

Peter Møller^a

Bernd Kramer^b

Jacques Serrier^c

Michèle Ravaille-Veron^c

^a Department of Psychology,
Hunter College of the City University of
New York, New York, N.Y., and
Department of Herpetology and Ichthyology,
The American Museum of Natural History,
New York, N.Y., USA

^b Department of Zoology, Universität
Regensburg, Regensburg, Germany
C.N.R.S., Institut Alfred-Fessard,
Gif-sur-Yvette, France

Thomas Szabo has died, and we have mourned his passing. Now, the time has come to celebrate his legacy and relive some of the memories we have of him as a colleague, a friend, a mentor, and an extraordinary human being. We who shared a short stretch of time with Thomas wish to include in this celebration his wife, Helge, and his two daughters, Anne and Caroline.

Following a sleepless ride on the Night Express from Hamburg to Paris, I (PM) arrived at the laboratory one early morning in the Spring of 1968. Located on the top floor of the *Collège de France*, the place was bustling with people speaking a foreign, unintelligible language, and hundreds of fishes in aquaria, strangely wired up to loudspeakers, intoned clicks and hums all over the place, presenting an even stranger cacophony still. Thomas emerged, calm and all smiles, one of his hallmark characteristics, introduced me to my future colleagues, and graciously provided me with six square feet of table space. Two weeks later, he phoned me in the middle of the night (the hotel concierge woke me up) and announced that I would present a talk on electric communication at the annual meeting of the French Physiologists that summer. Neither did I speak the language (a lack I quickly remedied), nor had I any idea whether I would have presentable data. Naturally, the data were forthcoming, I learned the speech by heart, and Thomas fielded the questions, which I did not understand.

Throughout our respective tenures in his laboratory, we all observed that Thomas knew how to challenge his students. He did it gently, but he did it consistently, and he

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always provided a safety net. In his own way, Thomas was very demanding. There was always a quest for perfection, and he applied the highest standards to himself, in his personal and scientific conduct, and also to his co-workers. As a result, collaborators did, on occasion, leave the lab, but Thomas maintained excellent relations with his in-house staff.

Thomas loved classical music, a trait carried over from his youth. As long as his daughters attended the *Ecole Alsacienne*, Thomas was a violinist with the school orchestra, and attendance at the Salzburg Festival was a high point of each summer for him and Helge. When Peter Schlegel and I (BK) were postdocs in Gif, the three of us met once a month and, with Thomas playing first violin, this memorable trio immersed itself in chamber music, mostly Mozart, Boccherini and Bartok. Thomas was self-confident, needed very little practice, and played flawlessly with a charming Hungarian temperament. I wish to dispel all rumors that have linked the name of this trio, 'Lady Killers', to any actual impact on attending females. Rather, these musical evenings always ended with a superbly prepared feast, and no one was ever hurt by the music or the food. With the departure of the musical postdocs to Germany, occasional gatherings were held in Ammerland on Lake Starnberg (Bavaria), where the trio turned into a quartet with the assistance of Frau Schlegel, Peter's mother. Towards the end of his life, Thomas joined the University Choir at Orsay, where, cognizant of his illness, he immersed himself in Brahms's German Requiem.

In addition to music, Thomas loved his garden, whose architecture he had helped to design, and he was proud to explain again and again the symphonic aspects of this creation. He was also a tinkerer who loved to fix things, the more complex the problem, the better. Thomas' longing for a perfect world permeated every aspect of his life. He disliked chaos and disorder, which made him visibly uncomfortable. With that in mind, all of us who house-sat in Gif while the Szabos were on vacation anticipated their return with some trepidation.

We will review Thomas' scientific career by highlighting some of the events that shaped and defined him as the gentle man and scientist we knew. Thomas' journey began in Budapest, Hungary, as an ambitious young medical student, unsure whether to do postdoctoral work in Australia, Sweden, or Switzerland, and it ended almost half a century later as Head of the Department of Sensory Neurophysiology of the C.N.R.S. (today's *Institut Alfred Fessard*) in Gif-sur-Yvette, France. Along the way, he contributed the pioneering work on the anatomical and physiological bases of electroreception, and he stood out as one of the godfathers of modern neuroethology.

This account is based in part on talks that two of us (PM and BK) presented at a conference in Montreal in August, 1992. We have also relied on material from Thomas' extensive travels (the African expeditions), which he made available to one of us (PM) in January of 1992, in Gif, during a series of interviews that covered several days. These

conversations were recorded, and direct quotes are so indicated. Thomas talked about his career, about important events in his life, about very personal matters, and about science and scientists. (Sadly, these were my last conversations with him.) He was a very happy man then, relaxed, serious and thoughtful at times, but also very witty and exuberant, providing delightful glimpses into the past and looking forward to 'research in retirement'. In spite of severe and painful restrictions imposed by the French Government on his laboratory and research program, Thomas was proud and optimistic to see his work continue with Kirsty Grant, Jean-Pierre Denizot, Jacques Serrier, and a cohort of new students. Thomas' career spanned so many projects and people that it is impossible to discuss each important contribution or mention every significant colleague. We hope that the lists of Thomas' publications, doctoral students, postdoctoral fellows and longtime collaborators will fill in the gaps and attest to the richness and breadth of his research interests and choice of colleagues.

The Formative Years (1924–1950)

Thomas Szabo was born on 23 March 1924 in Budapest, Hungary, to Reszö and Olga Szabo (née Karap). Thomas' father was a sculptor, educated at the Munich Academy of Fine Arts, and he ran a successful business as a stone mason in Budapest. Thomas' mother, one of the first women to graduate in Hungary with a baccalaureate degree, dedicated most of her time to the education of her sons in languages and music. A fascination with the sciences and medicine was also prevalent in the home, and in Thomas' words, 'I must have inherited a considerable portion of these "genes" from my parents'.

Having received his baccalaureate from St. Emericus College, Budapest, Thomas attended Medical School at the University of Budapest and obtained his MD degree (*summa cum laude*) in 1947. Lectures by Professors A. Szentágothai and A. Horányi on neurology and neuronal pathways made a deep impression on the young medical student and hooked him for life on the neurosciences. After short periods as assistant at the University's Institute of Anatomy and Institute of Neurology (1946, 1947, respectively), Thomas gained a fellowship from the Swiss government to work for three years at the Institute for Brain Anatomy and the Department of Physiology of the University of Zurich, under Professors M. Minkowski and W.R. Hess. Although the research there focused on the physiology and anatomy of feline and human central nervous systems, his first published paper (1949) dealt with the central integration of the postrotatory nystagmus in rabbits.

Six months into his stay in Switzerland, Thomas was summoned to the Hungarian embassy, where he was asked to return immediately to Budapest (no reasons were given). Thomas refused to comply, his passport was confiscated, and when the 'iron curtain' fell, he found himself a refugee, a 'citizen without a nation'. This period was certainly the most taxing in his life, and he seldom talked about it. Swiss immigration laws prohibited an extension of his stay, resulting in painful 'battles' with that country's authorities. Thomas disliked disputes and battles of any kind! In 1950, his brother Laszlo (a chemist on fellowship at the Institut Pasteur) invited Thomas to visit him in Paris, where friends had already 'decided' he should stay. They also concluded that the only laboratory he could possibly join was that of Alfred Fessard, the eminent French physiologist.

France, Alfred Fessard: From Mammals and Frogs to Electric Fishes (1951–1957)

Alfred Fessard had been appointed professor at the *Collège de France* in 1949, and, because laboratory space was in short supply in the 'old fortress' in the 5^e arrondissement, Fessard was given the *Institut Marey* in Paris' nice 16^e arrondissement (today's site of the French Open tennis tournament). Here, in collaborations with Mme D. Albe-Fessard, among others, Thomas renewed his interest in comparative physiology. For almost two decades, Alfred Fessard had been interested in the peripheral control of the electric organ discharge (EOD) in *Torpedo*, and he was now focusing on its underlying command system. He asked Thomas to search for the cranial interneurons that he, Fessard, thought linked the electrosensory pathways and the electromotor neurons. Thomas' summers were spent at the Marine Biological Station, Arcachon, where, together with Mme Albe-Fessard, he discovered the command nucleus that organizes the EODs during predatory behavior (nucleus ovalis) and studied its anatomy and physiology.

The first brush with electric fishes was followed by a series of neuroanatomical studies (several co-authored with Mme Albe-Fessard) on stretch receptors in frogs, spinocerebellar projections in cats (Thomas might have been the first to record from Purkinje cells), and pharmacological aspects of the iris sphincter muscle in pigs (a project that put him at the Paris slaughterhouses every morning before dawn). By the mid-1950's, Thomas realized he could not successfully pursue a medical career at the C.N.R.S., and he elected to complete his Ph.D. degree (*Thèse d'Etat*). For his thesis topic, he resumed his work on electric fishes: a comparative anatomy of the central electromotor command structures in both strongly and weakly discharging species (*Torpedo*, *Malapterurus*, *Electrophorus*, *Raja*, *Gymnarchus*

niloticus and the Mormyridae). Thomas' relentless, but unfortunately unsuccessful, search for an electric stargazer (*Astroscoptes*) is documented in many pleading letters to embassy attachés, research institutions, and leading scientists working on electric fish. Typical and telling, Thomas declined one 'hot lead' because the fish were not correctly preserved. He completed his thesis in 1956, the fateful year when Soviet troops crushed his people's uprising. Thomas decided to stay in France and become her citizen in 1957.

Expeditions to Africa (1958, 1959, 1961) and South America (French Guyana, 1959; Amazon River, 1964, 1967); the Conference on Bioelectrogenesis in Rio de Janeiro (1959)

At the urging of Fessard, in 1958, Thomas decided to explore his fish in the field: 'the place had to be a French colony with established ORSTOM laboratories, had to have a nearby airport and, most importantly, be in close vicinity of a river'. The place was Fort Lamy, today's N'Djamena, in the Republic of Chad on the River Chari.

The river provided an abundance of live material: *Marcusenius senegalensis*, *Petrocephalus bane*, *Mormyrops deliciosus*, *Mormyrus rume* and *M. hasselquisti* (with its large cerebellum), and in Lake Chad, Thomas spotted his first live five-foot *Gymnarchus niloticus*. The work on these mormyriforms, together with his thesis findings, laid the foundations for many future studies on the functional anatomy of the EOD central command system. Thomas returned to Fort Lamy in 1959 and for 6 months continued his journey to the former Belgian Congo, this time well equipped with an oscilloscope and other recording devices. On location, he worked on the anatomy and development of electric organs, studied mormyrid behavior, and collected specimens of juvenile mormyrids for further developmental studies in Paris. During his 3rd Africa expedition (1961) to Chad and the former French Congo, Thomas discovered the epidermal spike activity of knollenorgans [Szabo, 1962], which he first thought provided some form of sensory information but later found originated from the sensory cell itself [Szabo and Roth, 1967]. Aside from the wealth of scientific data, his travelogs rave about the journey by railroad from Brazzaville to Pointe-Noire and the 3-week voyage by boat back to Bordeaux, with ports of call in Abidjan and Dakar. Shortly after his return, he and Fessard published the germinal paper on electroreception: 'Mise en évidence d'un récepteur sensible à l'électricité dans la peau d'un mormyre' [Fessard and Szabo, 1961].

To acquaint himself equally with gymnotiforms, Thomas ventured to South America three times: briefly, in 1959, to French Guyana; in 1964 to Belém (together with

S. Hagiwara, L. Kruger, H. Lissmann, and H.O. Schwassmann); and in 1967, as guest scientist aboard the Scripps Institution of Oceanography Research Vessel *Alpha Helix* (in the good company of, among others, M.V.L. Bennett, T.H. Bullock, P.S. Enger, H. Markl, and A.B. Steinbach). Among the many species studied, the freshwater ray, *Potamotrygon*, remained an enigma for years because it apparently lacked the obligatory elasmobranch ampullae of Lorenzini. Under high magnification, Thomas eventually found the intradermal microampullae [Szabo et al., 1972], and the order of nature was restored. The scientific harvest from the *Alpha Helix* expedition led to one of Thomas' most comparative contributions: a paper on sound production in a Brazilian cicada [Enger et al., 1969]! Also during that expedition, Ted Bullock was stricken with a dangerously high fever for two weeks. As the only medical doctor abroad, it was Thomas that 'saved Ted's life'. After fruitless consultations with the ship's library, radio contact was established with Los Angeles, and Thomas announced that the patient had come down with 'rainforest fever'. With that therapeutic knowledge, Ted recovered fully within days.

Thomas was invited to participate at the 'Bioelectrogenesis' conference in Rio de Janeiro in 1959 where he enjoyed meeting with the major contemporary contributors to the study of electric organs (A. Cuceiro, J.C. Eccles, H. Grundfest, R.D. Keynes, and D. Nachmansohn among them). As noted, Thomas strongly disliked disputes, and he vividly recalled the animosity between Grundfest and Nachmansohn at the Rio meetings. For professional and personal reasons, 'Nachmansohn, the champion of chemical synaptic transmission, did not want to hear anything electric'. Thomas also noted that 'at this conference, nobody really seemed to appreciate the work' that he and two other participants, Michael Bennett and Hans Lissmann, were conducting on electric fish. 'There was hardly any discussion about electroreception, let alone ecology and behavior.' All this was to change with Thomas Szabo's scientific contributions and achievements.

America (1963/1964, 1966)

Two long-term research visits to the US, the Amazon expedition in 1967, and a short stay in Stockholm at the Karolinska Institute with J. Wersäll concluded the 'migratory phase'. The 1961 paper with Fessard had made its impression on 'the Americans', for T.H. Bullock and colleagues in Los Angeles had also discovered electroreceptors in the lateral line of gymnotiforms [Bullock et al., 1961]. Bullock had met Thomas while on a visit to Fessard's laboratory, and, as the great *spiritus rector* he was and still is, had sent Hagiwara to France (1962/1963),

where he met with Thomas at the Marine Biological Station at Arcachon. 'And surprise, surprise', Thomas recalled, 'only days later, Hagiwara invited me to come to Los Angeles to work with him.' Under Bullock's auspices, Hagiwara and Szabo joined forces and, together with Per Enger, conducted a series of landmark studies that established the neurophysiological bases for electroreception [Enger and Szabo, 1965; Hagiwara et al., 1965a, b; Szabo and Hagiwara, 1965, 1967]. In April of 1964, Lissmann joined the group with a dozen live specimens of *Gymnarchus niloticus*. Thomas finished his tenure in Los Angeles with a hallmark paper on sense organs in the lateral line system in electric fishes, including the Gymnotidae, Mormyridae, and Gymnarchidae [Szabo, 1965]. In 1965, he invited Hagiwara to France, where they investigated electrosensory pathways in mormyrids [Szabo and Hagiwara, 1967] and attempted to record from hair cell activity in the vesicles of Savi, which Thomas had investigated earlier [Fessard and Szabo, 1958; Szabo, 1958]. During a second stay in the US in 1966, Thomas worked with Hagiwara and H. Sakata on sensory pathways in *Gymnotus carapo* [Szabo and Sakata, 1967].

By then it had become clear that tuberous and ampullary electroreceptors encoded information either about non-homogeneous impedances in the environment or about foreign or self-generated EODs. It was thus important to investigate the integration processes for primary electrosensory information. A major event for students of behavior in weakly electric fishes was Thomas' discovery of 'rapid' and 'slow' electrosensory systems, which he described and characterized from the receptor to the mesencephalon.

In 1966, at the Lateral Line Conference in New York (organized by Phyllis Cahn), Harry Grundfest seriously tempted Thomas to stay in the US permanently. In the end, it was probably his loyalty to Alfred Fessard that made him return to Paris and to realize his dream, forming his own group of students and associates.

The Laboratories in Paris (1967–1972) and

Gif-sur-Yvette (1972–1993):

Laboratoire de Physiologie Nerveuse Sensorielle

Comparée at the Collège de France and Institut Marey

Within the C.N.R.S. (National Center for Scientific Research) Thomas was promoted from *Attaché* (1951–1956) and *Chargé de Recherche* (1957–1960) to *Maître* (1961–1973) and, finally, *Directeur de Recherche* in 1974. The Laboratory of Neurophysiology had its beginnings in 1967 at the *Collège de France* and the *Institut Marey*, which together occupied not more than 300 square feet. At the *Collège*, histologists (C. Baillet-Derbin, C. Derbin, J.-P.

Denizot, M. Ravaille) and behavioral physiologists (R. Bauer, P. Belbenoit, P. Moller, J. Serrier) shared their space with probably all known electric fish species (except the strong 'electricians', which were always in abundance in Arcachon during the summer; review in Belbenoit, 1986). The Institut Marey was home to the electronics maven (M. Boudinot), electrophysiologists (A. Roth, P. Schlegel) and a little cubby hole that served as office (B. Consigny). Thomas shared his time equally with both groups, commuting between the two places in a relic of an automobile, a two-stroke Auto Union DKW, and later in a real car, a VW beetle. When the two labs could no longer accommodate the research, Belbenoit and the histology group moved into temporary quarters at the Orsay campus of the Université de Paris. A new home had become a necessity!

In 1972, the long overdue move into new and more spacious quarters in Gif-sur-Yvette marked the beginning of a truly comparative approach to the study of electric fishes. In an amazingly short time, Thomas assembled a research team consisting of his old core group, new collaborators, former students and postdocs, and guest scientists whose areas of expertise included anatomy, animal behavior, comparative physiology, developmental biology, electrophysiology, histochemistry, histology, immunocytology, microscopy, taxonomy, and traditional zoology. Two huge aquarium rooms in the basement of the institute were the envy of every visitor and guest scientist. In short, at the Institute in Gif, the secrets of electric fishes were in serious jeopardy. Between 1972 and the time of his death, Thomas authored or co-authored over 300 papers and abstracts, in addition to other publications that resulted from work in his laboratory but did not bear his name. (Typically, Thomas never allowed his name to appear on a paper covering work with which he was not directly involved.) Over the years, Thomas' resident senior scientists (J.-P. Denizot, K. Grant, and J. Serrier) supervised their own students, spawning a second generation of electric fish disciples in Gif.

Thomas was not a behavioral physiologist, but he keenly realized the importance of relating laboratory findings to natural behaviors. Thus, in the 1970's a large contingent of animal behaviorists adorned the premises on the second floor of the Institute at Gif (including B. Kramer, G.W.M. Westby, and ichthyologist F. Kirschbaum, review in Kramer, 1990). In addition, several of Thomas' students (M.-J. Toerring, C. Teyssèdre, and P. Jacob) produced significant behavioral studies. In all these endeavors, Thomas always took an ardent interest. Although overwhelmed at times by new terminology and techniques, he listened, learned, and commented constructively. Thomas never went back into the field again, but he generously supported several expedi-

tions of his co-workers to Central and West Africa [review in Moller, 1995].

Thomas Szabo was both a delightful guest and a wonderful host. He understood how to cultivate relationships with friends and colleagues both at home and abroad, and he organized several 'roundtables' and symposia: in 1977 on 'Electroreceptors' (as a satellite symposium to the XVIIth International Congress of Physiological Sciences in Paris), and the First International Symposium on Electroreception and Behavior in Gif (who can ever forget the host's hospitality, which extended far beyond the facilitation of scientific discussions!). In 1980, the Second International Symposium on Electroreception was held in Keszthely, Hungary, and in 1986 another memorable electric fish symposium took place at the meetings of the European Neuroscience Association.

Once the Department in Gif was up and running, Thomas, alone or accompanied by Helge, came to the US almost every year to attend the meetings of the Society for Neuroscience, and New York City was their obligatory port of entry. Memories of these stop-overs with one of us (PM) abound: hiking in the Catskills, strolling along the ocean shore on Long Island, and working in the greenhouse of the American Museum of Natural History (under tropical conditions), where behavioral experiments underscored the role of the nucleus mesencephali exterolateralis for electrocommunication in *Gnathonemus petersii* [Moller and Szabo, 1981].

Thomas served on the advisory board of the *Journal of Comparative Physiology*, and he was a member of several societies: *Association des Physiologistes* (France), *Association des Anatomistes* (France), Society of General Physiologists (USA), Society for Neuroscience (USA), the New York Academy of Sciences (USA), the International Society for Neuroethology, and the J.B. Johnson Club. Among the many honors, he received the *Prix Godard* of the French Society of Biology (1965) and the *Prix Cuvier* of the French Academy of Sciences (1967). In 1975, he was elected a member of the *Deutsche Akademie der Naturforscher Leopoldina*, and in 1978, he was elected Honorary Fellow of the National Academy of Sciences of India.

During the last years of his life, Thomas became even more 'comparative', extending his interest to other sensory systems (olfactory, vestibular, mechanosensory, and acoustic) in fishes and their central integration with the electric sense. He was also looking forward to exploring the existence of possible acoustic projections to cerebellar units and investigating the inductive capacities of the command system in the central nervous systems of fishes. These research plans, sadly, were unfulfilled.

Thomas Szabo died on 28 November 1993, losing his most painful battle with cancer. The disease had just been diagnosed when we honored his career and scientific contributions at a symposium in Montreal in August of 1992 [Bell et al., 1993]. His death was, and still is, a great personal and scientific loss for his family, close friends, and a large community of neurobiologists and comparative anatomists. We are comforted that the legacy of Thomas Szabo as a scientist and exemplary human being will affect many future generations of scientists and electric fish enthusiasts. No one who heard it will ever forget Thomas' laughter,

which came from deep in his heart and was so overwhelmingly contagious!

Acknowledgements

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Permanent Collaborators (1965–1993)

- | | | |
|-----------------------------------|------------------------------------|------------------------------|
| Claude Derbin (1965–1975) | Bernadette Consigny (1969–1973) | Denise Rouilly (1975–1990) |
| Pierre Belbenoit (1967–1986) | Michèle Ravaille-Veron (1970–1993) | Kirsty Grant (1980–1993) |
| Michel Boudinot (1967–1993) | Jacques Serrier (1970–1993) | Catherine Bretey (1991–1993) |
| Claude Baillet-Derbin (1968–1986) | Simone Libouban (1974–1990) | |
| Jean-Pierre Denizot (1968–1993) | Danielle Kemenovic (1974–1991) | |

Doctoral Students (Year of Thesis Defense and Thèse d'Etat)

- | | | |
|----------------------------------|-------------------------------------|-----------------------------------|
| Claude Derbin (1974) | Chail Srivastava, India (1975) | Christian Graff (1986) |
| Claude Baillet-Derbin (1987) | Ursula Kramer-Feil, Germany (1976) | Sylvie Clause (1986) |
| Jean-Pierre Denizot (1970, 1977) | Marie-Jose Toerring, Germany (1979) | Borhane Djebbar, Algeria (1989) |
| Pierre Belbenoit (1971) | Françoise Haugedé-Carrée (1980) | Raffaella Niso, Italy (1990) |
| Jacques Serrier (1974, 1982) | Claudine Teyssède (1983) | Philippe Jacob (1991) |
| Hans Lugmair, Austria (1973) | Marie-Hélène Favarger (1981) | Mourad Bensouilah, Algeria (1992) |

Post-Doctoral Students

Erich Schwarz, Germany (1967)
Anton Roth, Germany (1967–1968)
Peter Molleir, Germany (1968–1969)
Peter Schlegel, Germany (1969, 1971–1972)
Fernando Pimental de Souza, Brazil (1969–1971)
Richard Bauer, Germany (1971–1973)

Mihail Retheliy, Hungary (1971–1972)
Bernd Kramer, Germany (1971–1974)
Frank Kirschbaum, Germany (1973–1976)
Max Westby, UK (1974–1977)
Karoly Elekes, Hungary (1979–1980)
David Caird, UK (1977–1979)

Diane Ellis, USA (1978–1980)
Manfred Fetzter, Germany (1982–1985)
Donald Rooney, Ireland (1987–1989)
John New, USA (1988–1989)

Visiting Scientists

Per Enger, Norway (1977–1978)
Peter Moller, USA (1978, 1979, 1987)
Curtis C. Bell, USA (1981–1982)
Carl D. Hopkins, USA (1981–1982)

Andrew H. Bass, USA (1981)
Giulya Lazar, Hungary (1983–1984, 1987)
Eli Kastoun, Libanon (1984)
Pal Toth, Hungary (1985)

Peter Laming, UK (1990)
G.N. Akoev, USSR (1990, 1991)
George N. Andrianov, USSR (1991–1992)

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