiological measures, I defined neuronal cell types as follows:

> Probably all neurones of the cortex can be defined, recognized and compared on the comprehensive application of the following measures: (i) brain area- and cell domain-specific distribution of input and output synapses, (ii) expression of proteins involved in cell signalling, (iii) intrinsic membrane properties reflecting the expression of ion channel proteins, and (iv) temporal distribution of firing *in vivo*. Based on the above range of parameters, each cell will fall into a tight cluster, *the cell type*, in this multidimensional space. (Somogyi and Klausberger, 2005)

Such a definition is difficult to achieve and requires many experts. With the dawn of single cell transcriptomics, a simpler, but more easily scaled up approach emerged and provided transformational results on the richness of neuronal diversity (e.g., Yuste et al., 2020). But for explaining the roles of cell types, the information in my definition is still required.

In the visual cortex, the next distinct local interneuron type I studied was the "double bouquet cell," which had a tight 50–100 micrometer diameter axonal bundle descending from the cell body in layers 2 and upper 3 to layer 6 and was particularly recognizable in primates. Professor Szentagothai and others envisaged that the axonal bundle innervated the apical dendrites of deeper layer pyramidal cells. Instead, we established with Alan Cowey (see volume 5) at Oxford that in the visual cortex of cats and monkeys their boutons mostly made synapses with small dendritic shafts and preferentially with dendritic spines, well above the proportion of so-called type 2 (often erroneously called symmetrical) GABAergic synapses in the overall bouton population (Somogyi and Cowey, 1981). In other words, double bouquet cells preferentially innervated dendritic spines that also received a glutamatergic synapse. By combining retrograde axonal transport of ^{3}H-GABA in the monkey visual cortex, we

demonstrated that double bouquet cells were GABAergic (Somogyi et al., 1981). This was again a contribution to the concept of synaptic target selectivity. Later, with Gabor Tamas, then a graduate student, and Eberhard Buhl, we proved by paired intracellular recordings *in vitro* that double bouquet cells acted through GABA-A receptors (Tamas et al., 1997a). Much more recently, having access to live surgically removed human cortical slices, we showed with my last graduate student, Istvan Lukacs, that double bouquet cells were immunopositive for the calcium-binding protein calbindin as well as somatostatin, acted on GABA-A receptors, and preferentially innervated dendritic spines (Lukacs et al., 2024). My original hypothesis that the dual glutamatergic and GABAergic innervation of single dendritic spines provides a privileged regulation of plasticity of some synapses on spines by double bouquet cells is now being tested by pioneering imaging techniques.

In the 1970s, I also realized that the marking of the terminals of long-range projections by anterograde axonal degeneration following electrolytic lesions of the cell bodies can be connected to Golgi-impregnated synaptic target cells by EM. I placed electrolytic lesion in the lateral geniculate nucleus (LGN) of rats and, after a few days of recovery, traced the recognizable degenerating synaptic terminals to Golgi-impregnated pyramidal and spiny stellate cells in area 17. I first photographed the selected cells in the light microscope and mastered the recovery of any single dendritic spine or bouton in the electron microscope for testing synaptic relationships. If a cell received LGN input, I could then follow its Golgi-impregnated axon to its local synaptic target. I demonstrated synaptic feedback input to aspiny interneurons from pyramidal cell axon collaterals, thus identifying three monosynaptically connected neurons in a chain (Somogyi, 1978). Later, with Alan Cowey and graduate student Zoltan Kisvarday, we repeated the experiment in the monkey and identified monosynaptic input to both spiny stellate cells and a small local GABAergic neuron, the "clutch" cell (Kisvarday et al., 1986b). Although the technique was a feat that contributed to some awards, the small scale, the low numbers of successful hits, and the poor penetration of the embedding resin into the dense Golgi crystalline precipitate meant that it did not gain popularity.

Two technical developments led to major advances in the study of identified neurons: (1) the stable gold toning of Golgi-impregnated neurons for EM, and (2) the intracellular labeling of electrophysiologically recorded neurons by horseradish peroxidase (HRP). In 1977, the year that I published my first Golgi EM paper, Alfonso Fairen in Alan Peter's lab developed the conversion of Ag_2CrO_4 to gold-decorated silver particles, which were embedded well and stable in the EM resin and only partially filled the impregnated processes, allowing for much better EM detail of synapses and intracellular organelles (Fairen et al., 1977). Initially, I was devastated that I had wasted so much effort on developing my technique,

as it was obvious that the gold-toning technique was superior and was going to be used more widely. However, after the initial shock, I had a go and realized that the visibility of the interior of the Golgi-impregnated neurons provided the opportunity to combine it with other techniques, such as autoradiography (Somogyi et al., 1981c), enzyme histochemistry (Somogyi et al., 1979), and later with EM immunocytochemistry (Freund et al., 1983).

A turning point in my life came from a visit to Budapest by David Smith in 1976, with whom I desperately tried to keep in touch as a potential escape route to the free world. He was hosted by Professor Szentagothai, and I was keen to show him my results using Golgi EM. His main interest at that time was the basal ganglia, as he was teaching the pharmacology of aminergic neurotransmission in relation to Parkinson's disease. David was frustrated by the lack of direct information on synaptic neuronal connections in the basal ganglia. He immediately realized that my methods could advance knowledge and soon after his visit, he made an offer for a working visit to Oxford. There were no mechanisms for working abroad for junior scientists and both Professor Szentagothai and I were keen to maintain my job and contribution to the Anatomy Department in Budapest. Through some very high-level political connections, Professor Szentagothai managed to convince the authorities that I would return if they let me out with my family, including our two children. I gave my word to him and kept it. We had two very intense and wonderful years in Oxford. Initially, I was a departmental demonstrator teaching in practical classes, then as a postdoc on David's grant, with total freedom in what I wanted to do.

Circuits of the Basal Ganglia: Oxford 1977–1979 and Beyond

We arrived at Oxford in the autumn of 1977 with Klara and two sons ages one and three. David Smith helped to find a small house for us to rent in a friendly street within walking distance to the lab through the University Parks. I got down to setting up a lab and activating a very old electron microscope helped by David's graduate student Antony Hodgson, who became a friend and close colleague. With both the basal ganglia and the neocortex in mind, we set out to combine Golgi impregnation with retrograde axonal labeling of the cell bodies by HRP that identified the projection area of the cells, and with anterograde HRP labeling of nerve terminals to test synaptic inputs (Somogyi et al., 1979). As Golgi impregnation for the visualization and identification of neurons required a block of tissue of several mm thickness, we introduced a novel chromogen for HRP reaction that could penetrate such thick blocks. To label the origin of the nerve terminals, we made small electrolytic or pharmacological lesions in the brains that were also injected with HRP in restricted areas for retrograde tracing of connections. In an extensively illustrated paper, with David and Antony,

we demonstrated by retrograde HRP labeling that striatal medium-size neurons with densely spiny dendrites projected to the substantia nigra. We also traced direct striatal synaptic input to dendrites of nigro-thalamic projection neurons and showed axo-axonic cell synaptic input to callosally projecting pyramidal neurons in the visual cortex (Somogyi et al., 1979).

The results attracted grant support, and soon Paul Bolam joined us as David's postdoc, and he took over the basal ganglia program and maintained the lab after my return to Budapest in 1979. I could return for a few months in the summers every year, and we closely collaborated over distance, Paul also visiting Budapest. With Paul, we demonstrated direct cortical input to Golgi-impregnated striatal medium spiny neurons and traced the synaptic targets of their local axon collaterals within the striatum (Somogyi et al., 1981a). He also discovered a second type of striato-nigral neuron (Bolam et al., 1981). Much later, Paul joined the Medical Research Council (MRC) Anatomical Neuropharmacology Unit (ANU), established by David in 1985, bringing his theme of basal ganglia as a group leader.

Through the combination of several anatomical techniques, we could tackle any question on synaptic relationships, but the results did not reveal anything about the molecular mechanisms of those synapses or about their functioning. By the late 1970s, intracellularly recorded neurons were increasingly labeled with fluorescent dyes or HRP for EM, revealing cell identity in the context of physiological information. At the same time, pharmacology was increasingly complemented by immunohistochemical dissection of neuronal populations both for signaling molecules and their receptors. My visit to Oxford allowed me to have insight into the use of these techniques as well as to meet outstanding pioneers (figure 2), one of whom was Tomas Hökfelt (see volume 12) from the Karolinska Institute, the other Claudio Cuello, who joined the Department of Pharmacology as a lecturer. Claudio studied the basal ganglia, so our collaboration had natural synergy, and he trained me in immunohistochemistry, which was exciting and fundamental



Fig. 2. British Pharmacological Society meeting Oxford 1979, poster session discussion. From left to right, Professor Marthe Vogt from Cambridge, Peter Somogyi, David Smith, and Tomas Hökfelt.

for my development and future contributions. With Claudio, his graduate student John Priestley and David Smith, we dissected the synaptic targets of enkephalin or substance P containing nerve terminal connections in the basal ganglia (Somogyi et al., 1982b, 1982c).

Exploring Neuronal Circuits of the Visual Cortex

After the intellectual, scientific, and societal freedoms experienced in Oxford, returning to the hierarchical and closely watched environment of the Anatomy Department at Budapest and resettling the family was challenging. Klara took care of our home and the schooling of our children in Leanyfalu, a small village by the Danube Bend 27 km to the north of Budapest. She also enrolled in university distance training to become a biology teacher and, after graduation, took a job in the village. One tangible benefit of our Oxford visit was that we managed to save enough money from my salary to buy our first car, an East German Trabant with a cotton fiber-strengthened resin exterior and a two-stroke engine. We could get it within a few months for hard currency, while those queuing for it in Hungarian currency had to wait five years, such was the demand of this affordable car. The plan was that I was going to commute to work, but soon we realized that on the day that I used the car for the return journey of just over 60 km, I used 75 percent of my salary on that day for the petrol. This was clearly unsustainable. Soon I was back to hitchhiking on the way to Budapest and facing the long commute home in the evenings, six days a week. Often, I left in the dark in the morning and came home after the family went to bed, not communicating with my children for days. Fortunately, during the summer collaborative visits to Oxford, I could save money again and supplement our income for the rest of the year.

On arriving back to Budapest from Oxford, Jozsef Hamori had accepted that I would form an independent group and even generously provided a newly arrived technician, Klara Peto, who became a lifelong friend and later accompanied me to Oxford on and off. We got a small room and remained part of the EM facility and contributed to its maintenance for several groups. I realized that on my own I could not exploit the many developments that were underway, so I put up an advert at my old university for volunteer student interns. The first two that turned up were an enormous stroke of luck; Tamas Freund (see volume 11) and Zoltan Kisvarday, two biology undergraduates who just started their second year of studies. They were exceptionally talented, were creative in different ways, and took the university course easily, so they had plenty of time on their hands. They were in the lab on most days, including weekends and during holidays, and soon became very productive scientists as well as buddies. By 1981, we published several papers together while Tamas and Zoltan were still undergraduates, including one in *Nature* on the

radial projection of a special population of GABAergic neurons in monkey primary visual cortex (Somogyi et al., 1981b). We collaborated with Tamas and Zoltan for years, and they established separate collaborations with David Smith. We also worked with Alan Cowey on the primate visual cortex and with Kevan A. C. Martin (see volume 12) and Professor David Whitteridge on the cat visual cortex. I also explored the molecular diversity of GABAergic neurons comparing visual cortex and hippocampus for neuropeptide expression with a technique I developed that enabled me to cut the soma of neurons into 0.5 micrometer thick sections and test up to six antibodies on the same cell. We demonstrated that somatostatin and cholecystokinin were expressed in separate distinct neuronal populations (Somogyi et al., 1984b). The comparison of two very different laminated cortical areas convinced me that the hippocampus was very promising and more easily interpreted in terms of cell types and connections, which I returned to later throughout my studies.

The four of us worked day and night, pushing the boundaries of regulations, which caught the attention of the then head of department, Professor Terez Tömböl, who thought that we should not be in the lab without permission outside normal working hours. She duly confiscated our keys to the department and lab, keys that fortunately were of a very primitive type. The department had a mechanical workshop, and the technician was a buddy, so we chiseled our replacement keys side by side with my students from blank keys—I doubt that many scientists had to overcome such hurdles to contribute to progress.

Kevan was a student of Whitteridge, and they were interested in visualizing the neurons that they recorded for classical receptive field properties. The question was if the striking differences in the action potential responses of simple and complex cells correlated with their cell type identity. They used sharp glass intracellular electrodes containing HRP for recording and visualizing the cortical cells, and also the axons of neurons of the LGN. We realized that having developed the "section Golgi-impregnation" method with Tamas Freund (Freund et al., 1983), we could visualize the HRP-labeled neurons in the tissue section of cortex that also had randomly Golgi-impregnated neurons, some of which by chance were monosynaptically contacted by HRP-labeled LGN terminals (Freund et al., 1985). We provided the first precise determination of the location of physiologically characterized LGN terminals on the soma, dendritic shafts and spines of visualized cell types, and immunocytochemically identified GABAergic neurons targeted by characterized LGN afferents. With Kevan and Zoltan Kisvarday, we identified a novel type of small basket cell in layer 4 of the cat primary visual cortex that Kevan named the "clutch cell" for its claw-like termination on the cell bodies of spiny stellate cells (Kisvarday et al., 1985).

The novel results and Kevan's originality greatly contributed to the setting up of the MRC's ANU, which he joined as a group leader in 1985.

The collaboration flourished in the MRC Unit and was extended to the primate cortex. Kevan intra-axonally recorded and visualized distinct types of LGN afferents and, with Tamas Freund and Ivan Soltesz, an undergraduate from Hungary, we identified their layer-specific synaptic targets (Freund et al., 1989b). Eventually, Kevan Martin left in 1995 for the Swiss Federal Institute of Technology (ETH) in Zurich and continued a program along the same lines. Thus, visual cortical physiology came to an end in the MRC Unit. We continued collaborating with Alan Cowey on the pathways mediating blindsight in the monkey (Kisvarday et al., 1991) and with talented visitors among them Clermont Beaulieu from Canada (Beaulieu et al., 1992) and Mary Kritzer from the United States (Kritzer et al., 1992) on quantitative synaptic and interlaminar relationships.

For these results, some recognitions followed. A great surprise was the Charles Judson Herrick Award of the American Association of Anatomists in 1984. A most memorable occasion was the Krieg Cortical Kudos–Cajal Club Cortical Discoverer Prize of the American Anatomical Society that I shared with one of my heroes Professor Alan Peters. In the same year (1991), my graduate student and collaborator Tamas Freund received the Cortical Explorer award.

Australia, the Land of Promise: Joining Ian Chubb and Antony Hodgson

As the results built up about both the visual cortex and basal ganglia, I felt increasingly despondent with the stale atmosphere of the Anatomy Department in Budapest and the commuter life both to Budapest and to Oxford, and I longed for a stable creative environment with longer-term perspectives. It seemed that the Soviet Empire and the regime of Janos Kadar's "goulash communism" in Hungary would never end, and I felt that my life was just ticking away. In 1980, Ian Chubb visited me in Budapest from Australia, and we discussed the option of joining him. Ian had returned to his native Australia from a Royal Society Research Fellowship in Oxford and became professor at the Department of Human Physiology at Flinders University in Adelaide.

Possibly, the wanderlust of my 20s still had not been extinguished by my high-octane life. To a biologist, Australia just sounded like the "promised land." So, after Ian invited me in 1982, I persuaded Professor Szentagothai to help me to obtain a work permit and exit visa with my family to join Flinders University. I promised that I would continue my contribution to the Department of Anatomy and publish the ongoing projects under both my Hungarian and future affiliations. Nobody objected, it was a win-win situation, and as it turned out, the results flowed with papers in which I was under Flinders, Oxford, and Semmelweis affiliations. We left with the family in the winter of 1983 from frozen Hungary and landed in Adelaide

into a 40 degree Celsius exceptionally dry and hot summer with the infamous bush fires burning in the hills.

Ian was interested in the unconventional roles of AChE and in neuropeptide processing, projects that I could complement with my immunohistochemical and EM skills. I set up an anatomy lab with the help of a wonderful technician Dimitra Beroukas whom Ian allocated for our projects. Antony Hodgson from Oxford was already in Ian's lab as a postdoc, and our group's work was greatly facilitated by the stimulating neuroscience community, most eminently represented by Professors Marcello Costa and John Furness, pioneers on the enteric nervous system. Ian gave us free hand in what we did, and we collaborated on mapping the distribution of chromogranins, the major adrenal chromaffin granule proteins, discovering that they were constituents of many peptidergic vesicles in nerve terminals in the brain of sheep (Somogyi et al., 1984a). This involved perfusion fixation of sheep (cheaper than laboratory rats there) through the heart, which is not for the fainthearted and required copious volumes of fixative.

I also persuaded Ian to support the characterization of the antisera to GABA and glutamate, which I brought to Australia from Hungary. The antisera had been developed following the pioneering work of Jon Storm-Mathisen and Ole Petter Ottersen (Storm-Mathisen et al., 1983), who applied the method of raising antibodies to small neurotransmitters like GABA and glutamate by conjugating them to carrier proteins for immunization. In Hungary, in a fortuitous collaboration with the immunologist Anna Erdei, whom I knew from university years and later became the head of the Immunology Department of Loránd Eötvös University, where we both studied, we managed to raise antisera to GABA and glutamate with the help of a chemist, Botond Penke, who produced the antigens. With Antony Hodgson, we completed the characterization of the antisera to GABA (Hodgson et al., 1985). We also managed the first EM immunocytochemical localization of GABA in synaptic terminals using colloidal gold-labeled secondary antibodies for visualization (Somogyi et al., 1985). The EM immunogold technique was relatively new; I was much encouraged by a friend from the United States, Anthony van den Pol (1949–2020), who was a professor at Yale and a frequent visitor to Oxford. He first visited me in Budapest in the 1970s and took up EM as a result of our interaction. Call it a truly international effort: The spectacular results attracted attention, and we distributed the GABA antisera worldwide freely, contributing to many studies, but declining authorship.

By the early 1980s, immunocytochemistry was flourishing and a few labs pioneered the absorption of secondary antibodies onto colloidal gold particles that could be made to different distinct sizes in a range of 5 to 40 nm. In contrast to immuno-enzyme methods, these discrete particles provided high resolution, did not obscure the labeled subcellular components, and were eminently countable. Our immunogold localization of GABA opened

the way to identify GABA in physiologically recorded HRP-labeled neurons (Somogyi and Soltesz 1986) and also in Golgi-impregnated cells, providing the neurotransmitter identity of fully visualized cell types (Somogyi et al., 1985). I also initiated a collaboration with Ole Petter Ottersen and Jon Storm-Mathiesen. Ole came to Oxford to learn immunogold EM, which he then developed further to great effect for many transmitters and systems (Ottersen et al., 1988). Later at Oxford, with Jozsef Somogyi, we identified high-glutamate neurotransmitter content in the terminals of cerebellar mossy fibers and parallel fibers, demonstrating quantitatively the difference from GABAergic terminals, which had lower glutamate content (Somogyi et al., 1986).

Life in Australia was idyllic; I walked to the lab through a beautiful park with centuries-old eucalyptus trees; in the evening sulfur-crested cockatoos landed on them to roost in front of my window as the sun sank into the ocean in the distance. Ian was very supportive. In a country of immigrants, we felt at home and developed many friendships; social life revolved around the beach, half an hour away, and the barbeques. After we bought an enormous old eight-cylinder Holden Kingswood car, we explored the many reserves and natural parks around. Once the science was on solid footing, we made long journeys, the most memorable of which was a drive from Adelaide to Alice Spring and back, at that time mostly on a dirt road that was very worn and rutted, shaking us and the car into pieces. We lost our windscreen when a lorry overtook us and were driving for days without one. The late Professor Anthony van den Pol joined us on this trip, helping with navigating the terrain in the front, while Klara sheltered with the children in the back under a blanket. Perhaps the sunshine, or the radiating optimism of the place, or the great wines, whatever the reason, Klara became pregnant, and we had our third child, Lilla in 1984, after an eight-year gap. All the time, I kept in touch with the Oxford crowd writing up many projects and with the Budapest lab, where Tamas Freund and Zoltan Kisvarday kept the projects going. I even visited from Australia and Zoltan also visited Adelaide to finish projects, working on GABA localization and immunogold labeling.

In 1988, I managed to return to Adelaide for a few months' sabbatical and collaborated with Professor John Chalmers on the brain stem control of blood pressure and heart rate, identifying several novel excitatory amino acid pathways (Somogyi et al., 1989a) using retrograde axonal transport of ^{3}H-D-aspartate. John was a world leader with an amazing group of talented people, who helped reveal to me the beauty of seeing the physiological effects of minute, 5–10 nL volumes of neuronal tracers, such as aspartate or even HRP, depending on the pipette tip location. After appropriate axonal transport times and fixing ^{3}H-D-aspartate in the brain, I used an autoradiograph to visualize the neurons that were responsible for the effects from areas, such as the cortex and brain stem nuclei. I wish I

could have continued the exploration of the cortical control of autonomic function, but there was simply not enough capacity.

Back to Oxford: Establishing the MRC ANU

By the end of 1983, David Smith felt that the novelty of our published results and the talented young people we interacted with deserved a more stable funding structure at Oxford. He consulted me and made an application to the MRC for a unit, a type of small flexible research institute that was a very cost-effective mode of MRC support, five years at a time, but also renewable. He was fortunate that through our prior collaborations he could include Paul Bolam and Kevan Martin as potential group leaders with distinguished track records. After a bumpy evaluation process, the MRC finally agreed to the funding, conditional on my returning to Oxford. David was to become the director, I requested a role as associate director, and they made an offer that I could not refuse. This was to the great disappointment of Klara, who preferred Australia. After the decision in 1984, the ANU started as I arrived from Adelaide on my 35th birthday and signed the contract. At the airport, Klara and I separated; she continued to Hungary with the three children and told me that she had enough of our nomadic life and would join me only when there was a furnished house to live in. In six months' time, all was ready, and the family reunited.

In Oxford, Kevan and Paul already had their labs and facilities in different departments, but I had to start all over again, and there was little physical space for a new lab. David was never short of creative thinking and duly persuaded the faculty of the department that the two large old-fashioned toilets separated for men and women were a huge waste of space, and everybody could fit into one facility with some reorganization and lots of goodwill. The female toilet was then converted to a lab, where I expanded my projects, even supplementing it with a portable cabin at the side of building that we entered through a previous window. It looked hilarious, but the scientific opportunities were great, and we were optimistic about attracting talent from around the world. Once the ANU was operational, David wasted no time and won an award from the drug company Bristol-Squibb-Myers to build a modern Department of Pharmacology for Oxford, where the ANU was also accommodated in a separate wing. We moved in in 1991, and the ANU flourished for 30 years in all, on a rigorous five-year review cycle at a time with brilliant independent but interacting group leaders, like Paul Bolam, Sean Eaton, Jeff McIlhinney, Marco Capogna, Jozsef Csicsvari, and Thomas Klausberger (figure 3). I took over as director in 1998, after an evaluation led by the then–chief executive of the MRC, Professor George Radda. I stepped down as director in 2015 and had to leave the unit in 2016. Nevertheless, I took my group to a new laboratory within the Department of Pharmacology and completed another MRC

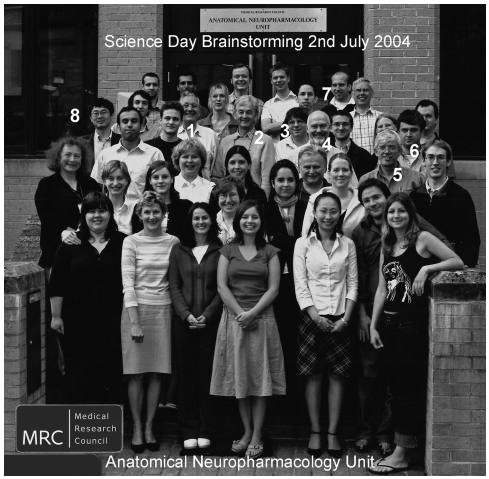


Fig. 3. MRC ANU Science Day meeting of staff, students, and visitors. (1) David A. Smith, honorary director; (2) Peter Somogyi, director; (3) Marco Capogna, group leader; (4) Jeff McIlhinney, group leader; (5) Paul Bolam group leader; (6) Jozsef Csicsvari, group leader; (7) Thomas Klausberger, future group leader; and (8) Masahiko Watanabe, visiting professor from Japan.

program until 2020, followed by a European Research Council Grant with the late Marco Capogna (1958–2022), who became professor in Aarhus, Denmark. I never had a tenured position; my salary and my family's security depended on the previous five year's results and the quality of my proposal for the next five years in a competitive grant system from 1985 until my retirement in November 2023.

Opportunities in the ANU: Cellular Electrophysiology of Identified Neurons *in Vitro*

The cyclic five-year form of grant support in the unit, the shared facilities and intellectual complementarity of the small groups, and David's empathetic leadership freeing us from administration provided a great opportunity for novel scientific ventures. We could already tackle any question on synaptic relationships in the two systems we studied, the basal ganglia and the cerebral cortex, but we lacked the pharmacological analysis of the connections and the exploration of the dynamic behavior of the different cell types that we identified. To improve our contributions, I initiated *in vitro* slice physiology and the high-resolution localization of neurotransmitter receptors in relation to identified neurons.

First, I sent a talented visiting student from Hungary, Ivan Soltesz, for training in cellular electrophysiology and pharmacology to Vincenzo Crunelli in London in 1988. There Ivan discovered that a GABA-B receptor

antagonist inhibited a potassium current in LGN neurons *in vitro*; he studied the LGN previously in Oxford. Upon his return, he wired up an *in vitro* slice setup and started recordings in 1989 but soon took a postdoctoral position elsewhere. The setup was activated again by an experienced Hungarian electrophysiologist Gabor Czeh in 1990, and we managed to record and label neurons in hippocampal slices. At the time, Eberhard H. Buhl (1959–2003) joined us as a postdoc from Germany, who could intracellularly label single neurons in fixed brain slices, and with Gabor Czeh, he soon learned to record live neurons, and we labeled them with HRP or biocytin for visualization. Eberhard loved the project, was meticulous, attentive to detail, and highly critical, which was much needed as we were inexperienced. We started with hippocampal slices and later continued with slices of the visual cortex involving an extraordinary Hungarian student Gabor Tamas with legendary spatial abilities (e.g., Tamas et al., 1998). The question was, how did different types of GABAergic neurons that differed in shape, reflecting their pre- and postsynaptic relationships, varied in their synaptic effects on the target cells? What specialized synaptic effects do the great diversity of axonal shapes predict? The answer required recording and visualizing both the pre- and postsynaptic neurons followed by the EM identification of the location and number of synaptic junctions that mediated synaptic effects along with pharmacological testing. We did not lack ambition.

Following much trial and error by Eberhard, with the help of Katalin Halasy, an expert electron microscopist from Hungary, we completed an unmatched study, identifying the synaptic effects of axo-axonic and basket cells as well as that of a novel GABAergic neuron that I named the *bistratified cell* in the rat hippocampus (Buhl et al., 1994). The latter cell ignored the axon initial segment and the soma that the other two GABAergic neurons targeted and only innervated the small dendrites of CA1 pyramidal cells in conjunction with the glutamatergic input from CA3 pyramidal cells. They all acted on GABA-A receptors, but on different membrane domains. As the dendrites of the bistratified cells were aligned with the CA3 input as well, I recognized that the synaptic targeting of the pyramidal cell dendritic domain was a feedforward regulatory circuit. This turned out to be a principle that applied to many other paired, local GABAergic and distant glutamatergic pathways. With Katalin and Eberhard, we had an exciting period of many detailed studies on hippocampal GABAergic neurons (e.g., Buhl et al., 1996).

A great stroke of luck happened when the program was in full swing and Ole Paulsen joined us from Norway, who now holds the Chair of Physiology (1883) at Cambridge University. Ole had a deep background in ion channel physiology and concepts of oscillatory neuronal activity. He and Eberhard jointly supervised one of our graduate students, Stewart Cobb, and together they tested how the synaptic effect of a single GABAergic

neuron influenced the firing of pyramidal cells *in vitro*. In a true breakthrough, one of those thrilling moments, they found that inhibitory postsynaptic potentials (IPSPs) evoked by individual identified basket cells, but not so much by other interneurons, could reset the firing of pyramidal cells in relations to ongoing theta frequency intrinsic membrane oscillations. These ~4 Hz voltage oscillations of the plasma membrane appeared just near the firing threshold *in vitro*. In ingenious experiments, they demonstrated that IPSPs evoked simultaneously in two independently oscillating pyramidal cells reset their firing phase and synchronized them, and this synchrony remained for several theta cycles even without further IPSPs. These results were conceptually novel and technically outstanding, so we submitted the paper to a high-profile journal, from which it was duly rejected without review. We protested, and I sought support from respected physiologists, eventually achieving that the editor sent it out for review and the paper had a smooth ride—an increasingly rare event as time went by. For all of us, this remains our most recognized experimental study (Cobb et al., 1995). We proudly demonstrated our results in the Royal Society's summer science exhibition to the public and in the evenings to the Society Fellowship and their guests in the soirées, which are black-tie social events (figure 4).

The success of paired intracellular recording prompted us to return to the visual cortex, and in view of our previous experience, we chose the cat, which in retrospect was not a bright idea, as later the mouse visual cortex became the area of choice of physiological and pharmacological studies. Gabor Tamas joined us as a Hugh Blaschko European Research Fellow from Szeged University Hungary, where I had learned AChE localization decades

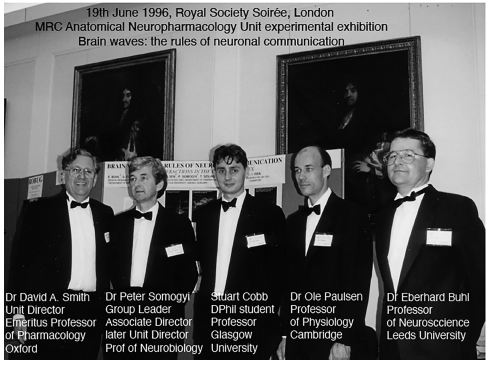


Fig. 4. Our team exhibiting electrophysiological recordings *in vitro* in brain slice and microscopic neuron identification at the 1996 Royal Society Summer Exhibition and Soirée, London; their later positions indicated under the names. The identification of the synaptic effects of distinct GABAergic hippocampal neurons (Buhl et al., 1994; Cobb et al., 1995) resulted in the invitation to exhibit. During the day, we showed our work to the public and in the evening to the Society Fellowship and their guests.

earlier. Today he is full professor and a world leader on the circuits of the human cortex based at Szeged University. Gabor, Eberhard, Katalin, and Ole completed detailed experiments on the number, location, and synaptic effect of GABAergic neurons and pyramidal cells, which are unmatched to this day (Buhl et al., 1997). In addition to the usual suspect basket cells, we identified a type of GABAergic neuron we named "dendrite targeting cell" that similar to bistratified cells in the hippocampus, only innervated the dendrites of pyramidal cells. Gabor also proved that GABAergic "double bouquet cells" acted on GABA-A receptors and preferentially innervated dendritic spines (Tamas et al., 1997a). He also discovered an extraordinary dense and cell type–dependent autaptic innervation by cortical GABAergic neurons (Tamas et al., 1997b), in addition to many selective interneurons to interneuron connections (Tamas et al., 1998). Making all this extraordinary effort in the cat instead of the mouse was a potential "mistake"; but we still do not know how these parameters compare in the mouse. The other missed opportunity was that despite our skills in immunohistochemistry, we did not try to test the neurochemical profile of the recorded neurons. Nevertheless, the facts that we established, and their conceptual significance, were widely recognized (see Somogyi et al., 1998). We had learned our lessons and made up for our mistakes later by recording *in vivo* and identifying multiple parameters of visualized neurons in the rodent hippocampus (Klausberger and Somogyi, 2008).

Quantitative Neurotransmitter Receptor Localization by Immunogold Labeling

Predicting the nature and dynamics of synaptic communication is facilitated by identifying the neurotransmitter receptors. The cloning of a multitude of receptors for the same transmitter revealed the great diversity and complexity of synaptic interactions. As antibodies were raised for receptor subtypes and even splice variants, I saw an opportunity for high-precision neuroanatomical analysis, starting with GABA-A receptors (Somogyi et al., 1989b; Soltesz et al., 1990). The immuno-enzyme reactions, such as HRP for EM, made precise localization difficult because of the spread of the reaction product. The differentiation of synaptic versus extrasynaptic receptors was particularly difficult. Having introduced immunogold labeling of GABA and other transmitters (see above) we attempted to localize receptors with discrete silver and gold particles, which is now in routine use at about 10–20 nm resolution. But the beginning was difficult. Under conditions of localizing the highly concentrated transmitters, we got no signal for the much scarcer receptors. I was fortunate to work with my long-time expert electron microscopist colleague David Roberts, who was one of the first appointees to the ANU and who introduced acrylic resin

embedding for EM postembedding immunoreactions on the thin sections, which provided deeper access for antibodies into the sections than the routine epoxy resins. The first success came in a collaboration with Nomi Eshar, who was a visiting student from Israel, bringing her antibody for the localization of a suspected glutamate receptor, which later was named chicken kainate-binding protein. To our surprise, this protein was localized to the membrane of Bergmann glial cells in the chicken cerebellum and completely absent from the synapses that the glial lamellae surrounded (Somogyi et al., 1990). With the sensitive postembedding localization method, a whole new chapter opened up. Soon talented students and visitors joined to learn the methods from David Roberts.

Agnes Baude, a fresh doctoral graduate, arrived from Marseille in 1991 and set out to explore the subcellular location of metabotropic glutamate receptors (mGluRs). I will never forget the thrill that we had when in the EM we realized that postsynaptic mGluR1a on the dendritic membrane of hippocampal and cerebellar neurons was largely excluded from the postsynaptic junction proper and was concentrated in a perisynaptic ring of glutamatergic synapses (Baude et al., 1993). This was so surprising that we kept testing the result with both pre- and postembedding immunogold labeling, as well as in cryo-EM sections cut by David Roberts, a very difficult technique. Attending a conference, I was keen to show the results to Professor Shigetada Nakanishi, who was at the forefront of receptor cloning and an authority on metabotropic receptors. He realized the significance of the finding and the potential for the many receptors they were working on and recommended that we collaborate through a visit by his doctoral student Ryuichi Shigemoto; the rest is history. Ryuichi arrived with his family in 1995 with great training in molecular biology, but with no electron microscopic experience. In no time, he was taking electron micrographs. Today Ryuichi is a world-leading innovator of quantitative EM immunocytochemistry and a professor at the Institute of Science and Technology Austria in Vienna.

Ryuichi brought to our lab in Oxford antibodies that he developed to several receptors for his doctorate, among them one to mGluR7. In light microscopic preparations, he had discovered that mGluR7 richly decorate the soma and dendrites of some neurons in the hippocampus, but it was difficult to make out in which subcellular domain the signal was located. We prepared pre-embedding silver-intensified immunogold specimens, in which the receptor-specific primary antibody is first recognized by a secondary antibody attached to a 1 nm gold particle. This particle is then made visible by growing a larger reduced silver shell on it, a method introduced to the lab by David Roberts from the literature. Once again, I remember the shock and the thrill of the unexpected when I first saw that the particles were in the active zones of presynaptic terminals innervating a select population of GABAergic neurons,

collectively outlining the cell's shape. Ryuichi understood that if these terminals were so rich in presynaptic mGluR7, then either they came from a specific source of neurons expressing high levels of mGluR7, or the postsynaptic cell determined the deposition of a high level of presynaptic mGluR7 selectively in its inputs. By following the axons of single-labeled hippocampal pyramidal cells and serial section EM analysis, he proved that the latter was the case. We discovered the target cell–specific deposition of presynaptic mGluR7 in synapses in individual boutons along the same individual axon (Shigemoto et al., 1996). As presynaptic mGluRs inhibit neurotransmitter release, we predicted that these neurons would be subject to stronger presynaptic inhibition than neurons innervated by low-mGluR7-expressing boutons, implying that the postsynaptic cell type influences the probability of transmitter release to itself. This hypothesis was more recently proven, but through a different molecular mechanism independent of glutamate release; the inhibition is mediated by protein-protein interaction of mGluR7 with a postsynaptic protein, Elfn1, across the synaptic cleft (Stachniak et al., 2019). Ryuichi eventually completed a gigantic description of all the metabotropic glutamate receptors in the hippocampus, which is now a classic (Shigemoto et al., 1997).

The success of our immunogold/silver particle localization of receptors attracted talented visitors and staff to the unit, and we extended the program to many neuronal systems and receptors. Francesco Ferraguti brought molecular biology expertise and, with Yannis Dalezios, we expanded the exploration of all the presynaptic mGluRs in the cortex and hippocampus (Ferraguti et al., 2005). Supported by Ryuichi, we demonstrated that all group III mGluRs were also in the presynaptic active zone of GABAergic terminals (Somogyi et al., 2003). This localization is probably explained by their proximity to calcium channels involved in transmitter release. With Rafael Lujan from Spain, we showed that the perisynaptic enrichment of dendritic group I mGluRs also applied to mGluR5 forming strategic microdomains on the spines of hippocampal pyramidal cells (Lujan et al., 1996).

In parallel studies, we also investigated the synaptic and extrasynaptic location of ionotropic glutamate receptors, raising antibodies with biochemists Elek Molnar and Jeff McIlhinney, the latter who was one of the unit's group leaders. A visiting undergraduate from Hungary, later graduate student at Oxford, Zoltan Nusser was a key and energetic investigator whose sharp focus led to significant progress. In a seminal study, Zoltan proved that in a population of glutamatergic nerve terminals originating from CA3 hippocampal pyramidal neurons and innervating the CA1 area, the so-called Schaffer collateral commissural pathway, the number of AMPA-type glutamate receptors varied according to size of the synaptic area and the target cell type—synapses on GABAergic interneurons contained significantly

more AMPA receptors than pyramidal cell spine synapses. On large spines, there was a higher density of AMPA receptors, whereas many small spines had undetectable levels, demonstrating the basis of the now accepted use-dependent synaptic plasticity mechanism (Nusser et al., 1998a).

Receptor subunits of the GABA-A receptor were also cloned in quick succession arriving at a total of 19 different subunits in mammals, five of which form an anion channel, consisting usually of three different subunit species. Such diversity provided the opportunity for hundreds of receptor varieties differing in composition, dynamics, and pharmacological properties. To test if the many different GABAergic interneuron subtypes could have used different receptors, I collaborated with scientists who raised subunit-specific antibodies. One of them was Professor Werner Sieghart in Vienna, who understood the functional importance of receptor location in diverse synapse populations and enthusiastically supported our efforts. Beyond the joint achievements, we also formed lifelong friendships and visited each other. With Zoltan Nusser, we showed that the GABAergic synapses on the axon initial segment of a pyramidal cell innervated by the axo-axonic cells had a higher alpha-2 subunit content than the somatic synapses originating from basket cells; the latter were dominated by the alpha-1 subunit (Nusser et al., 1996). The most unexpected result was obtained by Zoltan, who was the first to test Professor Sieghart's antibody to the delta subunit in the cerebellum. He found that the receptors incorporating this subunit were excluded from the synaptic junction and only occurred in the extrasynaptic membrane, in contrast to all the other receptor channels (Nusser et al., 1998b). Later studies showed that the high affinity of the delta subunit-containing receptor was responsible for much of the tonic GABA-A receptor current that regulated the input resistance, hence the excitability of neurons.

My collaboration with Ryuichi resulted in invitations as a visiting professor to Kyoto and Okazaki where he had his labs. I loved every minute of it, leaving my administrative responsibilities behind, while being able to totally focus on projects in a well-equipped lab, I could do experiments as well as continue writing and the distant supervision of my group in Oxford. Living in student dormitories, mostly within easy walking distance to the labs, surrounded by natural wonders and exotic shrines and gardens, I felt liberated. Ryuichi was a wonderful host, an expert cello player, and a tolerant group leader. The pace of lab work there was very different from that in Oxford; in Japan the lights were almost never turned off, students nodded off at their desks, hardly the most productive practice.

In Kyoto, I met Kazushi Fujimoto (1954–2003), a technical genius, who developed a highly sensitive electron microscopic membrane freeze-fracture replica immunolabeling method using sodium dodecyl sulphate (SDS) digestion (Fujimoto, 1995). I immediately realized that this method was the way forward for quantitative subcellular immunocytochemistry of

membrane proteins, and indeed, in addition to Kazushi, some other groups started to use it as well. It is a method that demands extreme dexterity and patience: The fixed or unfixed tissue is rapidly frozen and broken in a way that many of the membranes split between the two lipid layers taking the membrane proteins either to the intra- or extracellular half of the plasma membrane. The proteins are trapped by an evaporated carbon layer followed by platinum shadowing to show the distribution of proteins in the replica as bumps in their original location. The tissue is washed away with SDS, and the replicas can be probed with antibodies visualized by gold particles of different sizes for different proteins in the same replica. The whole process can be made quantitative by comparing different parts of the membrane, different cells, and synaptic junctions. There is no penetration barrier to antibodies, and because of the SDS treatment, immunoreactivity of proteins is excellent.

Kazushi was a friendly but withdrawn scientist and sadly his efforts were undervalued in his department. He taught me and Ryuichi about the elaborate processing and instrumentation, and we both established the method in our labs, followed by Francesco Ferraguti at Innsbruck and Zoltan Nusser at Budapest. Ryuichi had a flair for technical innovation; he introduced many improvements, combined receptor counting with measurements of synaptic physiology of the same population of synapses, and put several people on its applications. I visited several times with David Roberts to learn, until finally we could also do it in Oxford on a small scale, but we did not have the capacity for expanding it. I shared the supervision with Ryuichi of a graduate student, Yu Kasugai, at Okazaki. Kasugai visited Oxford, and we completed the mapping of several GABA-A receptor subunits on the surface of hippocampal pyramidal cells (figure 5). We found that although the receptors were concentrated in postsynaptic junctions, as expected, the total population of low-density extrasynaptic receptors was several times larger than synaptic receptors (Kasugai et al., 2010). Less than 1 percent of the somatic surface was covered by synaptic junctions. Ryuichi trained several students and postdocs, and they discovered many unexpected rules in the location and quantitative relationships of receptors and voltage-gated ion channels (Eguchi et al., 2022).

The collaboration with Werner Sieghart had a major effect on my development and life beyond GABA-A receptors. Werner asked me to host his freshly graduated doctoral student at Oxford for widening his horizons. Thomas Klausberger had a deep molecular biology background and figured out the molecular domains of interacting GABA-A receptor subunits for his doctorate. After an initial EM training and receptor localization, it was clear to me that Thomas could go much further than I could guide him, and indeed, today he is a full professor and Director of the Center for Brain Research in Vienna. But before he could set out to form an independent laboratory, we got down to the

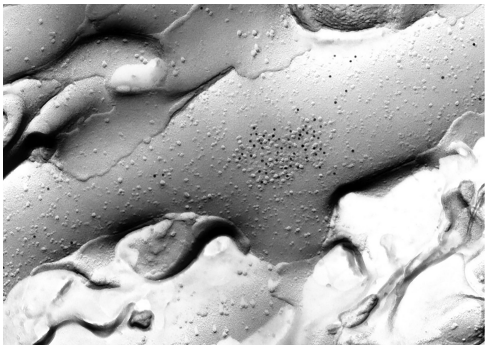


Fig. 5. Electron micrograph of membrane freeze-fracture replica immunolabeling of the dendritic shaft of a hippocampal pyramidal cell with 10 nm gold particles (black dots) for the beta-3 subunit of the GABA-A receptor. The receptor is highly concentrated in the postsynaptic junctional membrane marked by the high density of intramembrane proteins; a lower density of labeled extrasynaptic receptors is also present. I took this image in the laboratory of Ryuichi Shigemoto in the National Institute of Physiology, Okazaki, Japan, and dedicate it to the memory of Kazushi Fujimoto, the inventor of the technique. (Data in Kasugai et al., 2010).

business of widening his scientific horizons even more, so I sent him to my friend Professor György Buzsáki (see volume 13) for additional training in Newark at Rutgers University.

System Electrophysiology of Identified Neurons *in Vivo*

Our paths crossed many times with György Buzsáki (Gyuri) who has had a great influence on my thinking about the brain. Gyuri also started in Hungary and received neurophysiology training from Professor Endre Grastyan, a great neurophysiologist and a contemporary and friend of Professor Janos Szentagothai. Eventually, once the MRC ANU was set up, I had the opportunity to host Gyuri when he visited for the training of Tamas Freund and me in electrophysiology *in vivo*. We collaborated on a project to test recovery of electrical activity following brain ischemia (Freund et al., 1989a). Gyuri is a stimulating partner with strong views about most things and with exceptional technical and analytical skills. We collaborated on the hippocampus repeatedly when he was interested in the axonal projections of recorded, identified cell types, and I had the privilege to work in his lab (Li et al., 1994). Thus, it was natural that I arranged for Thomas to visit him, with the suggestion that they try the *in vivo* intracellular recording and labeling of single GABAergic neurons with sharp electrodes. Thomas spent a few months in New Jersey, and although they did not get the interneurons, he gained invaluable experience in physiology, particularly in network oscillations. Gyuri was typically recording interneurons with tetrodes, but that method did not allow for the identification

and visualization of the recorded neurons. By the time Thomas returned, Shone Eaton, a physiologist group leader in the unit, had managed to reproduce Didier Pinault's juxtacellular recording and labeling technique (Pinault, 1996). Thomas soon picked up the method and applied it to the hippocampus. He had learned from Gyuri how to differentiate between putative pyramidal cells and some GABAergic interneurons in the hippocampus based on their firing characteristics. Our question was, did the distinct types of interneurons that we recognized by their shape and molecular cell markers differ in their *in vivo* firing? More generally, what factors drove the evolutionary differentiation of GABAergic cells?

I shall never forget that, when after several attempts of labeling, one day Thomas brought to the microscope a neurobiotin-labeled and HRP-visualized section of the first neuron that he predicted would be an interneuron. The whole lab gathered: It was clearly an interneuron, a basket cell, later published as figure 1 of our first paper from the anaesthetized rat CA1 region (Klausberger et al., 2003). Many more followed, including the first-ever axo-axonic cell with identified firing pattern in several brain states, which I reconstructed from many sections and included in figure 2 of that paper. The significant advance was that each neuron could be monitored during different brain states, such as theta oscillation, or slow-wave sleep with sharp-wave ripple events. The combination of their behavior was so characteristic that Thomas and later other colleagues he trained could tell which of the about 25 GABAergic interneurons they were recording while the electrode was still in the brain and the animal was alive. Initially, Gyuri guided us in the analysis of firing time series in relation to the phase and frequency of oscillations, such as theta, gamma, and high-frequency ripple oscillation. The firing patterns, along with the shape of the dendrites reflecting input and that of the axon reflecting output, as well as the combination of signaling molecules that we visualized in the labeled neurons, and their terminals defined the cell types. Thomas managed to record a population of bistratified GABAergic neurons, which only innervated the dendrites of pyramidal cells and fired at the trough of theta oscillations at a later phase than basket and axo-axonic cells did, and they were very active during sharp-wave ripples (Klausberger et al., 2004). The many different cell types that we identified and named cooperatively formed the system that carried out "the unity of network operations" (Klausberger and Somogyi, 2008).

At that point, it was obvious that we finally had the tools to dissect the contributions of cell types in relation to the roles of the system, so I increased our capacity by appointing new students and postdocs, some of whom turned out to be brilliant. Thomas and Damien Lapray constructed microdrives for glass electrodes carried on the head of the rat, and they could move it just next to the cell for recording (Lapray et al., 2012). Linda Katona and Tim Viney were the first to record and label axo-axonic cells in

naturally sleeping and freely moving rats. Just as in anaesthetized animals, during theta oscillations, on average, axo-axonic cells fired the most just after the peak of theta cycles, when pyramidal cells fired the least, and when pyramidal cells fired the most at the trough of theta, axo-axonic cells were silent (Viney et al., 2013). This double-reverse correlation makes it very likely that GABA release to the axon initial segment is a major mechanism governing the pyramidal cell-firing threshold. Linda, who started as a visiting undergraduate from Romania and continued as a doctoral student, with her colleagues managed to record and label somatostatin-expressing interneurons: the bistratified cell and the O-LM cell, innervating completely different dendritic domains of pyramidal cells in naturally sleeping or moving rats (Katona et al., 2014). Refuting the dogma that somatostatin-expressing interneurons had a unified role, Linda demonstrated that the spiking of the two cell types could be differentiated in several network states.

The nights were long and the success rates were very low, but the rewards of the results were great. John Tukker and Balint Lasztoczi tackled recording different types of GABAergic basket cells, defining how those expressing the calcium-binding protein parvalbumin differed from a non-overlapping population expressing cholecystokinin, yet converging with their terminals on soma and proximal dendrites of the same postsynaptic pyramidal neurons (Tukker et al., 2013; Lasztoczi et al., 2011). They also became experts in analyzing the specialization of interneurons during various forms of gamma frequency network oscillation (Tukker et al., 2007; Lasztoczi and Klausberger, 2016). Thomas and Pablo Fuentealba recorded slow-firing neurogliaform cells, one population of which we named the *ivy cells* after their characteristic axons. An image of a reconstructed ivy cell and the ivy plant climbing in my back garden made it to the cover of *Neuron* (Fuentealba et al., 2008). This successful program made it through the five-year unit review, earned Thomas a group leader position in the unit and later a professorial position in the Medical University of Vienna. He had a clear vision to place identified neurons into the network operation reflecting the behavioral context of the animals. He extended his studies to the prefrontal cortex with his students Katja Hartwich and Lema Massi and continued his program in Vienna (Massi et al., 2012; Passecker et al., 2019).

Other groups internationally greatly contributed to the ever-evolving scheme of neuronal spatiotemporal network diversity using similar approaches. Ivan Soltesz, who started as an undergraduate visitor from Hungary to Oxford and became a system physiologist and the James R. Doty Professor of Neurosurgery and Neurosciences at Stanford University, made brilliant contributions on a large scale. With Csaba Varga, who earlier was a visitor to Oxford, they measured oscillatory phase-specific interneuron-type firing sequences in the hippocampus in mice during

theta, gamma, and high-frequency ripple oscillations discovering that, on average, the same sequence was followed irrespective of the oscillatory frequency (Varga et al., 2012). Independently, I also noticed that during theta rhythm the preferred firing phase of axo-axonic, basket, O-LM, bistratified, and CCK GABAergic neurons followed a sequence that resulted in a traveling wave of GABA release starting at the axon initial segment near the peak of the theta wave, through the soma to the dendrites from cycle to cycle (Somogyi et al., 2014).

The complex synaptic temporal interactions between the firing of pyramidal cells, interneurons, and hippocampal afferents did not make it obvious how the average cell type–specific peak excitability and spike output of neurons arose rhythmically. It was well known that input from the medial septum and brain stem were major regulatory inputs for the hippocampal theta rhythm, which reports a brain state associated with movement, sensory-motor processing, or paradoxical sleep. After Thomas Klausberger left for Vienna, we sought to dig deeper into the role of the medial septal input containing GABAergic, cholinergic, and glutamatergic afferents, synaptically influencing both pyramidal cells and interneurons. Particularly, the GABAergic septal input to interneurons, on which Tamas Freund did seminal work at Oxford was the most relevant (Freund and Antal, 1988). Our hypothesis was that different populations of GABAergic neurons may already be in the septum that provided differential rhythmic inputs to different interneuron types in the hippocampus. In collaboration with David Dupret, a previous group leader in the ANU and now professor at Oxford, we set out recording and visualizing individual septal neurons *in vivo* with neurochemical identification aiming to analyze their axons in the hippocampus. Luck was on our side, as a very talented and determined graduate, Abhilasha Joshi, joined us from India for her doctoral studies. She learned from Tim Viney the technique of *in vivo* juxtacellular recording and the labeling of single neurons in head-fixed awake mice in a virtual reality environment. Tim learned the method from Thomas's group in Vienna. Soon Minas Salib, another of Tim's talented students, joined them from Germany to record medial septal neurons.

From extracellular silicone probe recordings in the medial septum, an astonishing diversity of firing patterns of individual cells emerged even without cell visualization, contradicting the prevalent simple model of the medial septum being a "pacemaker." Sure enough, there were neurons in the medial septum that displayed highly theta-modulated rhythmic firing dynamics and disrupting the septal input to the hippocampus stopped theta oscillations. However, just as the long-maintained simplified basket cell to hippocampal pyramidal cell rhythmic inhibition scheme did not fully explain the operation of the network composed of diverse cell types, the simplified rhythmic septal GABAergic inhibition of hippocampal basket cells could not explain the reality of diverse firing phases

of distinct hippocampal cell types. The medial septal rhythmic neurons displayed highly variable rhythmicity, different firing phases relative to hippocampal theta, and different burst durations. Abhilasha focused on two frequently encountered rhythmically firing cell types and managed to visualize them, proving that they were GABAergic. She named them in Sanskrit based on the firing patterns converted to sound on a speaker during recording. The Teevra (sharp sound) cells were the most rhythmic neurons, had short burst duration, and did not change their firing rate during movement, whereas the rhythmic Komal (soft sound) cells had longer burst duration and increased their firing rate during movement, and surprisingly had different preferential theta firing phases (Joshi et al., 2017). In a tour de force analysis, after labeling the recorded cell's axon from the septum to the hippocampus, Abhilasha proved that GABAergic Teevra cells preferentially projected to the CA3 area of the hippocampus, where they selectively innervated axo-axonic GABAergic cells and a population of cholecystokinin-expressing interneurons. She could identify axo-axonic cells based on Tim Viney's discovery that they lacked detectable SATB1 transcription factor in contrast to other parvalbumin expressing neurons (Viney et al., 2013). Thus, we identified not only the *in vivo* activity, as well as the location and projection area of certain medial septal neurons, but also the hippocampal interneuron types that they synaptically targeted. More surprises followed including the "orchid" GABAergic neurons from Tim (Viney et al., 2018), Minas Salib (Salib et al., 2019), and the Hugh Blaschko Fellowship awardee Gunes Unal (Unal et al., 2018). We obtained ample evidence for our hypothesis that target-selective medial septal neurons are major contributors to setting up the cell type–specific firing phase of distinct hippocampal interneuron types. Sadly, with the termination of the grant and when I had to leave the MRC ANU in 2016, the wonderful group of talented people dispersed, although much more remains to be discovered. Nevertheless, several of these colleagues were influenced by the experience in the Oxford lab. Thus, Abhilasha continues an exciting program on rhythmic brain activity in relation to movement in India, Gunes Unal carries on in Turkey, and Tim Viney now runs his own laboratory at Oxford, where I am a lucky guest.

Human Cortex and the Visits to My Family from Neurodegeneration

My last major program was aimed at dissecting GABAergic interneuron types in the human neocortex in collaboration with Marco Capogna, a previous group leader in the ANU. We obtained a grant from the European Research Council to explore neuronal circuits in surgically removed live cortical tissue, following in the footsteps of my previous student Gabor Tamas, a professor at the University of Szeged in Hungary, and others. We

found that double bouquet GABAergic neurons selectively innervate pyramidal cell dendritic spines and small dendritic shafts in a narrow cortical column and hypothesized that they regulate synaptic plasticity of glutamatergic inputs to the same spines (Lukacs et al., 2024). Some dendritic spines also have dual glutamatergic and GABAergic innervation, the latter from terminals expressing a high level of presynaptic cannabinoid type-1 receptor (CB1) as shown by electron microscopic immune-localization. However, the majority of CB1-expressing GABAergic terminals innervate dendritic shafts, where they regulate synaptic plasticity. We also found that specific types of GABAergic neurons express vesicular glutamate transporter type-3 in their terminals along with the vesicular GABA transporter, and hence likely release both amino acids as transmitters (Somogyi et al., 2025).

The human cortex is affected in a wide range of neurodegenerative diseases leading to dementia. An increasing number of gene variants are identified contributing to the risk. My father passed away at 90 because of heart failure; he was mentally still clear even if a bit slower. He had a strong essential tremor that I probably inherited, which is starting to bother me. Cerebellar degeneration is thought to be involved. It used to be called benign, but I do not find anything benign about it. My mother passed away at 87 because of some form of slow neurodegeneration that was never fully diagnosed but could have been Alzheimer's disease or fronto-temporallobal degeneration, or one of the many atypical, combined catastrophes. I organized medical care and supervision for them, visited them regularly, and they had a dignified exit. Curiously, I did not use to worry about my own possible neurodegeneration or look into the relevant research until my wife, Klara, was diagnosed with a mysterious condition in 2016. Then it all changed, and I joined Tim Viney's efforts to better understand neurodegenerative mechanisms (Viney et al., 2022; Sárkány et al., 2024).

As a neuroscientist, I now recognize that I have a duty to learn more about brain mechanisms underlying the condition of my late wife and give my children the opportunity to plan their lives, should there be some genetic predisposition for the disorder. While Klara's mind was still clear, we both decided to donate our brains to the Oxford Brain Bank. Upon her passing in 2024, her brain was processed and the whole tragedy of neurodegeneration was dramatically illustrated by the multiple proteinopathies upon neuropathological analysis. Studying our family histories and meeting her relatives indicates that there may be genetic predisposition for her late-onset neurodegeneration, but none of the well-known risk factors have been identified as causative to her death. My last project, alas with noticeably decreased capacity, is to try to find out what condition killed her. This is the question that I wake up with every day. In the process of testing for risk gene variants, I was identified as a heterozygote carrier of a significant risk factor, but this has not changed my life. On the contrary, I joined several clinical research projects in Oxford as a research subject. I also

coordinate an effort by a consortium of leading experts to get to the bottom of identifying Klara's condition. Along the way I learn both past and the latest progress in understanding neurodegeneration, which is exciting. My mentor and friend David Smith, who has been working on neurodegeneration for decades, along with Professor Helga Refsum and others at Oxford University, established that lowering homocysteine levels in the elderly with mild cognitive impairment significantly slowed the progression of cognitive decline (Douaud et al., 2013). Exercise has emerged as another preventive mechanism, and for decades, I have been running regularly 5–10 km distances for fun and the occasional race, such as the Oxford Town and Gown 10 km Cystic Fibrosis Charity race every May. This is a family event, and often I run with my children. As the years pass, one of the rewards of aging is that in the 5 km parkrun races on Saturdays, I can come first in my age category, often helped by the fact that I am the only one in my age range out of 500–800 runners. Where are all the others?

Authorship Ethics

The memory of my professor Janos Szentagothai's generosity of taking his name off the axo-axonic cell manuscript that I drafted in 1976, so that I could be the single author, remained with me. Later, I tried to accept authorship on research papers from my colleagues only when I did observational or significant analytical contributions and encouraged them to follow this practice. Several colleagues, including Tamas Freund, Zoltan Nusser, and Tim Viney, published papers with other scientists without me as an author while employed in my group, which may helped the development of their identities. Of my past colleagues, Thomas Klausberger and Zoltan Nusser adopted this practice. Authorship today largely follows the feudalistic practice of the grant holder being a senior author irrespective of the actual scientific contribution to the research. To justify this, vague terms like "conceptualization" have been introduced as a contribution. Coming from paternalistic, hierarchical, postwar/feudalistic Hungary, as a junior scientist, I was very keen to demonstrate my distinct contributions and use the papers to establish communication with scientists worldwide. I insisted to be among the corresponding authors. In the less regulated publication era of the 1980s, some of my papers had a note stating "correspondence to any of the authors," which should be the norm. But later this was no longer possible, as journals refused to implement my requests and restricted corresponding author numbers. The trend is for large multicenter, collective studies with dozens to hundreds of authors, where individual contribution is given over to the collective wisdom, which may be a productive mechanism to tackle large challenges. I worked in an era in which the insight and often the key contribution happened in the creative mind of a few privileged individuals.

Services to Science and Education

I taught in some undergraduate courses and practical classes at Oxford to a small extent and mainly supervised graduate and visiting students in research. My disadvantaged beginning haunted me all my life, and I feel a compulsion to provide opportunity and help to young people to realize their talents. Once I was reasonably stable in my job and family, I began to dedicate more of my capacity to help others. Apart from the individuals studying and working with me, I founded three organizations. The first was the Transylvanian Academic Exchange Trust (TAET, 1991–1996), at a time when the Romanian dictator Nicolai Ceausescu attempted to wipe out the culture and language of the nearly two million Hungarian ethnic minority in Romania. He introduced a plan of demolishing Hungarian villages and moving the people into concrete blocks of flats near newly created industries and moving ethnic Romanians from other parts of the country into Transylvania, where most Hungarians lived. I traveled to Romania in support of Hungarian academics in Targu Mures, where there was a bilingual (Romanian and Hungarian) medical school, where some doctors were educated in Hungarian. I initiated campaigns to withdraw the Honorary Doctorate of Elena Ceausescu in the United Kingdom, the chemist wife of the dictator, and to expel her from the New York Academy of Sciences. Fortunately, the Ceausescus were executed before their plans were fully implemented. With academics such as David Smith and Alan Cowey in Oxford, we established and registered the charity TAET and brought young scientists and fresh graduates from Targu Mures for international experience and research training. Many of them became professors at their home country later. Sadly, Hungarian language education has been gradually eroded in Romania and because of low birth rate and high emigration, the population greatly decreased with consequences for their culture and identity.

Transylvania, now part of Romania, is a multiethnic region of Central Europe and has changed countries many times during its troubled history. A significant population of the Hungarian minority lives in small villages often far from towns with high schools. Two linguist academics, Professor Janos Pentek and Professor Katalin E. Kiss, realized that many disadvantaged talented pupils never have a chance to attend high school because of the cost of commuting and a lack of residential accommodation. They founded the Nyilas Misi Talent Support Association (www.nyilasmisi.ro), in which a given promising pupil in the upper 20 percent of achievement in all subjects, is paired with a specific sponsor, who provides a monthly scholarship to enable the pupil to finish high school and who may also help during university studies. When there were not enough sponsors in 2011, I joined the association coordinating my family, friends, and academic colleagues from around the world as sponsors. I worked with the director of

the office, Zsofia Cseke, who remains a friend. At the height of our group's activity, 73 sponsors supported about 80 children per year, many of whom have already completed university. Now, out of about 300 sponsors, in our group, 32 of us support 38 children and university students.

Remembering my excellent education, particularly in the Zsigmond Moricz Gimnazium (high school) in Szentendre, I founded the Ramon y Cajal Scholarships competition in the town, first for all high schools then extending it to the Aron Marton Liceum in Csikszereda, Romania, and to the High Schol of Dunaszerdahely in the Slovak Republic to demonstrate cooperation among neighboring nations with loaded histories. Each year (2005–2016) I provided a not-so-straightforward theme around neuroscience and evolution that required original scientific thinking and scholarly research by the pupils to compete with an essay. The first prize was a summer internship in Oxford, mostly in my lab. The second prize was an internship in the Institute of Experimental Medicine in Budapest, where I had an honorary position, and the third prize was a significant book. A committee of neuroscientists scored the essays. The prizes were handed out in my high school on a special science meeting of the alumni and pupils in natural sciences organized by the excellent chemistry teacher Gabor Maknics, a friend of mine. Many talented pupils were awarded, most of them graduating later from universities; some of them have already completed their doctorate and work as postdocs in various parts of the world.

In 2011, I was awarded the Semmelweis-Budapest Prize of Semmelweis Medical School in Budapest (figure 6), which carried a prize



Fig. 6. With pioneering ex-pupils and friends in the Hungarian Academy of Sciences after delivering the Semmelweis-Budapest Award lecture on November 12, 2012. The award led to the foundation of the Stephen Kuffler Research Foundation in Budapest under the chairmanship of Zoltan Nusser. From left to right, Zoltan Nusser, Tamas Freund, Peter Somogyi, Zoltan Kisvarday, Gabor Tamas, and in the front, Klara Peto, a friend and longtime colleague.

of EUR10,000. It was the year of the first attack on higher education by the Orban government, which severely reduced funding for education, and I felt that I could not take the money when universities struggled to pay their staff. I offered the prize as seed money to the university toward a foundation awarding young talent in sciences. As the university was unable to organize this, I asked my previous pupil Zoltan Nusser to set it up in the Institute of Experimental Medicine, where he was a group leader. The director, Tamas Freund, who was another previous student of mine, approved it, and Professor Sylvester E. Vizi, a previous Academy president who was an emeritus professor there, accepted the request to be one of the founders. The Stephen Kuffler Research Foundation was born in 2012 (https://kuffler.site.ox.ac.uk). We chose the name with my friend Jozsef Somogyi in recognition of Kuffler's seminal discoveries establishing neuroscience as a discipline. I invited living pupils of Kuffler as trustees, and they all enthusiastically supported the idea; David Hubel, Torsten Wiesel, John Nicholls, Ed Kravitz (see volume 4), and Eric Kandel (see volume 9) were joined by David Smith and Sylvester Vizi. These founders and others donated to the foundation, some of them on a yearly basis, which was greatly extended by Nusser's energetic fundraising in Hungary. The aim was to identify and reward those early talented students who already in their undergraduate years were showing originality and scientific potential, which we later extended to doctoral students. The fields included all aspects of biology and medicine and applied computational and related physical sciences.

To reflect Kuffler's international roots—he studied medicine in Vienna and was born in Hungary during the Austro-Hungarian monarchy—and to demonstrate cooperation in Central Europe, an area of long-running historical ethnic tensions, applications were open to all countries of Central Europe, including Poland, which produced several awardees. Under Nusser's chairmanship of a board of eminent active scientists, awardees were selected once a year and an award ceremony was held at the Hungarian Academy of Sciences, several of which were attended by Kuffler's children. I tried to attend most of the award events, and David Smith and John Nicholls gave talks and handed out awards. We were all very proud of this scheme, which attracted a lot of attention; I presented our initial results in 2013 at the Kuffler Centenary Symposium at Rockefeller University, which was attended by Professors Kandel, Wiesel, and Kravitz. Some of the more than 50 awardees of the Foundation are now established scientists. Sadly, following my dismissal from the Institute of Experimental Medicine in Budapest in 2020, Zoltan Nusser felt that he could no longer work with me and resigned, which was painful. I could not organize a replacement and the incorporation of the Foundation was terminated in Budapest and has remained dormant. I have moved the website to Oxford and hope to resurrect it on a smaller scale.

The David Smith Lectures in Anatomical Neuropharmacology at Oxford (2008–2025)

In recognition of the success of exploring identified neuronal circuits in the ANU, on the 25th anniversary of the MRC's decision to establish it, I decided to mark each year by recognizing outstanding scientists who shared our vision or contributed to the unit's work. Namely, I established the David Smith Lecture in Anatomical Neuropharmacology, with the inaugural lecture given by Antoine Triller from the Pasteur Institute, France, in 2008. The awardees receive a unique laser-engraved wooden plaque illustrating the brain, the Oxford Sheldonian Theatre, the GABA molecule, and a stainless-steel engraved electron micrograph or, more recently, a drawing of David's scheme representing the neuron as a secretory cell. The lectures were initially only in neuroscience, but from the time of the relocation of our group to the Department of Pharmacology in 2016, they were opened to all areas of pharmacology. Nominations are made by group leaders and voted on democratically. We have been honored by outstanding scientists giving stimulating lectures, in chronological order: Antoine Triller, György Buzsáki, Tamas Freund, Ryuichi Shigemoto, Ann Graybiel, Peter Jonas, Ivan Soltesz, Tomas Hökfelt, Andreas Björklund (see Volume 10), Zoltan Nusser, Jean-Marc Fritschy, Thomas Sudhof, Andreas Luthi, Hannah Monyer, Tim Bliss, Hugh Williamson, Anette Dolphin, John Hardy, and Thomas Klausberger (in 2025). The lectures are followed by a dinner in one of the colleges and are attended by David Smith (www.pharm.ox.ac.uk/seminars-and-lectures/david-smith-lecture).

As the founder of the lectures, I could not accept giving one, but in recognition of the 50th anniversary of the publication of our first paper with David Smith (Somogyi et al., 1975), I accepted his and the department's invitation to give a special lecture on June 5, 2025: "50 Years with David Smith on Location: From Chromaffin Granules to Neurodegeneration via Synapses" (https://ox.cloud.panopto.eu/Panopto/Pages/Viewer.aspx?id=4e264046-7b68-4d6d-b6d6-b30100806329).

Participating in the Hungarian Academy of Sciences, 2004–2021

I have a strong Hungarian identity and dual Hungarian and British (1995) citizenship and feel responsibility for both people. I have been supporting numerous Hungarian students and scientists, and three of my students, Tamas Freund, Gabor Tamas, and Zoltan Nusser, are members of the Hungarian Academy of Sciences and among the top scientists in Hungary. Membership of the Hungarian Academy of Sciences (the Academy) is a much sought-after recognition of scientific achievement in Hungary. The Academy was founded in 1825 at the initiative of Count István Széchenyi,

who offered a year of his personal income to support it, and other nobles joined in with donations to support science and the nurturing of the Hungarian language. Széchenyi traveled widely in Europe, including Great Britain, and his mission was to promote scientific research and develop the Hungarian language for scholarly use. Nomination for membership is only by members and is a complex process with many conditions—for example, there can only be 365 members at any one time, which is ironic as life expectancy is increasing and scientific research is expanding in the world. The Academy includes the whole spectrum of learning, natural sciences, and humanities as well as law and economics, and until recently, it was directing the national research institutes.

I was nominated at an unusually young age of 42 by a distinguished group of academicians, including professor Janos Szentagothai, who was president of the Academy at the time; my university zoology professor, Janos Balogh, who was a previous vice president; and the neuropharmacologist professor Sylvester Vizi, who later became president. At the time of the debate of my credentials in the Biology Section of the Academy, I was working in Oxford on unpaid leave from my job in the Anatomy Department, where I kept my affiliation. My formal boss was Jozsef Hamori who had ample personal experience of my generally critical attitude, and he informed the debate that I was a British citizen already, which was not true, but it excluded me as a candidate for election. I had not even applied for British citizenship until then, but nobody bothered to ask. The meeting concluded that while recognizing my scientific contributions, as a foreign national, I could only be elected as a foreign member, which was considered a great honor, but gives no voting rights for the member in the Academy's business, a critical issue for those who may wish to influence proceedings and decisions. I was saddened by the obvious intent of exclusion and declined the honor, as I would have been the only Hungarian citizen ever elected as foreign member. Later in 2003, when Sylvester Vizi became president, he proposed a new nomination, which was led by my previous student and colleague academician Tamas Freund. The Biology Section finally honored me with membership in 2004.

The Academy was, and remains, a conservative institution rooted in feudalistic traditions and rituals, where connections and alliances play a great role in both nominations and the allocation of funds, as they do all over the world. However, unusually in terms of international practice, since 1989 following the collapse of the Soviet Union–maintained regime, when academic salaries were very low, the academicians receive a significant monthly stipend for life on top of their normal salaries or pensions, irrespective of their continued work. This provides a high incentive to become a member and a potential for feudalistic dependence of candidates from nominators. Using my own stipend for travel from Oxford, I attended monthly Biology Section meetings, met outstanding scientists, learned

about brilliant scientific advances, and attempted to propose the introduction of reforms. These attempts mostly failed and can be summarized in three themes. First, I proposed the introduction of international peer review for all decisions and selections involving funds, such as scientific grants, academy membership, and senior posts at research institutes. Second, in 2016, when not a single female candidate was elected for membership and the total female membership of the Academy was 7 percent, I documented and published the historical injustice of discrimination of women, demonstrating that at the rate of their election, it would take 150 years for women to reach 30 percent of membership. I proposed a mechanism for change. Hungary historically is a paternalistic, semifeudal society. A well-intentioned debate ensured, but the leadership ignored their responsibilities, and little has changed. My third effort was directed toward persuading the academicians to give up, selectively and gradually, their stipend that we received from the government, as it hampered the representation of academic values independent of the directions of the political wind. My proposal created a great outcry, but soon enough, the consequences of being on the payroll of the government became apparent. The only success I can show for my labors was the election for honorary membership of my colleagues Alan Cowey from Oxford and Werner Sieghart from Vienna, both of whom gave great inaugural lectures at Budapest.

In 2018, the government initiated the confiscation of the assets of the national research institutes that were legally the property of the Academy, and the taking over their management, justified by claims of improving efficiency. However, the government's real goal was to bring all academic activity and education under political control and generally to intimidate academics. The mechanism they invented was "to borrow" the buildings and research equipment at zero rent and force the researchers to resign their employment rights, and then reappointing them on the same day under much less secure conditions. The plan worked, as I concluded in a lecture to the General Assembly: "We Have Become a Country of Fear" (Somogyi, 2019; in Hungarian and English, https://mersz.hu/dokumentum/matud_430/#matud_f17649).

There were some protests. The then President Laszlo Lovasz tried to negotiate, but because of the intimidation, fear, and opportunism of the academics, the institutes were eventually brought under political control, which was increasing by the day until the fall of the Orban government in 2026. The ensuing mismanagement that followed has damaged morale, reduced output, and has led to an exodus of scientific talent from the country as well as accelerated the lack of applicants for science education and careers. In the subsequent election for new leadership, including the president, there were two internationally outstanding natural scientists as candidates. I gave a speech at the General Assembly on December 2, 2019, warning my fellow academicians of the government's damaging

actions and the potential consequences of the election (Somogyi, 2020). I intended to publish my speech both in Hungarian and English, the latter to inform the foreign and honorary members. The article was accepted in the Academy's official periodical, *Hungarian Science*, so I circulated it to all academicians. Without informing me, President Laszlo Lovasz and Tamas Freund, the vice president for life sciences, agreed to pressure the chief editor and fellow academician Professor Andras Falus to cancel my article, effectively censoring it to prevent debate, which could have irritated the political regime. My speech that they both heard in person without objection could not appear in the Academy's periodical and was published in full on an online forum *Qubit* (Somogyi, 2020, in Hungarian and English, https://qubit.hu/2020/02/25/oxfordi-akademikus-orban-viktor-kormanya-masfel-eve-rombolja-a-tenyeken-alapulo-bizalmat).

In 2020, members of the Academy elected Tamas Freund as president, who previously as vice president wrote to Prime Minister Viktor Orban without the knowledge of the presidium, apologizing for not having been able to get rid from the Academy of "unproductive social scientists" critical of the government. His letter became known before the election to the electing academicians and other representatives. I found the conduct of the newly elected president unacceptable and realized that Tamas Freund's support of the government's actions would prevent me from working for any reform. I resigned my membership after his election on August 1, 2020. Nevertheless, I maintained my honorary, unpaid post and affiliation at the Institute of Experimental Medicine in Budapest, where I was invited by the then director Professor Sylvester Vizi when my previous boss Jozsef Hamori sacked me from Semmelweis University. Several of my pupils joined the institute and I collaborated with scientists, and thus I considered myself not only a British but also a Hungarian scientist, which was very important to me. This came to a sticky end with my final humiliation of being dismissed by the director of the institute, my previous Oxford graduate student, Zoltan Nusser. He justified it by Orban's latest "catch-all law," mandating the resignation of all employees to make them more dependent under a new regulatory regime, and those who did not resign "voluntarily" were dismissed. I did not sign my resignation in a symbolic act of resistance to authoritarian control but instead asked Zoltan for any other position to maintain my Hungarian scientific affiliation. I received none and ceased to be an affiliated Hungarian scientist on December 31, 2020.

Epilogue

I hope that through hard work and dedication I have contributed to a better understanding of the brain. This history does not contain all the controversial events in my life, as it is difficult to document them briefly. The main

regret I sometimes have is the time and energy I spent on conflicts with colleagues, superiors, and administrators at the expense of creative thinking and research. I cannot tell how many of these conflicts could have been avoided with more wisdom on my behalf. On balance, I think my personality is unusually sensitive to noticing and objecting to dishonesty, injustice, and scheming, which others manage to put to one side without getting involved. Sometimes, I raised issues mistakenly and had to live the consequences. At other times, I was right but lacked the wisdom and power to change things and lost many sleepless nights in vain (e.g., Somogyi, 2019). I must consider myself lucky in how much I achieved in spite of all the turbulence in my life. The students, postdocs, and visitors who I trained and the collaborators I interacted with as well as the unknown number of scientists whose work I influenced will continue to use and develop the knowledge to which I contributed. This ensures the immortality of scientists, as even after their names are forgotten, the knowledge they helped to produce becomes part of the universal scientific culture of mankind.

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I express my gratitude to my parents who provided an exciting environment and care as well as allowed me to study and to make my decisions. I owe my development to many brilliant and motivating teachers. My contribution to science was most helped by my wife, Klara Molnar (1950–2024), who shouldered responsibilities, stood by me in times of trouble, maintained a stable family environment, and was part of our social collegiate community. She pruned my excesses and ensured with great determination that the family had the fair share of my attention and energy. She bravely supported us through our moves from country to country and accompanied me to conferences and lectures.

I owe my professional development to some outstanding scientific teachers with whom I enjoyed friendship and close personal interactions as they shaped my scientific conduct. I learned EM from Istvan Benedeczky, biochemistry and pharmacology from A. David Smith and Ian Chubb, neuronal circuit organization from Janos Szentagothai, immunohistochemistry and disease states from Claudio Cuello, visual neuroscience from Alan Cowey, and system neuroscience from György Buzsáki. The interactions with my younger colleagues helped me to fly with them on the journeys into the unknown. I was very lucky to have the support of excellent research assistants, including Klara Peto, Klara Szigeti, Eva Toth, Naomi Berry, Dimitra Beroukas, Frank Kennedy, Paul Jays, Ben Micklem, David Roberts, Kristina Detzner, Diane Latawiecz, Kathryn Newton, Philip Cobden, Wai Yee Suen, Zai Ahmed, Michael Howarth, and Emily Hunter to name a few, who maintained the facilities, made innovations, assisted in the experiments, and provided the continuity of

the knowledge pool. I had the privilege of benefiting from the support of dedicated, loyal secretaries, and personal assistants, including Dorothy Rhodes, Laura Lyford, Pamela Twynam, and Mary Gilgunn-Jones, who protected my creative time from the relentless administrative demands. I am grateful to them all.

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